

Geese on a green wave:

Flexible migrants in a changing world

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Geese on a green wave:

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Introduction



Figure 1.1: The Goose Barnacle (*Lepas anatifera*) and the Barnacle Goose (*Branta leucopsis*)

Background

The biology of the European species of *Branta* geese (including *Branta leucopsis* (Bechstein), the Barnacle Goose, and *Branta bernicla* (Linnaeus), the Brent Goose) was long shrouded in mystery. These geese were present in large numbers during winter and early spring but disappeared from European shores in late-spring, only to return again in autumn with their offspring. This stimulated imaginative ideas on the origin of these birds. The Barnacle Goose and the Brent Goose derive their common (barnacle) and Latin names (*bernicla*) respectively, from the legend that the *Branta* geese actually developed from shells of the mollusc species Goose Barnacle, *Lepas anatifera* (*Cirripedia* family *Lepadidae*) (Figure 1.1).

Because nobody had seen nesting Barnacle Geese or goslings, people believed that geese hatched from shells that grew on trees on logs near the sea (Figure 1.2). The hair-like appendages used for catching food were thought to be goose feathers. When the shells matured they would split open and reveal the legs of the birds hanging out. The bird would hang by its bill until fully mature and then would drop into the sea. The supposed stages of development of the geese are described and illustrated in Gerarde's "Herball, or Generall Historie of Plantes" (1597). This legend not only provided a plausible explanation for the origin of geese, it also proved highly convenient because geese could be classified as "fish" and therefore eaten during fasting periods. On 21 June 1596 the crew of Barentsz' expedition, on their expedition to find the North-East Ship Passage to eastern Asia, went ashore on Spitsbergen and found Brent Geese on their nests (as described by Gerrit de Veer in 1598), however the tales of the Barnacle Goose Tree were popular until the 18th century.

Nowadays we can observe breeding Barnacle Geese all over their western European wintering range; however, the above story illustrates that this has not always been the case. Traditionally, Barnacle Geese were true migrants and were never observed breeding outside their Arctic habitat. Their recent population growth and breeding range expansion to temperate areas (Figure 1.3) formed the motivation for the research presented in this thesis.



Figure 1.2: The Barnacle Goose Tree as described by Gerarde in his “Herball, or Generall Historie of Plantes” (1597).

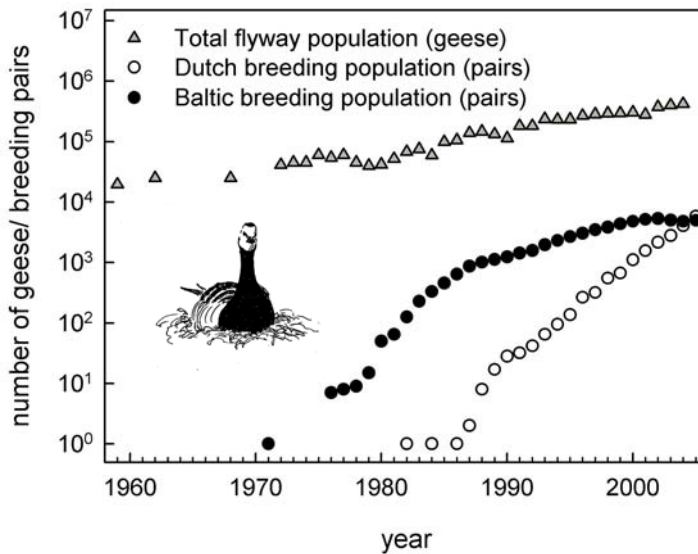


Figure 1.3: Population trend of the total population of Barnacle Geese as well as the numbers of breeding birds in the more recently established Baltic (included are birds breeding on the Swedish islands of Öland and Gotland) and Dutch colonies.

Foraging choices of Barnacle Geese, along the flyway

Before we start to speculate about reasons for the recent breeding range expansion, we will examine why Barnacle Geese undertake such a long, energy-demanding journey to breed. Why do they leave temperate staging sites at the end of spring? We have to assume that traditionally migration to and breeding in the Arctic conferred some advantage as compared to breeding in temperate regions. Being herbivores, geese have to rely on high quality forage. They have an inefficient digestive system, characterised by a rapid passage of plant food through the alimentary tract (Prop and Vulink 1992; Jefferies *et al.* 1994). They, therefore, have to consume large quantities of nutrient-rich plant material (Prop and Deerenberg 1991) and forage for a large part of the daylight period (Stock and Hofeditz 1997; Stahl *et al.* 2001a). Recent studies suggest that breeding at high latitudes can be explained partly by the seasonally declining forage quality of maturing swards in temperate regions (Boudewijn 1984; Prins and Ydenberg 1985; Prop and Deerenberg 1991), in contrast to the high forage quality of newly emerging shoots at Arctic sites (Sedinger and Raveling 1986; Manseau and Gauthier 1993). Additionally, the longer daylight period at higher latitudes, allows the geese and their goslings to forage almost 24 hours per day (Prop *et al.* 1984). Geese might follow a green wave of highly nutritious fresh spring growth of plant tissue on their way from temperate staging sites, via several stopover sites, to their breeding areas in the Arctic (Drent *et al.* 1978; Owen 1980). At these breeding areas the peak in spring growth and quality is expected to coincide with gosling hatch and thus the peak presumably will facilitate gosling growth (Sedinger and Raveling 1986; Lepage *et al.* 1998). This hypothesis is called the “*green wave hypothesis*” and it stands central in this thesis.

An important part of the green wave hypothesis is the assumption that geese do not gather all the necessary resources for breeding at the breeding site itself, but have to bring at least part of these resources from their different staging sites (Gauthier *et al.* 2003; Klaassen 2004; Morrison and Hobson 2004); in other words geese are supposed to be partly capital breeders (Gauthier *et al.* 2003; Klaassen 2004; Morrison and Hobson 2004). This makes the choice of staging sites even more critical: not only do they have to gather enough reserves for the migration; they also have to obtain reserves for subsequent breeding. Larger amounts of body reserves prior to the start of migration often ensure higher breeding success (Ankney and Macinnes 1978; Ebbinge and Spaans 1995; Prop and Black 1998; Madsen 2001). Moreover, highly nutritious food resources during the gosling rearing period ensure higher gosling growth rates resulting in a higher adult body size (Cooch *et al.* 1991; Sedinger *et al.* 1995; Loonen *et al.* 1997; Larsson *et al.* 1998), higher survival probability (Loonen *et al.* 1997; Van der Jeugd and Larsson 1998) and even a higher probability of future breeding of the goslings (Sedinger *et al.* 2004). Therefore, the availability of high quality food resources must be one of the key factors that determines the optimal timing of migration and the choice of foraging and breeding sites along the flyway.

Flexible migrants in a changing world

Food resources along the flyway are scattered and usually only temporarily available within each season. Not all areas along the route are suitable for geese; they do not provide suitable forage species, are perceived as too dangerous, or are not close enough to water bodies that provide drinking water and safety during moult. Many of these areas are suitable for only part of the year: forage species, in the absence of grazing by livestock or mowing by man, will become too tall for geese to handle and the nutritional quality of these tall swards is lower compared with grazed swards (Van der Wal *et al.* 1998b; Lepage *et al.* 1998). Food availability and quality at these sites can be influenced by management, other grazers and by the geese themselves. Previous studies have shown that Dark-bellied Brent Geese, as well as Barnacle Geese prefer areas that are grazed by livestock (Summers and Critchley 1990; Vickery *et al.* 1994; Hassall *et al.* 2001; Van der Graaf *et al.* 2002; Bos *et al.* 2005b). These areas have a low sward height, high tiller density and the grass is of high nutritional quality. Recent environmental changes, such as intensification of agriculture at coastal sites may have improved the quality of coastal grasslands in a way that geese now have access to high quality food on their traditional spring-staging sites all-year round (Van Eerden *et al.* 2005). On the other hand, the cessation of livestock grazing in many coastal grasslands along the migration route, either from a nature conservation viewpoint as for example in northern Germany (Bakker *et al.* 2003), or due to a lack of profitability of traditional agricultural practices, as in the Baltic states (Ehrlich *et al.* 2002), is likely to lead to a lower overall availability of high quality forage at these coastal stopover sites in the future. The two extremes of management (abandonment or intensification of agriculture) are not the only forms of human impact on food resources along the flyway: global warming will become more and more significant over the next decades. Average temperatures are predicted to rise between 1 and 5 °C in the present century (IPCC 2001), this may affect timing of spring warming and hence the start of plant growth and consequently the optimal timing of exploitation by the geese.

Study Sites

Whereas most studies concentrate on one stage of the life cycle of migratory herbivores and therefore on one area, my study focuses on the interactions between Barnacle Geese and their food resources along the entire flyway. During my investigations, I had the unique opportunity to conduct research at the major staging sites along the migration route of Barnacle Geese and so follow the geese on their migration. All research in this thesis has been conducted on three sites along the East-Atlantic Flyway; a winter- and spring- staging site in the Wadden Sea, a stop over site in the Baltic Sea and a breeding site in the Barents Sea in the Russian Arctic (Figure 1.4). Additionally some data will be shown on a newly established breeding site in the Netherlands in the final chapter and synthesis of this thesis.

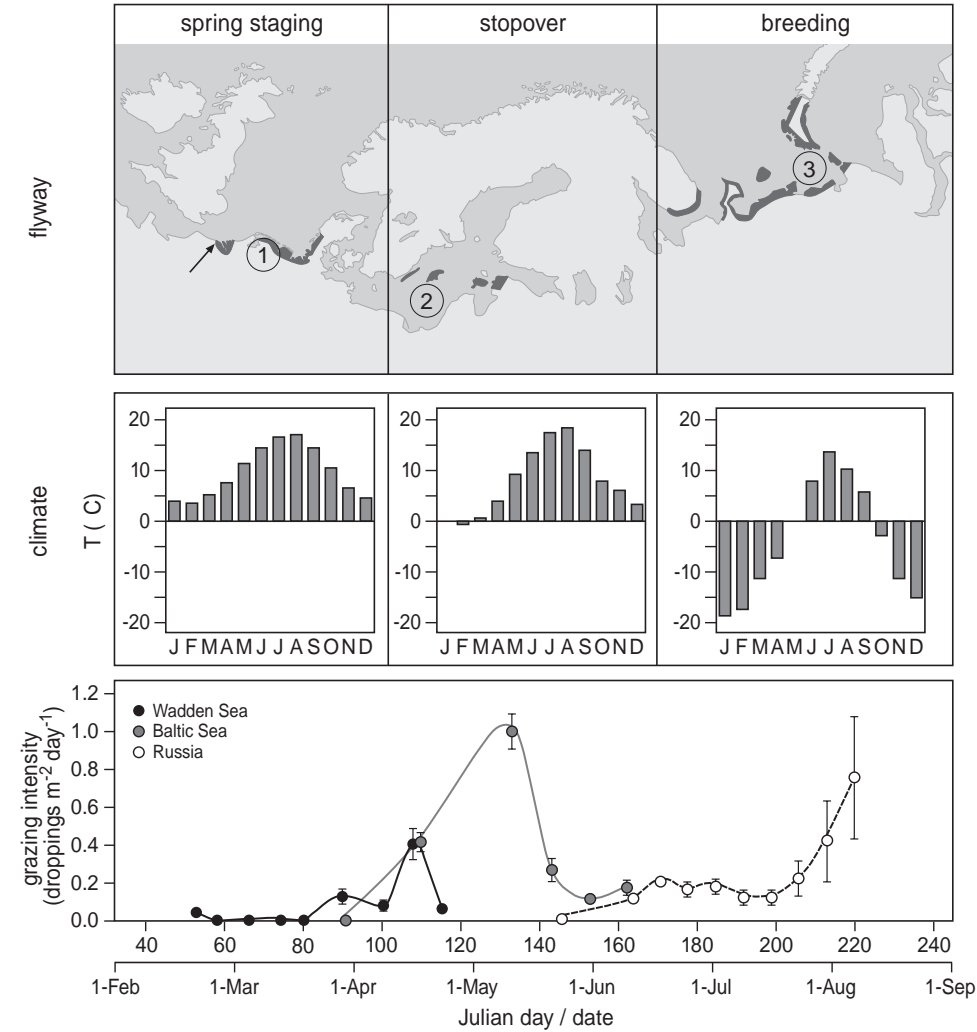


Figure 1.4: The traditional flyway of the Barnacle Geese, average monthly temperatures and goose grazing intensity on the spring staging, stopover and breeding sites in the Wadden Sea (1), Baltic Sea (2) and Russian Arctic (3). Arrow indicates the Dutch Delta, a recently established breeding area.

(1) *A Wadden Sea staging site: Schiermonnikoog*

The island of Schiermonnikoog is situated in the Dutch Wadden Sea (53°30'N, 6°10'E). The island consists of an agricultural polder area (265 ha), surrounded by a seawall, a small village and a natural salt marsh area (1500 ha). Most of my research has been carried out on this salt marsh. Schiermonnikoog is used as a wintering and spring staging site by thousands of Dark-bellied Brent and Barnacle Geese. In the winter months the majority of the geese are restricted to the agricultural grasslands in the polder, but they shift to the salt marsh in early spring (Prins and Ydenberg 1985; Bos and Stahl 2003). I call this period “spring staging” (March-mid-May). During this period the geese forage intensively in order to gather large body reserves for their journey to the Arctic and subsequent breeding. Barnacle Geese leave Schiermonnikoog around mid-April, Brent Geese stay until mid-May. In Box 1, I give an overview of the morphology and vegetation of the island, herbivores present, their foraging preferences and the importance of the spring staging period for migrating geese.

(2) *A Baltic stopover site: Gotland*

The first stop of Barnacle Geese on their way to the Arctic Russian breeding sites is in the Baltic Sea. Traditionally, a large proportion of the Russian barnacle geese have used the island of Gotland as a stopover site during migration. They utilise narrow strips of coastal grasslands along the shore of southern Gotland (57°07'N, 18°27'E) for a few weeks at the end of April/early May before continuing their journey. In this short period the large numbers of geese deplete forage resources on the relatively small marshes. Since the 1980s, some geese have remained on small islands along the coast of Gotland during the summer period and have started to breed here (Larsson *et al.* 1988). At present about 10% of the total Barnacle Goose population breeds in the Baltic, the majority near Gotland (Ganter *et al.* 1999). Geese that breed on the small islands along the coast return with their families to the mainland of Gotland soon after hatch. The geese remain on these marshes, which are also grazed by cattle and sheep throughout the summer. Box 2 contains a detailed description of one of the major stopover sites on Gotland. This site is used by adult birds and goslings later in the season.

(3) *A Russian breeding site: Tobседа*

After a few, briefly used stopovers in the Baltic and in the White Sea, the geese move to their breeding areas in the Barents Sea region, northern Russia. Here, my main study site was located near the village of Tobседа in the Kolokolkova Bay (68°35'N, 52°18'E). After human abandonment of the village in the late 1980s, a large breeding colony of Barnacle Geese developed in the late 1990s (Mineev and Mineev 2004). In 2003, the colony consisted of 1,324 breeding pairs (Van der Jeugd *et al.* 2003). The geese breed on small

sandy islands just off the coast and on the main marsh since ground predators only rarely visit the peninsula (Van der Jeugd *et al.* 2003). Snow melt takes places here in the second half of May, after which time the geese soon arrive. They start nesting immediately upon arrival. When the chicks hatch the geese swim to the foraging grounds on either side of the bay and rely on the now green salt marshes during post-hatch brood rearing and wing moult. In late September or early October, winter sets in rather abruptly and the geese migrate to their temperate wintering sites. In Chapter 2, I give a detailed description of this Arctic salt-marsh site.

(4) A recently established breeding site: the Dutch Delta (SW Netherlands)

Since the early 1990s Barnacle Geese breed in the Dutch Delta area (Meininger and Van Swelm 1994). Here they mainly choose small islands for breeding and forage on the surrounding agricultural grasslands close to the shoreline. Geese from the colonies in the Dutch Delta do not migrate over a long distance anymore, but have become resident birds within the Netherlands, at sites that were originally within their wintering area.

Outline of the thesis

In the first part of my thesis “Foraging choices of Barnacle Geese, along the flyway” I will describe the traditional migration of Barnacle Geese and the foraging choices geese make along the flyway. First, I will illustrate some of the main sites on the migration route and the habitat choices within these sites (Chapter 2, Box 1, Box 2). Second, I will use an experimental approach to gain insight into these foraging choices (Chapter 3, Chapter 4). Finally, I will test one of the underlying assumptions of the green wave hypothesis, namely that there are waves of food availability along the flyway and that the geese synchronise their migration with the northwards developing waves (Chapter 5).

In the second part of this thesis “Flexible migrants in a changing world” I will use an experimental approach to demonstrate the influence of other herbivores, temperature rise and changes in human land use on the availability of food resources of Barnacle Geese; these factors are summarised in Figure 1.5. Other herbivores can affect food resources and can compete with the geese for these resources (Chapter 6). Geese have facilitative effects on their forage resources by restricting the build-up of necromass, by keeping the growth of the vegetation in a young state (Chapter 7), and by fertilising swards with their droppings (Chapter 8). Ambient temperature affects the vegetation development within one growing season and the phenological timing of food peaks. Differences in spring temperatures between years are the primary cause for deviations in the timing of these food peaks every year (Chapter 9). Global warming will advance food peaks and the foraging behaviour of Barnacle Geese will have to prove very flexible in order for the birds to keep up with an advancing green wave.

Humans are a major factor influencing the food availability for Barnacle Geese, not only as a result of their influence on global climate, but also because of changes in agricultural land use. Recently, Barnacle Geese have expanded their breeding range dramatically; I will describe the new breeding sites in Chapter 10, and discuss whether changes in land use may have facilitated the recent expansion of the breeding range of Barnacle Geese towards temperate areas.

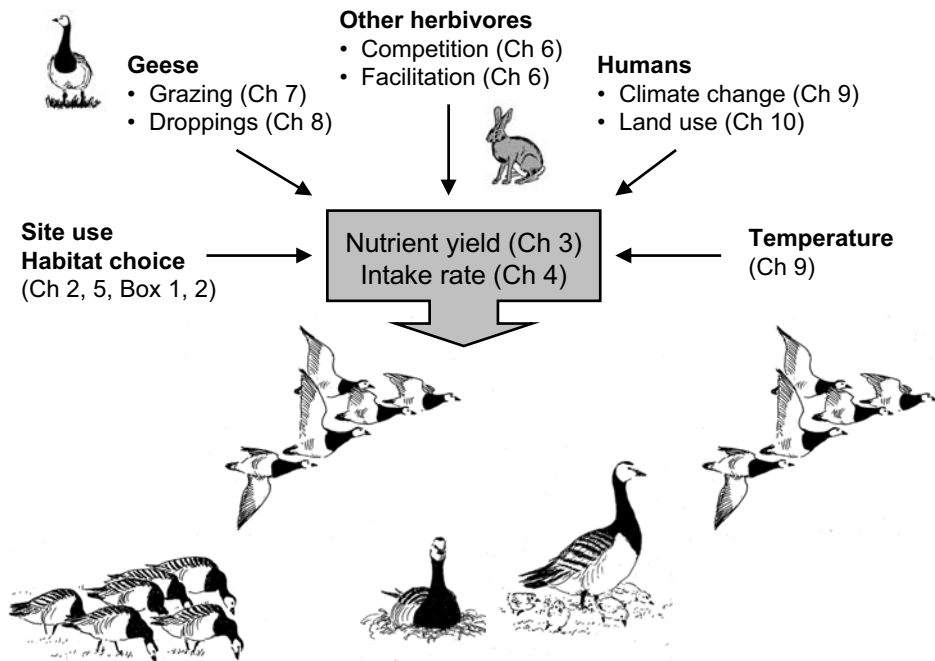


Figure 1.5: Factors affecting food resources of Barnacle Geese.



The meeting of the fleets of Jan Huygen van Linschoten and of Willem Barentsz near Nova Zembla, August 1594 (van der Moer 1979).

Part 1

Foraging choices of Barnacle Geese: From temperate to Arctic



Box 1**Spring staging in the Dutch Wadden Sea: fuelling for migration**

Before Barnacle Geese, *Branta leucopsis*, start their migration to their Arctic breeding grounds, they have to gather sufficient body reserves for migration and subsequent breeding. During the months of March and April, we find them foraging intensively on salt marshes in the Dutch and German Wadden Sea. In my thesis I use the salt marshes on the Dutch island of Schiermonnikoog as an example of these salt marshes. Most of my research has taken place on these marshes and here I will give a brief overview of the island of Schiermonnikoog and its vegetation, the herbivores present and their foraging preferences and the importance of the spring staging period for geese.



Part of the livestock grazed salt marsh at Schiermonnikoog as seen from the dike dividing the agricultural pasture area and the salt marshes, looking in the direction of the Wadden Sea (South).

Schiermonnikoog: a spring staging site in the Dutch Wadden Sea

Schiermonnikoog is a relatively small island in the Dutch Wadden Sea, about 18 km in length and 3 km wide. It consists of an embanked agricultural pasture area (polder, 290 ha) with a small village, a forest and dune area, wide beaches on the North Sea coast and a large salt marsh at the eastern end (Figure B1.1). While there are only about 1,000 permanent inhabitants, the island is visited by about 300,000 tourists yearly. The entire island is part of the National Park Schiermonnikoog. The agricultural pastures are heavily fertilised with approximately $400 \text{ kg N ha}^{-1}\text{yr}^{-1}$. The western salt marshes (185 ha) are grazed in summer by cattle at a stocking rate of 0.5 cow ha^{-1} , the central marshes have been grazed by livestock until 1958 (100 ha), while the eastern marshes (1450 ha) have never been grazed by livestock. In spring about 2,000 Brent Geese (*Branta bernicla bernicla*) and 6,000 Barnacle Geese utilise the salt marshes of Schiermonnikoog. Besides large numbers of staging geese, the salt marshes harbour a large Spoonbill (*Platalea leucorodia*) colony, several large gull and tern colonies (*Laridae* and *Sternidae*), and they are also a breeding place for many species of waders (*Charadriiformes*) and ducks (*Tadorna tadorna*, *Somateria mollissima*). The central and eastern marshes are closed to the public from mid-April to late July to prevent disturbance to breeding birds. On the salt marsh of Schiermonnikoog, we find three small wild herbivore species: Dark-bellied Brent Geese, Barnacle Geese and Brown Hares (*Lepus europaeus*). Additionally rabbits (*Oryctolagus cuniculus*) are found in the dune areas. Brown Hares are present throughout the year, whereas the migratory Brent and Barnacle Geese only use the marsh during the spring period.

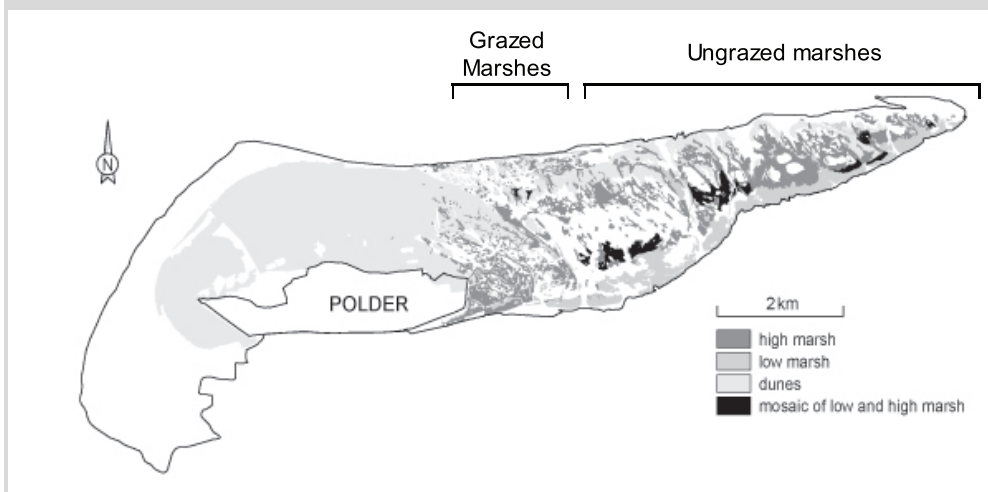


Figure B1.1: Map of the island of Schiermonnikoog, indicating the major habitats used by geese (Figure copied from Bos & Stahl 2003).

Vegetation succession and small herbivores

The island of Schiermonnikoog is continuously growing towards the east. Here, new salt marshes are developing. The gradient from east to west therefore represents a gradient from young marshes to old marshes (ca. 150 years old), a so-called chronosequence (Olff *et al.* 1997). Perpendicular to this age gradient is an elevation gradient from low marshes that are often flooded in the south to high marshes that are only rarely flooded in the north. As a marsh becomes older, more sediment is deposited and the thickness of the clay layer and the total amount of nitrogen in the soil increases. Along with this increase in soil nitrogen, productivity of the marsh rises. The youngest stages of the marshes have a low productivity and are therefore poor foraging places for herbivores. On the marshes of intermediate age and productivity we find the highest grazing intensity of both hares and geese (van de Koppel *et al.* 1996). In the absence of livestock grazing the next stage in succession is a tall canopy of *Atriplex portulacoides* at the lower marsh and *Elytrigia atherica* on the higher marsh. In the marsh of intermediate age (central marshes), hares have been shown to retard succession by at least 20 years, due to their grazing activity (van der Wal *et al.* 2000b; Kuijper and Bakker 2003; Kuijper and Bakker 2004). However, eventually the small herbivores lose control and succession continues (Kuijper and Bakker 2003). In this stage only grazing by livestock can prevent the dominance of tall species and keep the vegetation attractive for small herbivores (Bakker *et al.* 1993). Classification of the vegetation of the salt marsh follows de Jong *et al.* (1998). The marsh has been mapped by Kers *et al.* (1998). Both the ungrazed marshes of intermediate productivity (central marshes) and the older marshes (western marshes) that are grazed by livestock consist largely of a short sward with the grass *Puccinellia maritima* on the lower marsh, and the grass *Festuca rubra* and the rush *Juncus gerardi* on the higher marshes (van der Graaf *et al.* 2002). In these areas highest foraging intensities of hares and geese are recorded (Ytsma 1998).

Foraging preferences of small herbivores

In the winter geese are present on the island but forage only in the heavily fertilised agricultural pastures. In March, for Barnacle Geese, and mid-April, for Brent Geese, they switch their foraging activities to the salt marshes where they will remain until end of April and mid-May respectively (Boudewijn 1984; Prins and Ydenberg 1985). Prins and Ydenberg (1985) found that Barnacle Geese shift from pasture to salt marshes when the forage grasses are equal in dietary protein content. They suggest that the salt marshes are a more preferred habitat, but that the low nutrient content of the forage grasses prevents use of the marsh during winter. Additionally, studies on the spring staging ecology of Barnacle Geese in Norway, show that body stores acquired in natural habitats have a higher protein to fat ratio, which favours reproductive success (Prop and Black 1998). Finally, geese can

forage more efficiently on the salt marsh due to less human disturbance. Bos and Stahl (2003) found that when a non-disturbance policy was implemented in the agricultural pastures, both Brent and Barnacle Geese extended their use of the pastures and remained here until the spring migration.

In June 2005, we conducted a survey on part of the livestock grazed marsh in the western section (Figure B1.1). We identified patches consisting of a single plant community or a mosaic of communities in some cases, and within these patches we measured canopy height, goose and hare grazing pressure and estimated total cover and the cover of the three most dominant edible species. Details of the methods used are described in Box 2. Edible species were defined as the species preferred in the diet, they included *Festuca rubra*, *Juncus gerardi*, *Plantago maritima*, *Triglochin maritima*, *Agrostis* sp. and *Poa* sp. (unpubl. data). Table B1.1 shows the major plant communities on this salt marsh and their characteristics. The low-intensity cattle grazing on the older marsh (0.5 cow ha^{-1}) creates a mosaic of patches with tall vegetation dominated by *Elytrigia atherica* and *Juncus maritimus* and patches with a short sward dominated by *Juncus gerardi* and *Festuca rubra* (Table B1.1). We found that geese use plant communities with a low canopy and a high cover of edible species. In our study, we could not distinguish between Brent and Barnacle Goose droppings. However, it is known from previous studies (Ytsma 1998) that Brent Geese mainly use the lower marsh (Ll and Lp in Table B1.1) with *Puccinellia maritima* as their main diet component (70% of the diet; Van der Wal *et al.* 1998a), whereas Barnacle Geese mainly use the higher marshes (Hy-Hj in Table B1.1) and feed on *Festuca rubra* (90% of the diet; Van Dinteren 1988). This difference in choice of foraging site is probably related to a wider tolerance of salt-affected vegetation by Brent Geese (Stahl *et al.* 2003). Hares prefer vegetation of intermediate canopy height in the high marsh with high cover of *Juncus gerardi* and *Festuca rubra*. Their diet overlaps most with Barnacle Geese and consists largely of *Festuca rubra* (68% of the diet; Kuijper *et al.* 2004). Additionally, geese and hares supplement their diet with the species *Plantago maritima* and *Triglochin maritima*. These forage species have a low abundance in all plant communities but are rapidly depleted. *Plantago* and *Triglochin* have relatively high protein content in comparison to *Puccinellia* and *Festuca* and high gross food intake rate due to their larger plant size (Prop and Deerenberg 1991). Dominant birds obtain a higher proportion of these species in their diet in these marshes (Teunissen *et al.* 1985; Prop and Deerenberg 1991).

Table B1.1: Properties of the major plant communities on a livestock grazed salt marsh on Schiermonnikoog (>0.5 ha cover in total). Characteristic species of the plant communities in the table: Ll-*Limonium vulgare*, Lp-*Puccinellia maritima*, Hy-*Elytrigia atherica*, Hm-*Juncus maritimus*, Hz-*Serephidium maritimum*, Hf-*Festuca rubra*, Hj-*Juncus gerardi*.

	Plant community							Dune
	Low marsh		High marsh					
	Ll	Lp	Hy	Hm	Hz	Hf	Hj	
Total area (ha)	1.65	0.82	0.83	2.38	1.80	2.76	1.58	1.25
Patch size (m ²)	2358	635	360	881	1202	1102	406	780
Total cover (%)	81	78	97	97	96	96	95	96
Edible species (cover %)	28.6	58.2	12.7	16.5	39.6	70.4	79.2	1.2
Canopy height (cm)	2.88	2.07	25.69	24.97	8.95	4.28	4.89	14.95
Goose grazing pressure (droppings m ⁻²)	4.1	9.3	0.6	0.5	8.2	3.7	3.2	0.5
Hare grazing pressure (droppings m ⁻²)	0.16	0.29	0.10	0.24	0.68	1.54	1.56	0.75
<i>N</i>	7	13	23	28	15	25	39	16

Fuelling for migration

The spring staging period is a very important time in the life cycle of geese. Individual geese that depart from their staging grounds with larger body reserves have a higher chance of successful reproduction (Ankney and MacInnes 1978; Ebbinge and Spaans 1995; Prop and Black 1998; Madsen 2001). Female geese need adequate body reserves for migration, egg production and maintenance during the incubation period (Drent *et al.* 2003). If body reserves are insufficient to meet these demands, females will either leave the nest prematurely to feed or they will starve to death on the nest (Ankney and MacInnes 1978). During spring staging geese forage over 70% of the daylight period (Black *et al.* 1991; Stock and Hofeditz 1997; Stahl *et al.* 2001a). Dark-bellied Brent geese staging on Schiermonnikoog, increase their body weight by 25-35% (Ebbinge and Spaans 1995). Prop and Black (1998) compiled data on the rate of body mass increase during spring staging for several goose species and show that geese gain 11.5 to 28.8 g per day which amounts to 0.4-1.4 g per day per 100 gram body mass. For Barnacle Geese foraging on the salt marsh of Schiermonnikoog, Ebbinge *et al.* (1991) found a value of 17 g d⁻¹, or 0.95 g d⁻¹ 100 g⁻¹ body mass. This would mean that within one month staging Barnacle Geese can increase their body weight by about 25%. Heavy disturbance during the spring staging period can lead to a lower accumulation of body reserves or even a loss, which will have a negative effect on migration performance and reproductive effort (Drent *et al.* 2003; Mainguy *et al.* 2003). Prop and Black (1998) have shown that not only is the accumulation of body

reserves important in determining reproductive success in geese, but also the composition of these body reserves. Geese staging on agricultural areas acquire more fat in relation to protein and subsequently have a lower breeding success than birds foraging on natural habitats that acquire relatively more protein. The authors suggest that birds from agricultural areas that have acquired fewer protein reserves either lack adequate muscle development to carry sufficient reserves on migration, or lack the necessary proteins for egg production after arrival on the breeding grounds (Prop and Black 1998).

Thus, in order to reproduce successfully, geese not only have to gather sufficient body reserves during spring staging but also have to be highly selective in their choice of spring staging sites, foraging habitats and diets in order to obtain a good fat to protein ratio. The salt marsh of Schiermonnikoog, thanks to the fascinating facilitation processes between hares and geese on the younger marsh and livestock and geese on the older marsh, forms an important fuelling site for both Brent and Barnacle geese and an ideal study site for my research.

Acknowledgements

I want to thank all people that did so much research on Schiermonnikoog before me and created a solid background for my work. Students of the Community and Conservation Ecology Course 2005 helped with data collection and Julia Stahl, Roos Veeneklaas, Alma de Groot, Jan Bakker and Karin Bengtsson with supervision of this course.



Close-up of the livestock grazed marsh with a mosaic of tall and short patches. Shown is a small exclosure used for measuring production of the vegetation (as described in Chapter 2).

Box 2:**The brackish salt marsh of Grötlingbo-udd; a Baltic stopover site for migrating Barnacle Geese.**

The peninsula Grötlingbo-udd on the east coast of the Baltic island of Gotland (Sweden) near the southern tip, is a stopover site for large numbers of migrating Barnacle Geese, *Branta leucopsis*, in the months of April and May, as well as a foraging site for families and non- or failed- breeders of the Gotland breeding population of Barnacle Geese from end of May onwards (Chapter 5). The salt marsh stretches from the east point of the peninsula along the southern shore for about 1 km. The east point of the peninsula is protected as a nature reserve, whereas the southern part is private property of local farmers. The entire salt marsh is moderately grazed by cattle from early June onwards. Besides its function as a foraging site for Barnacle Geese, the area is a breeding site for many species of waders.

Because of the high numbers of Barnacle Geese in the area, this site was chosen as an experimental area for part of the studies presented in this thesis. In this Box, I will describe the vegetation of the area, the usage pattern by the migrating geese as well as conservation issues.



The livestock grazed salt marsh of Grötlingbo-udd, early in the season (mid-April 2003).

Salt marsh

In June 2005, 14 plant communities were defined within the southern salt marsh (Table B2.1). Each community was described by three relevés of 1 m², relevés were randomly placed within each community. Species presence in the relevés was noted and percentage cover of each species was visually estimated. Table B2.1 shows species that were present in more than two communities, species that were only found in two communities or less are given in the footnote. The lower salt marsh of Grötlingbo-udd falls within the *Juncetum gerardi* association, as described by Tyler (1969). He divided this association into three sub-associations: *Juncetosum gerardi*, *Festucetosum rubrae* and *Festuceto/caricetosum nigrae*. A second association was distinguished by Wallentinus (1973); the *Agrostis* association. Within each of these four (sub-) associations, except the *Festuco/caricetosum nigrae* subassociation, we distinguished two variants, based on the presence of characteristic species (Table B2.1). What we call higher marsh actually has few halophytes and is therefore not considered salt marsh in the literature. We chose to incorporate these types in our description, since the geese feed in the entire area. Directly adjacent to the marsh is either forest or a continuation of the meadows, without the presence of any halophytes. Our study area was enclosed by a stone wall and the geese rarely foraged in the area inland from the wall. This can probably be explained by an increase of the perceived predation risk in an area, where small shrubs and other obstacles reduce early predator detection and block the escape to safe waterbodies in case of an attack. In the study area Juniper shrubs (*Juniperus communis*) started to encroach the patches of meadow at a higher elevation, but farmers have been preventing further spread by regular burning and removal of this shrub. The cutting of shrubs is part of an EU program promoting the open landscape, which has been in action since 1990.



Cattle on the salt marsh of Grötlingbo-udd, June 2004.

Table B2.1: Plant communities on the marsh of Grötlingbo-udd as recorded in June, 2005. Mean cover percentage of three relevés (1 m²) is shown, 1 indicates a species is present. Boxes indicate characteristic species of the plant community. Footnote shows species that occur in 2 communities, species that occur in only one community are not given. For the lower marsh the communities as described in the literature are given (Tyler 1969; Wallentinus 1973): A- *Agrostis* association, J- *Juncetosum gerardi* subassociation, F- *Festucetosum rubrae* subassociation, FC- *Festuco/Caricetosum nigrae* subassociation.

	Pond	Low marsh				High marsh								Beach
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
(Sub) Association according to literature	-	A	A	J	J	F	F	FC	-	-	-	-	-	-
Plant community	<i>Ranunculus baudotii</i> / <i>Rumex crispus</i>	<i>Agrostis stolonifera</i> / <i>pioneers</i>	<i>Agrostis stolonifera</i> / <i>Potentilla anserina</i>	<i>Juncus gerardi</i>	<i>Juncus gerardi</i> / <i>Serephidium maritimum</i>	<i>Festuca rubra</i> / <i>Plantago maritima</i>	<i>Festuca rubra</i> / <i>dicots</i>	<i>Festuca rubra</i> / <i>Carex nigra</i>	<i>Carex flacca</i> / <i>Sesleria albicans</i>	<i>Festuca ovina</i> / <i>Juniperus communis</i>	<i>Festuca ovina</i> / <i>Lotus corniculatus</i>	<i>Festuca ovina</i> / <i>Anthyllus vulneraria</i>	<i>Festuca ovina</i> / <i>Hieracium pilosella</i>	<i>Honkenya peploides</i> / <i>Potentilla reptans</i>
Total cover (%)	22	3	18	97	90	95	94	70	73	97	65	77	63	42
<i>Ranunculus baudotii</i>	3													
<i>Rumex crispus</i>	11		1				1		1	1	1			3
<i>Salicornia europaea</i>		2			1	1								
<i>Spergularia salina</i>		2	2		1	1								
<i>Glaux maritima</i>	1	1	1	1										
<i>Puccinellia distans</i>	1	1	1		1									
<i>Potentilla anserina</i>	1		13	8		4	7	20	1					1
<i>Juncus gerardi</i>		2	1	83	15	4	1	1		1				
<i>Agrostis stolonifera</i>	3	2	3	3	1	1		1	1	1	1			
<i>Serephidium maritimum</i>					50		1		1					
<i>Plantago maritima</i>		1			15	14	4	1						
<i>Festuca rubra</i>			1			55	20	6	1	10	1	1		
<i>Bellis perennis</i>						1	10	1	1	1	1	1		
<i>Plantago lanceolata</i>							14	1	1	14	17	17	4	
<i>Potentilla reptans</i>							18	1	1	1		2	1	11
<i>Odontitis vernus</i>				1	1	4	1		1					
<i>Atriplex prostrata</i>				1	1	1	1		1					
<i>Carex nigra</i>								33	1					
<i>Carex flacca</i>								1	15	2				
<i>Sesleria albicans</i>									40					
<i>Festuca ovina</i>									7	32	25	27	27	
<i>Luzula campestris</i>							1		1	13	1		1	

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Juniperus communis</i>										7				
<i>Lotus corniculatus</i>						1	1	1	2	1	10	1	1	
<i>Filipendula vulgaris</i>										1		7		
<i>Anthyllis vulneraria</i>							1		1		1	5		
<i>Galium verum</i>									2	1	1	1	1	
<i>Galium boreale</i>										1		1	7	
<i>Hieracium pilosella</i>												1	12	
<i>Honkenya peploides</i>														25
<i>Urtica dioica</i>							2							2
<i>Cirsium arvense</i>							1				1			4
<i>Achillea millefolium</i>							1			1		1	1	
<i>Agrostis capillaris</i>										1	1	1	1	
<i>Allium vineale</i>										1	1	1	1	
<i>Bromus hordeaceus</i>							1		1		1	1	1	
<i>Centaurium littorale</i>						1	1	1		1				
<i>Cerastium fontanum</i>						1			1	1	1	1	1	
<i>Cirsium vulgare</i>							1	1		1	1	1		1
<i>Elytrichia repens</i>							1	1				1	1	1
<i>Erophila verna</i>										1	1	1		
<i>Linum catharticum</i>									1	1	1	1		
<i>Myosotis ramosissima</i>							1			1	1	1	1	
<i>Phleum phleoides</i>											1	1	1	
<i>Poa pratensis</i>							1	1	1		1		1	
<i>Ranunculus bulbosus</i>							1		1	1	1	1		
<i>Sagina procumbens</i>						1	1	1						
<i>Saxifraga granulata</i>									1	1	1			
<i>Stellaria gramminea</i>							1			1	1			
<i>Taraxacum sp.</i>									1		1	1	1	
<i>Trifolium dubium</i>							1		1	1	1		1	
<i>Trifolium micranthum</i>							1	1	1	1	1	1	1	
<i>Trifolium pratense</i>								1	1	1	1	1	1	
<i>Trifolium repens</i>						1	1	1			1		1	
<i>Veronica arvensis</i>							1			1	1	1	1	
<i>Veronica chamaedrys</i>							1			1	1	1	1	
<i>Vicia latiodens</i>											1	1	1	

Alisma plantago-aquatica (1,3), *Anthoxanthum odoratum* (12,13), *Arabis hirsuta* (10,12), *Avenula pratensis* (12,13), *Bupleurum tenuissimum* (6,9), *Carex spicata* (9,10), *Cochlearia danica* (5,6), *Galium palustre* (9,13), *Leontodon autumnalis* (8,10), *Lolium perenne* (7,11), *Ranunculus scleratus* (3,8), *Polygonum aviculare* (7,14), *Potentilla argentia* (11,12), *Potentilla tabernaemontani* (12,13), *Ranunculus cincinatus* (1,2), *Rumex acetosa* (7,10), *Saxifraga tridactylites* (10,11)

Foraging choices of Barnacle Geese

A large part of the southern marsh of Grötlingbo-udd was mapped using GPS-techniques (Figure B2.1). In each patch assigned to a specific community, we conducted measurements on grazing pressure by geese, canopy height and the cover of edible species (Table B2.2). We measured the cumulative spring grazing pressure (April to early-June) within each patch by counting goose droppings in five plots of 4 m² in mid-June 2005. We assumed that we counted only droppings from the same season and that dropping numbers thus reflected the use of the area in that year. Since some droppings might have disappeared within the season due to tidal or wind actions; the number of droppings we use is a net number. Canopy height was measured to the nearest 0.5 cm using a sward stick with a styrofoam disc (20 cm diameter, 24 g). Cover of individual species was estimated visually. Edible species were defined as the species preferred in the diet, they included *Festuca rubra*, *Juncus gerardi*, *Plantago maritima*, *Triglochin maritima*, *Agrostis* sp. and *Poa* sp (based on epidermal analyses of droppings collected in May-June 2004; Pardijs and Wolfs 2004).

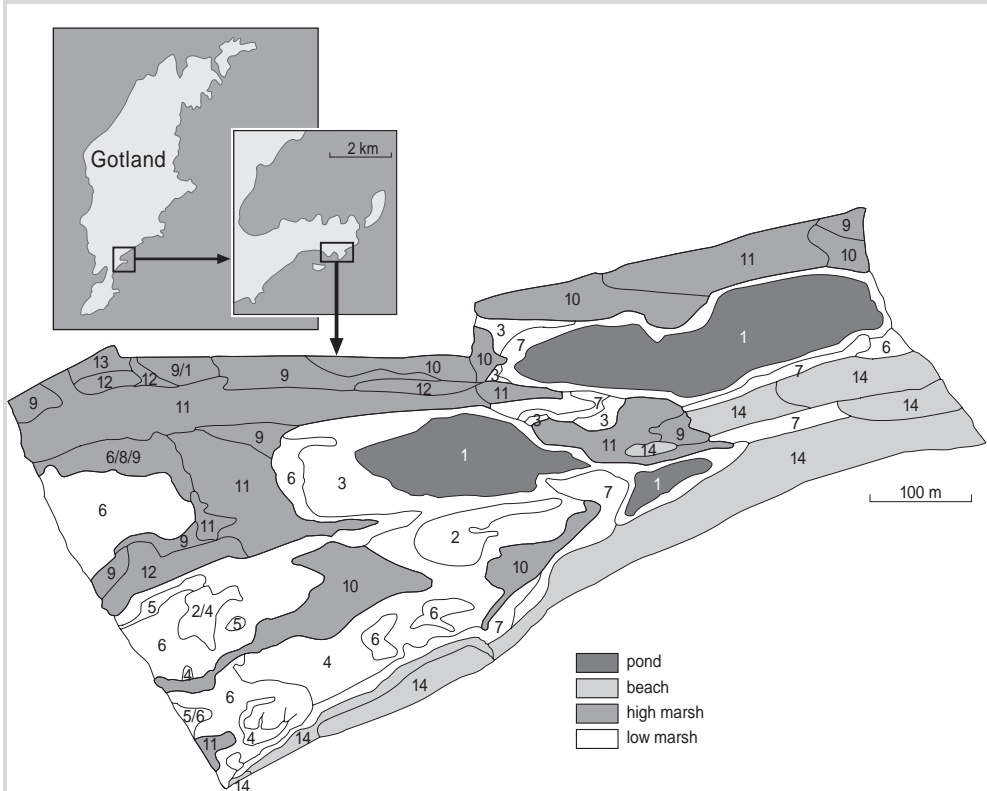


Figure B2.1: Location of Grötlingbo-udd and of our study area on Grötlingbo-udd and the vegetation map of our study area.

Table B2.2: Total surface area of each plant community (ha), cumulative goose grazing pressure April-June 2005 (droppings m⁻²), canopy height (cm) and cover of edible species (%) of all plant communities on Grötlingbo-udd described in Table B2.1. Plant community 8 was not found in sufficiently large patches to make measurements. N is the number of patches of each plant community in which the measurements were done.

Plant community	Surface area (ha)	Grazing pressure (droppings m ⁻²)	Canopy height (cm)	Edible species (cover %)	N
1 Pond	2.05	0.07	6.6	3.3	3
2 <i>Agrostis stolonifera</i> / pioneers	0.23	0.9	4.2	37.0	1
3 <i>Agrostis stolonifera</i> / <i>Potentilla anserina</i>	0.41	11.4	2.7	42.6	7
4 <i>Juncus gerardi</i>	1.22	14.3	3.7	62.3	3
5 <i>Juncus gerardi</i> / <i>Serephidium maritima</i>	0.04	9.4	3.0	42.5	2
6 <i>Festuca rubra</i> / <i>Plantago maritima</i>	1.83	21.1	3.8	77.9	8
7 <i>Festuca rubra</i> / dicots	0.71	16.6	3.3	40.6	8
9 <i>Carex flacca</i> / <i>Sesleria albicans</i>	0.60	3.6	5.4	29.0	7
10 <i>Festuca ovina</i> / <i>Juniperus communis</i>	1.83	5.8	6.0	48.6	7
11 <i>Festuca ovina</i> / <i>Lotus corniculatus</i>	2.59	8.0	5.2	44.5	8
12 <i>Festuca ovina</i> / <i>Anthyllus vulneraria</i>	0.15	2.4	4.8	30.7	4
13 <i>Festuca ovina</i> / <i>Hieracium pilosella</i>	0.06	0.5	4.6	26.5	2
14 <i>Honkenya peploides</i> / <i>Potentilla reptans</i>	2.68	4.0	5.9	4.0	9

Goose grazing pressure was highest in communities of the lower salt marsh, containing the species *Festuca rubra*, *Juncus gerardi* and *Plantago maritima*. A regression analysis showed that grazing pressure in each plant community is largely explained by the average cover of edible species (Figure B2.2a), as well as by average canopy height (Figure B2.2b). Canopy height and cover of edible species were negatively related ($R^2=0.34$, $P=0.04$, $N=13$). In line with previous studies on other sites, this study shows that Barnacle Geese at Grötlingbo-udd selected foraging patches with the highest cover of edible species and with low canopy height. The same relationship between grazing pressure and canopy height was found for a Russian breeding site of Barnacle Geese (Chapter 2). As discussed there, either the geese may prefer low canopy heights or the low canopy height might be a result of the high grazing pressure; and again it is impossible to disentangle these two processes here.

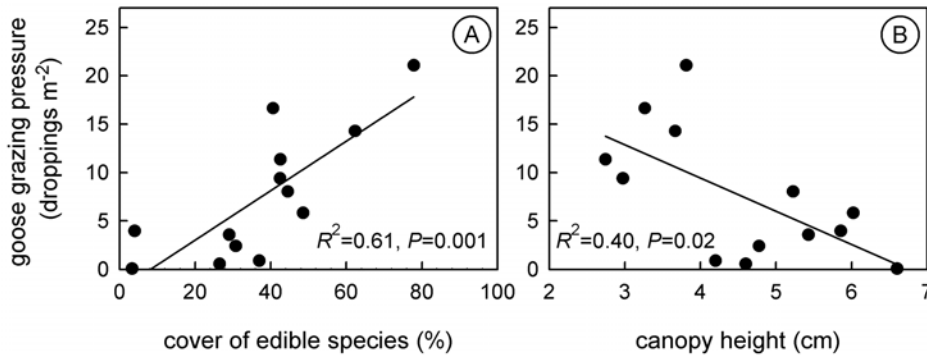


Figure B2.2: Relation between average cumulative goose grazing pressure from April-June 2005 (droppings m⁻²) in each community and the cover of forage species (A) and canopy height (B) in this community, as found on the salt marsh of Grötlingbo-udd, mid-June 2005. See Table B2.1 for descriptions of the plant communities.

Many other studies have also shown a relationship between canopy height and goose grazing pressure, usually concluding that geese prefer short vegetation (Van de Koppel *et al.* 1996; Vickery *et al.* 1997; Van der Wal *et al.* 1998b; Hassall *et al.* 2001; Van der Graaf *et al.* 2002; Bos *et al.* 2005b). Our measurement on grazing pressure is a cumulative measure for the entire spring period, but it is likely that some species are preferred only within a certain time frame. Additionally, we acknowledge that we probably underestimated grazing pressure on the pond community, since droppings that fall on wet soil disintegrate quickly. We noticed that the geese preferred foraging along the edge of the pond in wet areas that recently had dried.

Conservation Issues

Although the marsh of Grötlingbo-udd covers a rather small area (50 ha), it serves as an important stepping stone for many Barnacle Geese during migration. The vegetation is similar to many other Baltic brackish marshes (Dijkema 1990; Wallentinus 1973; Tyler 1969; Jutila 2001; Dupré and Diekmann 2001); however its location near breeding islands gives it a special status. Since the early 1990's, the adjacent islands are used as breeding sites; in recent years these islands have harboured approximately 1,500 breeding pairs of Barnacle Geese each year. The majority of these birds come to the mainland of Gotland soon after hatch or after a failed breeding attempt. They stay in the coastal meadows during moult and chick rearing and leave these areas only in autumn. As emphasized before by Dijkema (1990), grazing by livestock is of key importance for the maintenance of marshes

(Bakker *et al.* 2003). In the absence of large herbivores, halophytes will disappear and reed beds (on the lower parts of the marsh) or *Juniperus* shrubs (on the higher parts) will become more abundant and finally take over in the absence of preventive measures. In Estonia, many coastal marshes have already become overgrown due to the cessation of grazing on the coastal meadows (Ehrlich *et al.* 2002). Several studies on Baltic coastal marshes have demonstrated that species richness is higher in grazed than in abandoned marshes (Dupré and Diekmann 2001; Jutila 2001), with the exception of heavily grazed marshes (Dupré and Diekmann 2001). Cessation of livestock grazing will lead to a lower cover of edible species for the geese and a higher canopy height (Andresen *et al.* 1990; Aerts *et al.* 1996; Olff *et al.* 1997; Jutila 1999; Stock and Hofeditz 2002; Van der Graaf *et al.* 2002; Bakker *et al.* 2003). Concurrently, the carrying capacity of the marsh for grazing geese will decrease (Figure B2.2). Many studies show a decrease in goose numbers after the abandonment of grazing (Aerts *et al.* 1996), or where a relatively low number of geese are present in permanently or temporarily ungrazed areas as compared to nearby grazed areas (Van der Graaf *et al.* 2002; Bos *et al.* 2005b).

Finally, cessation of livestock grazing will not only result in a decreased diversity and a major loss of feeding habitat for Barnacle Geese, but also other species, in particular breeding waders, might suffer from the changing habitat. Waders have been shown to prefer moist habitats with short vegetation (Vickery *et al.* 1997). Many wader populations in Europe have been declining in recent years (conclusions of the International Wader Study Group Conference 2003, Cadiz, Spain). Coastal meadows in southern Sweden traditionally harbour a large breeding population of several wader species. Breeding densities in coastal meadows of Gotland and Öland range between 10–440 pairs/km² (Ottvall 2004), the most common breeding waders on these meadows are Redshank (*Tringa totanus*), Oystercatcher (*Haematopus ostralegus*), Lapwing (*Vanellus vanellus*) and Ringed Plover (*Charadrius hiaticula*). For all these species, whose population trends are declining overall, a positive relation was found between breeding density and grazing intensity (Ottvall and Smith 2004). In the Netherlands, breeding numbers of several species of waders declined rapidly after cessation of grazing, whereas the decline was retarded in grazed areas (Vulink *et al.* 2001). Though not yet an issue in this area, managers should be keen to ensure continuing grazing by livestock on Baltic marshes in order to maintain diversity and protect the foraging and breeding habitat of geese and waders.

Acknowledgements

Stellan Hedgren of Länsstyrelsen Gotland kindly allowed us to work on the marsh of Grötlingbo-udd. This work would have been impossible without the expertise of Jan Bakker and the supervision of Roos Veeneklaas and Julia Stahl, and the help of the students of the Community and Conservation Ecology Courses in 2004 and 2005.

Habitat use of Barnacle Geese at a sub-Arctic salt marsh in the Kolokolkova Bay, Russia

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Summary

Along the East-Atlantic migratory flyway, goose and swan species rely on the availability of suitable coastal habitats as staging sites during migration and for breeding. Especially for the Russian part of the flyway, detailed descriptions of these habitats in relation to use by herbivores are lacking. We report on salt-marsh characteristics and habitat use by Barnacle Geese in a recently established breeding site, near the village Tobseda at Kolokolkova Bay in the Pechora Delta, Russia. A classification of plant communities was made and vegetation and properties were measured. Goose visitation was assessed by counting droppings. From the bay towards the dunes there was a gradient of decreasing salinity, along with a gradual shift in plant communities from salt marshes to freshwater bogs, tundra and dunes. Barnacle Geese visited salt-marsh communities of the low and middle marsh more than high marsh and non-saline communities. Two low marsh communities were preferred. Both had high tiller densities and low canopy heights and were dominated by *Carex subspathacea*, a species of high forage quality. Those characteristics are selected for by geese, but might be maintained through grazing. The salt marsh at our site bears similarities to other marshes at similar latitudes along the Russian Coast and in Canada. We discuss whether processes, like grazing facilitation and habitat degeneration through overgrazing occur on our site.

Introduction

Recently, research on flight energetics and costs of long-distance migration in waterfowl have revealed that migrating geese and swans ultimately depend on “stepping stones” of suitable foraging habitats along the migration route to meet their energy demands for long-distance flight (e.g. Alerstam and Hedenström 1998; Nolet and Drent 1998). The integrity of the flyway depends on the persistence of appropriate staging sites. These sites serve as “fuelling stations” along the migratory route where birds acquire resources in order to continue their journey and gather a surplus of reserves that will allow them to initiate clutches upon arrival at the Arctic breeding grounds. Along the East-Atlantic migratory flyway, linking western Europe with Siberia, Barnacle Geese (*Branta leucopsis*), Dark-bellied Brent Geese (*Branta bernicla bernicla*), Tundra Bean Geese (*Anser serrirostris*), White-fronted Geese (*Anser albifrons*) and Bewick Swans (*Cygnus bewickii*), and a large variety of ducks rely almost exclusively on coastal habitats as staging (and breeding) grounds. From temperate to sub-Arctic sites, salt marshes play a central role in our understanding of the migratory schedules of herbivores.

The green wave hypothesis suggests that the migration of avian herbivores to Arctic breeding grounds is related to seasonal patterns of plant growth and in particular to changes in the nutrient quality of forage plants. Birds follow the temporal wave of spring growth of forage plants as they migrate North (Owen 1980). The spring production of leaf tissue, which offers nutrients in high concentrations, is the fuel for migration and subsequent breeding. The hypothesis also attempts to explain the traditional restriction of the breeding range of different herbivorous waterfowl species, like geese and swans, to high Arctic regions through limitations in food availability and production (Owen 1980). At Arctic breeding sites, the birds are confronted with a short-time window in which they have to lay eggs, incubate and raise their young. It is extremely important for young birds to be able to forage on high-quality vegetation in order to gain sufficient weight to undertake the southward migration to the temperate wintering grounds (Gadallah and Jefferies 1995; Piedboeuf and Gauthier 1999; Person *et al.* 2003). According to the hypothesis the quality of food on offer during peak standing crop in summer in more temperate regions would be insufficient to support the requirements of the birds and their young. However, the recent expansion of breeding range of a variety of goose species seems to contradict this hypothesis. A species that recently expanded its breeding range from the high Arctic to a wide range of habitats in sub-Arctic and temperate regions is the Barnacle Goose (Van der Jeugd *et al.* 2003). In this study, we use the Barnacle Goose as a model to understand the habitat use of herbivorous migratory birds at a sub-Arctic staging and breeding site.

Although salt marshes are key habitats in the life cycle of small avian herbivores like geese, our knowledge of salt marshes around the Arctic Circle of the Old World remains fragmentary. While several salt marshes in the Canadian and North-American Arctic are well described (Jefferies 1977; Jefferies *et al.* 1979; Vince and Snow 1984; Kincheloe and Stehn 1991), descriptions of salt marshes of the Russian part of the East-Atlantic flyway are either lacking, or are not accessible in Western literature. In this study we attempted to fill this gap by describing different plant communities and their characteristics and mapping the zonation of a salt marsh at an important stopover and breeding site for migrating geese in the Pechora Delta in Arctic Russia. We give special attention to habitat use by Barnacle Geese, as the area forms one of the westernmost breeding sites for the Russian population of this species.

Methods

Study site

Fieldwork was carried out near the village Tobseda (68°35.296'N, 52°18.183'E), in Kolokolkova Bay on the west coast of the Pechora Delta (Figure 2.1). The peninsula, where the village of Tobseda is situated, borders the Pomorsky Channel of the Barents Sea to the north and the Kambalnichya Pakha Gulf of Kolokolkova Bay to the south (Figure 2.1). It is a low coastal terrace, which is being formed in two parallel ways. First, from the sea-side of the terrace due to accumulation of sand on the open coast as a result of abrasion of the shores and sea bottom and, second, from Kolokolkova Bay as a result of sedimentation of clay deposits transported into the bay by the Neruta River. A dune system has developed along the terrace, and salt marshes have established along the shores of the Kolokolkova Bay. The groundwater depth in these marshes is shallow and, therefore, the groundwater salinity is often similar to that of seawater. Moving from the Kolokolkova Bay in the direction of the dunes, the marshes become less saline and gradually turn into sedge-moss mires where freshwater conditions prevail. Within the marshes there are a number of small water bodies differing in salinity.

The salt marshes are potentially of great importance for migrating geese and swans. Satellite telemetry shows that Dark-bellied Brent Geese use the area as a stopover site during spring migration (Syroechkovsky Jr. and Litvin 1998; Green *et al.* 2002). On the return migration in autumn, the area again serves as an important staging post (Van Eerden 2000). On earlier expeditions (1996, 1997), large numbers of Barnacle Geese, Tundra Bean Geese, White-fronted Geese and Bewick Swans were observed in these marshes (Van Eerden 2000). In the past decade the area has developed as a breeding area for Barnacle Geese (Syroechkovsky Jr. 1995; Van der Jeugd *et al.* 2003), probably as an outcome of a reduction in human disturbance, since the nearby village was abandoned.

Vegetation classification and mapping

Vegetation descriptions were made of 48 plots of 4m x 4m. All species of vascular plants, mosses and lichens were recorded. For vascular plants the nomenclature of Czerepanov (1995) was followed. The abundance of all species was recorded by estimating their percentage cover. The vegetation descriptions were arranged in groups of plots with different species and/or combinations of species with a high percentage cover. The resulting classification matched that of Leskov (1936), describing coastal salt-marsh communities of the Barents Sea.

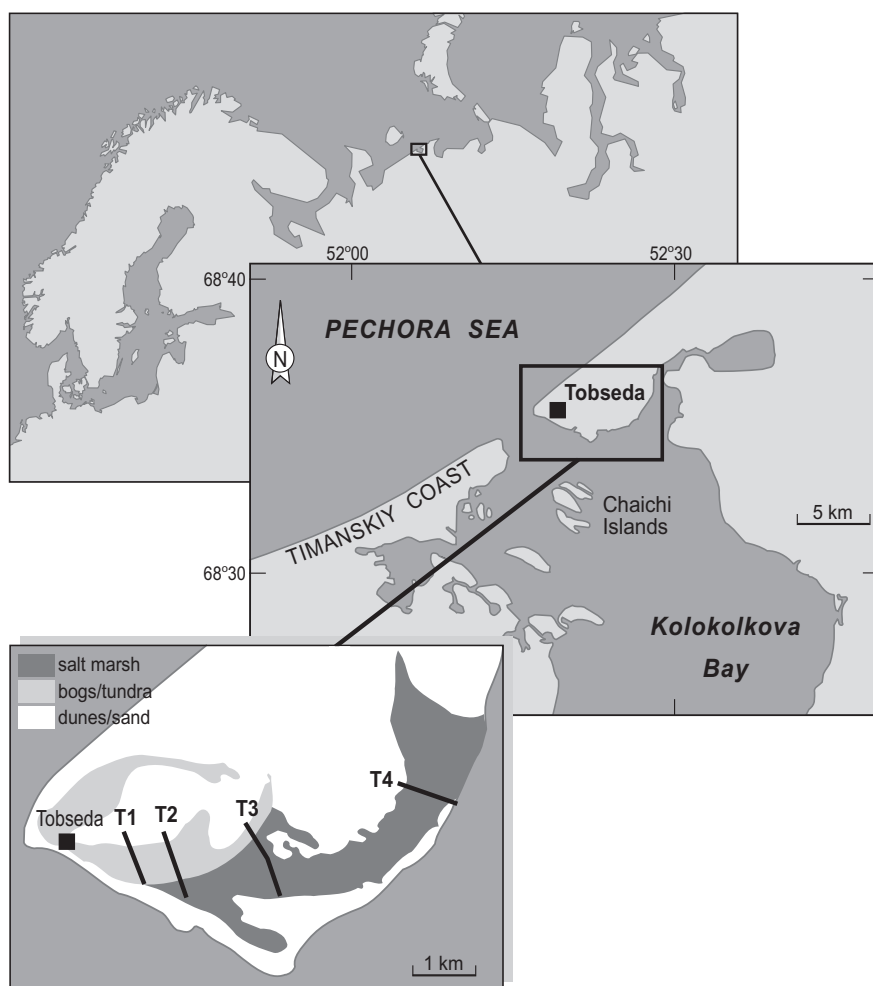


Figure 2.1: Location of the Pechora delta area, the village Tobседа and the transects within the study area. Figure is based on Landsat TM images (1995/1996).

Using this classification (Table 2.1), we determined salt-marsh vegetation zonation along four transects. The four transects were established on different parts of the salt marsh in the summer of 2002 and were considered as four independent replicates (Figure 2.1). Transects ran perpendicular to the coastline in order to map zonation from the low salt-dominated marshes to the dunes. Transects were 50 metres wide and transects 1-4 were respectively 890, 1130, 1280 and 770 m in length. Transects were situated at least 500 m apart from each other and were numbered from northwest to southeast. Transect 1 was close to the (abandoned) village, transect 2 was located in the goose breeding area and transects 3 and 4 were placed towards the east. Transect 4 was higher in elevation than transect 3 and also traversed another small breeding colony. In order to determine the vegetation zonation within each transect, we walked a line-transect of 50 m width, with five people evenly spaced over the entire width of the transect. The transect led from the intertidal flat to the dunes and plant community was recorded by every person every 10 m, using the classification in Table 2.1.

Measurements

For each plant community within each transect goose droppings were counted. Dropping counts were done in mid-July 2002. We assumed that we counted only droppings from the same season and that dropping numbers thus reflected the use of the area in that year, since some droppings might have disappeared within the season due to tidal or wind actions; the number of droppings we use is a net number. Resting piles were discarded. Dropping counts were made using two different methods and were repeated ten times within each vegetation type for each transect in randomly chosen plots. When droppings were abundant, we counted droppings in plots of 4 m². When dropping density was low, we counted plots of 10 m². Densities were expressed as x droppings m⁻². For all plant communities with dropping densities higher than 1 dropping m⁻², we measured tiller density (three replicates, each of 25 cm²), percentage of grazed tillers (three replicates, each of 25 cm²) and canopy height (five measurements to the nearest 0.5 cm) using a sward stick with a styrofoam disc (20 cm diameter, 24g). In addition for each of these plant communities along transects 1, 2 and 3, vegetation cover was estimated in ten randomly selected plots of 4 m². Additionally, we collected samples of leaf tips (approximately 3 cm) from the most abundant plant species for chemical analysis of forage quality. In Table 2.3 the number of replicates for each species is shown. Samples were dried at 60°C for 48 hours and thereafter ground and analysed for nitrogen and carbon contents, using an automated CNHS-analyser (automated element analysis, Interscience EA 1110).

In order to estimate standing crop, samples of aboveground biomass were taken in all plant communities for all transects between 21 and 25 July 2002. In each plant community, we sampled the upper 2-3 cm of soil, including the litter layer. We collected three or four round cores with a diameter of 16.6 cm in each plant community. In stands of *Salix reptans*, the aboveground biomass of willow was cut from an area of 1 m². Green biomass was cut, sorted and dried to a constant weight at 70°C.

In order to measure electric conductivity, surface water was sampled either in the root zone of plants in the *Hippurus tetraphylla*, *Carex mackenziei* and *Dupontia* communities, or in pools that were present in the marsh (all other plant communities; sample sizes are indicated in Table 2.1). Soil samples were collected from the rooting zone of plants (0-8 cm), dried to a constant weight at 70°C and homogenised using a porcelain mortar and pestle and sieved with a mesh-width of 0.25 mm. Every plant community was sampled once on each transect if present (Table 2.2). Contents of total nitrogen and carbon (% of dry matter) were determined by gas chromatography on an automated nitrogen-carbon analyser (ANA-1500) at the Ecoanalit Laboratory (Institute of Biology, Komi Science Centre, Russia).

In order to obtain information about the use of the area by other herbivores, we collected data on presence of other herbivorous birds and mammals. Sightings and counts of birds and mammals were not collected systematically, but were noted. During 10 days, three lines of 20 mousetraps, with bait of carrot and peanut butter were set in the proximity of the village and transect 1 in order to trap small mammals.

Taxonomy of bird species follows guidelines of the Dutch Commission for Avian Systematics (CSNA).

Statistics

As soil and vegetation properties were measured in different plots with different sample sizes, some data are not appropriate for detailed statistical analyses. Hence the results are presented in a descriptive manner. In order to compare goose visitation and vegetation parameters between plant communities we used a univariate ANOVA, combined with a post-hoc Tukey test. Visitation of other herbivores was analysed using a non-parametric Kruskal-Wallis H test. All statistical analyses were performed using the statistical package SPSS for Windows version 11.0.1. Barnacle Goose dropping density was log-transformed to reach normality criteria.

Table 2.1: Total cover percentage of the plant communities at our study site (Figure 2.1) in 2002 combined with a table of frequency and cover of individual vascular plant species. Roman numbers indicate the frequency of individual species (based on presence/absence in the relevés): I – <20 %, II – 21-40%, III – 41-60%, IV – 61-80%, V – 81-100%. Percentage cover of each taxon was estimated subjectively using the following variant of the Braun-Blanquet scale: “r” << 1%, “+” < 1%, “1” 1-5%, “2a” 6-12.5%, “2b” 12.6-25%, “3” 26-50%, “4” 51-75%, “5” 76-100%. Boxes specify the indicative species of the plant community.

Diagnostic species	<i>Hippuris tetraphylla</i>	<i>Puccinellia phryganodes</i> / <i>Carex subspathacea</i>	<i>Carex mackenziei</i> / <i>Wainstorfia exannulata</i>	<i>Carex subspathacea</i> / <i>Stellaria humifusa</i>	<i>Carex subspathacea</i> / dicotyledonous	<i>Calamagrostis deschampsiioides</i> / <i>Carex glareosa</i>	<i>Festuca richardsonii</i> / <i>Parnassia palustris</i>	<i>Salix reptans</i> / <i>Rhodiola rosea</i>
Number of relevés	4	9	6	3	5	12	5	4
Total Cover (%)	10-60	20-100	90-100	70-100	90-100	90-100	100	100
Cover of monocotyledons (%)	10-60	20-100	60-80	40-100	90-100	90-100	90-100	5-50
Cover of mosses (%)			30-100		10		1-10	20-50
Cover of lichens (%)								1-50
Cover of cryptogamic crusts (algae) (%)		20-75		60				
<i>Hippuris tetraphylla</i>	V/2a-4							
<i>Puccinellia phryganodes</i>		V/2a-4		V/1	V/+2b	I/r-2b		
<i>Carex mackenziei</i>			V/4-5					
<i>Dupontia psilosantha</i>			I/+					
<i>Triglochin palustre</i>			I/r		I/r	I/r		
<i>Carex subspathacea</i>		IV/1-3		V/2b-4	V/2a-4	V/+2b	V/r-1	
<i>Stellaria humifusa</i>		II/+	III/+	V/2a-2b	V/1-2b	V/+2b	II/r+	
<i>Potentilla egedii</i>					IV/+2b	V/+2a	III/2a-2b	
<i>Plantago schrenkii</i>					IV/r-4	IV/r-3	II/+1	
<i>Arctanthemum hultenii</i>					III/+1	V/+2a	V/+2a	
<i>Carex glareosa</i>						V/+5	IV/+2b	III/r+
<i>Calamagrostis deschampsiioides</i>						V/+4	V/r-2b	III/r-1
<i>Festuca richardsonii</i>							V/2b-4	I/+
<i>Parnassia palustris</i>							V/+2b	III/+
<i>Salix reptans</i>							I/1	V/2b-4
<i>Rhodiola rosea</i>							IV/r+	V/r+
<i>Carex rariflora</i>								V/1-3
<i>Empetrum hermaphroditum</i>								V/1-3

In the *Salix reptans* community, species with a frequency I include *Luzula wahlenbergii* (+) and *Carex concolor* (+).

Results

Classification of the vegetation

On basis of the vegetation classification 11 plant communities were recognised within the salt marsh (Table 2.1). Three plant communities not presented in Table 2.1 are the *Dupontia psilosantha* community (a community with a dominance of *D. psilosantha*), a community similar to the *Carex subspathacea*/dicotyledonous community, with a dominance of *Plantago schrenkii*, and a community that we call “beach wall”. The latter was situated on an elevated sandy ridge at the coast and was characterised by a low vegetation cover (10%), of which 77% of the cover was graminoids (36% *Puccinellia phryganodes*, 41% *C. subspathacea*). The remainder was *P. schrenkii* (23%); many nests of Barnacle Geese were found in this community.

We divided all non-salt-marsh plant communities into the following habitat classes: water/algae, dune/sand, mires and tundra. This distinction was made on basis of indicator species or groups of species (*Carex aquatilis*, *Carex rariflora* and the presence of a large percentage cover of mosses for mire habitat class, a substantial cover of lichens and dwarf shrubs for tundra habitat class) and substratum. We sub-divided the salt marsh into three habitat classes, based on salinity and location with respect to tidal inundation (low, middle, high). Plant communities belonging to the low salt marsh were the most saline communities: *Puccinellia phryganodes*/*Carex subspathacea*, *Carex subspathacea*/*Stellaria humifusa* and the beach wall community. Plant communities belonging to the middle high salt marsh were more brackish communities: *Hippurus tetraphylla*, *Carex mackenziei*/*Warnstorfia exannulata*, *Dupontia psilosantha*, *Carex subspathacea*/dicotyledonous, *C. subspathacea*/dicotyledonous with *Plantago schrenkii* dominant and *Callamagrostis deschampsoides*/*Carex glareosa*. The plant communities of the high salt marsh were *Festuca richardsonii*/*Parnassia palustris* and *Salix reptans*/*Rhodiola rosea*.

For all plant communities, the total nitrogen content of the sediment by weight was very low (< 1%). Table 2.2 gives the electrical conductivity of the surface water samples. An average electrical conductivity is close to that of seawater (21,000 $\mu\text{S}/\text{cm}$) was distinctive for pools on sites where the communities *P. phryganodes*/*C. subspathacea*, *C. subspathacea*/*S. humifusa*, *C. subspathacea*/dicotyledonous, and *C. deschampsoides*/*C. glareosa* were present, i.e., those communities that experience periodical or occasional flooding by seawater. All other communities showed values more similar to the conductivity of freshwater lakes in the dunes and the high marshes (54.2 $\mu\text{S}/\text{cm}$). However, high standard errors in conductivity values were recorded for the communities listed above, which shows that there was considerable heterogeneity in salinity of soil and lake water represented by these different vegetation communities. We found no significant correlation between salinity and total aboveground biomass (Pearson Correlation = -0.469, $N=8$, $P=0.241$).

Table 2.2: Soil and vegetation properties of salt-marsh plant communities: C/N ratio of sediment, fraction nitrogen in sediment (as a percentage of the dry weight of the soil), electrical conductivity of the groundwater, total aboveground biomass, tiller density and vegetation height. Numbers are means \pm standard error of the mean, sample size given in brackets. For tiller density and canopy heights results of a post-hoc Tukey test are given (see text), different letters denote significant differences at the $p < 0.05$ level.

	Fraction N in sediment (% of dwt)	Electrical conductivity ($\mu\text{S}/\text{cm}$)	Total above- ground dry biomass (g/m^2)	Tiller densities (tillers/25cm)	Canopy heights (cm)
<i>Hippuris tetraphylla</i>		229.5 \pm 81.0 (N=3)	81.40 (N=1)		
<i>Puccinellia phryganodes</i> / <i>Carex subspathacea</i>	0.16 \pm 0.06 (N=5)	14071 \pm 3556 (N=8)	59.34 \pm 8.25 (N=4)	19.04 \pm 1.68 (N=30) ab	1.26 \pm 0.06 (N=30) ab
<i>Carex mackenziei</i> / <i>Warnstorfia exannulata</i>	0.40 \pm 0.17 (N=3)	182.3 \pm 31.0 (N=6)	195.13 \pm 14.64 (N=3)		
<i>Carex subspathacea</i> / <i>Stellaria humifusa</i>	0.30 \pm 0.11 (N=5)	17600 (N=2)	127.20 (N=1)	26.53 \pm 1.93 (N=20) c	0.83 \pm 0.07 (N=20) a
<i>Carex subspathacea</i> / dicotyledonous	0.28 \pm 0.12 (N=4)	4901 \pm 3245 (N=3)	126.47 \pm 6.38 (N=3)	20.55 \pm 1.44 (N=10) abc	2.13 \pm 0.23 (N=10) b
<i>Calamagrostis deschampsii</i> - <i>oides</i> / <i>Carex glareosa</i>	0.31 \pm 0.07 (N=9)	2453 \pm 1494 (N=6)	217.02 \pm 24.33 (N=4)	13.68 \pm 0.88 (N=20) a	5.05 \pm 0.41 (N=20) c
<i>Festuca richardsonii</i> / <i>Parnassia palustris</i>	0.33 \pm 0.12 (N=3)	152.7 (N=1)	221.70 (N=2)		
<i>Salix reptans</i> / <i>Rhodiola rosea</i>	0.13 \pm 0.03 (N=2)	125.3 (N=2)	125.03 \pm 28.19 (N=3)		
Beach wall				25.27 \pm 1.38 (N=10) bc	0.70 \pm 0.04 (N=10) a

Description of the transects

From east to west (i.e. from transect 1 to transect 4), we observed a decrease of mire and tundra habitats and an increase in the area occupied by salt-marsh communities, especially plant communities dominated by *P. phryganodes* and *C. subspathacea* (Figure 2.2). Some plant communities occurred only in a single transect: the *F. richardsonii*/*P. palustris* community was present only in transect 3, the *C. subspathacea*/dicotyledonous community with *P. schrenkii* the dominant species, was present only in transect 4 and the beach wall community was found only in transect 2.

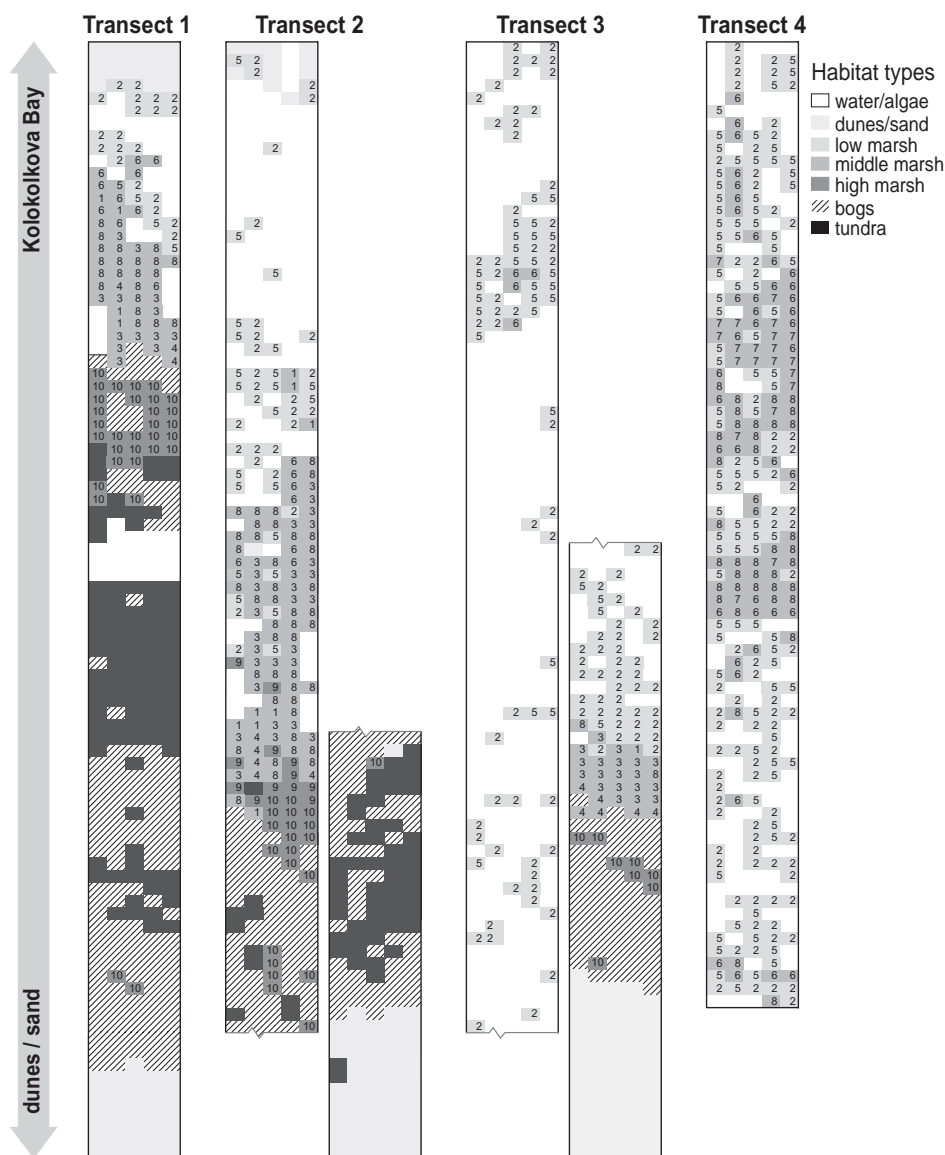


Figure 2.2: Vegetation zonation of the four transects with indication of the main habitat types. Transects were 50 metres wide and transects 1-4 were respectively 890, 1130, 1280 and 770 m in length. For the salt-marsh habitat types, numbers identify the plant community. 1 - *Hippurus tetraphylla*, 2 - *Puccinellia phryganodes*/*Carex subspathacea*, 3 - *Carex mackenziei*, 4 - *Dupontia psilosantha* (not present in Table 2.1), 5 - *Carex subspathacea*/*Stellaria humifusa*, 6 - *Carex subspathacea*/dicotyledonous, 7 - like 6 but with *Plantago schrenkii* dominant, 8 - *Carex glareosa*/*Calamagrostis deschampsoides*, 9 - *Festuca richardsonii*/*Parnassia palustre*, 10 - *Salix reptans*/*Rhodiola rosea*.

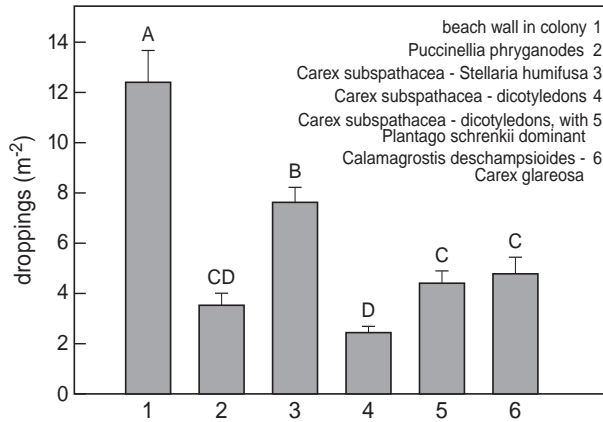


Figure 2.3: Average cumulative dropping densities for the most important vegetation communities (mid-May-mid-July 2002) \pm SE. Communities with dropping densities lower than one dropping per square metre are not included. Different letters denote significant differences (post-hoc Tukey test $p < 0.05$). Values are averaged for all transects, $N = 30$ except for communities 1 ($N = 10$), 4 ($N = 20$) and 5 ($N = 10$), which were only present in one transect.

Barnacle goose visitation in the plant communities

For the salt-marsh communities, we used a univariate ANOVA with plant community as a fixed factor and transect as a random factor, in order to test for differences in goose visitation between transects and plant communities. We found a significant effect of plant community on goose visitation ($F_{8,9} = 14.201$, $P < 0.001$), no effect of transect ($F_{3,9} = 1.516$, $P = 0.276$), and a strong interaction between transect and plant community ($F_{9,189} = 5.671$, $P < 0.001$).

Because the main differences occurred between plant communities and not between transects we grouped all data from the different transects for the analyses of habitat use by Barnacle Geese. A post-hoc Tukey test was used to depict differences between plant communities. All non-marsh plant communities and both the *F. richardsonii*/*P. palustris* and *S. reptans*/*R. rosea* communities did not differ in grazing pressure and had significantly lower dropping densities than those recorded for the other marsh communities. Dropping densities of these plant communities are shown in Figure 2.3. The beach wall community and the *C. subspathacea*/*S. humifusa* community had a significantly higher dropping density than the other communities. All communities that had average dropping densities lower than 1 dropping m^{-2} (non-marsh communities, the *F. richardsonii*/*P. palustris*, *S. reptans*/*R. rosea*, *C. mackenzeei*/*W. exannulata* and *Dupontia psilosantha* communities) were not used for the following analyses.

Vegetation parameters and barnacle goose visitation

Aboveground biomass accumulation was highest in plant communities of the middle and high marshes, where the grasses, *C. deschampsoides*, *F. richardsonii* and the sedge *C. glareosa* dominated. The *P. phryganodes*/*C. subspathacea* community was characterised by a low total net accumulation of biomass (Table 2.2).

Table 2.2 gives the average tiller density and canopy height. Both tiller density ($F_{4,85}=9.180$, $P<0.001$) and canopy height ($F_{4,85}=71.076$, $P<0.001$) were significantly different between plant communities (One-way ANOVA). Overall, the *C. subspathacea*/*S. humifusa* community and the beach wall community, used by breeding geese, had the highest tiller densities and the lowest canopy heights (Table 2.2 shows results of a post-hoc Tukey test). Table 2.3 shows the N content and the C/N ratio of some main forage species. The N content of species differed significantly (One-way ANOVA $F_{6,21}=9.378$, $P<0.001$). *C. subspathacea* and *T. palustre* appear to have the highest N content and the lowest C/N ratio. A post-hoc Tukey test shows that *C. subspathacea* had a significantly higher N content than *P. phryganodes* and *C. deschampsoides*, but the value did not differ significantly from *C. mackenziei*, *C. glareosa*, *C. rariflora* and *P. schrenkii*.

In order to investigate whether Barnacle Geese have a preference for specific vegetation properties, we tested for a relationship between Barnacle Goose dropping density and canopy height and tiller density (univariate ANOVA with plant community as a fixed factor and tiller density and canopy height as covariates). We found a significant effect of plant community ($F_{4,83}=12.657$, $P<0.001$), tiller density ($F_{1,83}=5.433$, $P=0.022$), and canopy height ($F_{1,83}=5.167$, $P=0.026$) on dropping density. In this model, tiller density had a positive effect on dropping density, whereas canopy height affected dropping density negatively. Interestingly, the most preferred communities (the beach wall and the *C. subspathacea*/*S. humifusa* communities) indeed had the highest tiller density and the lowest canopy height. When performing the same test for each plant community separately, we found a significant positive relation between canopy height and dropping density only for the *C. subspathacea*/*S. humifusa* community ($F_{1,17}=14.149$, $P=0.002$). Apparently, Barnacle Geese favoured higher vegetation in this preferred plant community where canopy height was generally low.

Table 2.3: Nitrogen content (as a % of dry weight of the leaf tissue) and C/N ratio of tissue for different species collected from 20-25 July 2002, ranked on ascending N content. Different letters denote significant differences (Tukey post-hoc test with significance level of $p < 0.05$, when $N \geq 3$).

Species	N	Nitrogen (%) \pm SE		C/N ratio
<i>Festuca richardsonii</i>	1	1.64		27.73
<i>Dupontia psilosantha</i>	1	2.00		22.97
<i>Calamagrostis deschampsoides</i>	3	2.34	± 0.05 c	19.75
<i>Puccinellia phryganodes</i>	5	2.58	± 0.22 bc	18.34
<i>Plantago schrenkii</i>	2	2.60		16.17
<i>Carex rariflora</i>	3	2.90	± 0.02 abc	16.26
<i>Carex glareosa</i>	3	2.92	± 0.09 abc	15.90
<i>Carex mackenziei</i>	3	3.27	± 0.14 ab	14.31
<i>Carex subspathacea</i>	9	3.79	± 0.15 a	11.86
<i>Triglochin palustre</i>	1	4.14		9.69

Other herbivores

White-fronted Geese and Tundra Bean Geese occurred in low numbers, some breeding pairs were found in the area but no flocks of non-breeders were seen. A non-parametric Kruskal-Wallis test showed a significant difference in dropping densities of *Anser* species between plant communities ($\chi^2=20.046$, $df=8$, $P=0.010$). Most droppings were found in the *D. psilosantha* community and in the beach wall community. No droppings were found in the *C. subspathacea*/*S. humifusa* and the *C. subspathacea*/dicotyledonous communities.

A couple of pairs of Bewick Swans were observed in the area. Swan grazing differed significantly between plant communities ($\chi^2=43.227$, $df=8$, $P<0.001$). Droppings were found only in the different bog communities and in the *C. mackenziei*/*W. exannulata* community. However, moulting groups of more than 100 birds were observed grazing on the *C. subspathacea*/dicotyledonous community, just outside the study area.

Droppings of Willow Grouse (*Lagopus lagopus*) were found only in one mire site outside the transects, (0.63 ± 0.20 droppings m^{-2} , $N=70$) and on a dry ridge running through that bog (0.95 ± 0.53 droppings m^{-2} , $N=40$). We found no droppings of Reindeer (*Rangifer tarandus*) or Mountain Hare (*Lepus timidus*) in the area. We did not catch any small mammals on our mousetrap transects, neither did we observe any tracks in the area.



Top: Mennobart van Eerden, Olga Lavrinenko, Vladimir Elsakov and Götz Eichhorn studying the vegetation on the salt marsh near the village of Tobседа (clockwise starting from the left, July 2002)
Bottom: Salt marsh area near the village of Tobседа, early-June 2003

Discussion

The Tobsteda salt-marsh bears similarities in vegetation composition to other marshes along the Russian coast (Korchagin 1935; Rebristaya 1997; Shoyna marsh, Kanin Peninsula, personal observations) and to marshes at similar latitudes in North-America, in particular the marsh at La Pérouse Bay, Canada (Jefferies *et al.* 1979). Just like the Canadian site, the lower salt marsh here is dominated by *P. phryganodes* and *C. subspathacea* and the soil nutrient content is very low. At the lowest elevation, *P. phryganodes*/*C. subspathacea* vegetation forms a mosaic pattern with bare soil (Figure 2.2). This pattern is probably typical for low salt-marsh areas in sub-Arctic environments, where mechanical disturbance (ice rafting) is prominent; and it has also been described for the Canadian sub-Arctic site (Srivastava and Jefferies 2002). At our site, the mosaic turns into a more distinct zonation along the elevational gradient where the *P. phryganodes*/*C. subspathacea* community grades into the *C. subspathacea*/*S. humifusa* and *C. subspathacea*/dicotyledonous community. All plant communities with high cover of either *P. phryganodes* or *C. subspathacea* are preferentially used by foraging geese.

As the Russian sub-Arctic salt marsh at our study site is heavily used by staging, breeding and moulting geese, processes similar to those acting in La Pérouse Bay may play a role: stimulation of plant production at modest levels of herbivory and habitat degeneration at high levels. At the salt marsh of La Pérouse Bay, appropriate densities of Lesser Snow Geese (*A. caerulescens caerulescens*) increase the production, density and nitrogen content of their forage plants (*P. phryganodes* and *C. subspathacea*) by grazing (Cargill and Jefferies 1984b; Kotanen and Jefferies 1987; Bazely and Jefferies 1989a). This is caused by accelerated nutrient cycling as a result of grazing and subsequent fertilisation of the vegetation by droppings (Bazely and Jefferies 1985; Hik and Jefferies 1990). The negative effects of large numbers of herbivores on their forage plants are cumulative and result in habitat degeneration. The negative effects are initiated by the grubbing of Lesser Snow Geese. As a result of the removal of the insulating mat of plant material, soil evaporation increases, which leads to hypersaline conditions in the upper layers of the soil, thereby reducing the growth of graminoids (Srivastava and Jefferies 1996). In grubbed areas, soil nitrogen and its mineralisation are decreased which, together with the hyper saline conditions limit the re-establishment of plants (Wilson and Jefferies 1996; Walker *et al.* 2003). Unlike the Snow Geese in the Canadian Arctic, Barnacle Geese do not forage destructively. They graze the aboveground plant material and do not grub for below-ground plant parts. At our Russian site, we found no evidence of negative effects of goose grazing on the graminoid sward and we do not expect habitat degeneration as a result of goose foraging to play a role in inducing vegetation change in this Russian sub-Arctic salt marsh. It is likely, however, that grazing optimisation does play a role in this marsh.

Vegetation selection by barnacle geese at a sub-Arctic marsh

Our data suggest that Barnacle Geese select forage sites on a combination of the forage parameters canopy height, tiller density and food quality. It is striking that the two most preferred plant communities both contain the two forage species with highest tissue quality: *T. palustre* and *C. subspathacea*. The preferred communities also had the highest average tiller densities and the lowest average canopy heights. Interestingly, these can either be the characteristics geese select for, or they can be caused by goose grazing. Grazing reduces canopy height and may increase tiller density of the grazed vegetation (McNaughton 1984; Kotanen and Jefferies 1987; Bazely and Jefferies 1989a). Dense swards of forage plant species are preferred by geese, as they result in increased food intake rates (Van der Wal *et al.* 1998b). At the same time, geese are known to prefer low canopy heights as short swards decrease handling time and enhance foraging efficiency (Van der Wal *et al.* 1998b; Hassall *et al.* 2001; Bos *et al.* 2002).

For Arctic and sub-Arctic systems, several studies demonstrated that quality of the vegetation is improved through grazing (Gauthier *et al.* 1995; Post and Klein 1996; Ruess *et al.* 1997; Fox *et al.* 1998). The alleviation of the nutrient limitation of the vegetation through the addition of herbivore faeces plays an important role in this process (Bazely and Jefferies 1989b; Ruess *et al.* 1997). Future studies on the Tobseda marsh will investigate nutrient availability for plant growth at that site and the role of foraging geese in regulating ecosystem processes.

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Patch choice of avian herbivores along a migration trajectory – from temperate to Arctic

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Summary

1. Many herbivorous waterfowl species are migratory and seem to track temporal and spatial pulses of optimal forage availability on their way from temperate wintering to arctic breeding sites.
2. In order to unravel the relative contribution of forage quality and forage biomass to foraging choices in avian herbivores, we experimentally manipulated biomass and quality of main forage plants through fertilisation and grazing exclusion at three sites along the migration flyway of Barnacle Geese, *Branta leucopsis*.
3. Fertilisation increased the nitrogen content of the forage and grazing exclusion increased biomass levels. Additionally, natural levels of tissue quality and biomass differed along the flyway.
4. Manipulated plots were offered to wild geese in a multifactorial, replicated design at each site and goose visitation was measured based on dropping counts.
5. At all sites, grazing pressure was highest on plots with a combined increase of biomass and quality. Generally, geese preferred plots with the highest nitrogen availability per surface area.
6. The numerical response of the geese to forage changes was supported by behavioural observations at one site. Plots with a combined increase of biomass and quality were defended vigorously against flock mates.
7. We show that geese maximise nutrient intake through distinct choices for forage of the highest quality and optimal biomass levels. These findings help to interpret changes in forage quality and availability induced by human land use in numerous coastal habitats.

Introduction

Avian herbivores of the Northern Hemisphere breed in the (sub-) Arctic and winter in more southern, temperate areas. During spring migration the birds have to balance their energy expenditure and food intake in order to build up sufficient energy reserves to be able to migrate to their breeding areas and breed successfully (Drent *et al.* 2003; Bety *et al.* 2003; Ward *et al.* 2005). The birds usually migrate in several distinct steps, and refuel and rest at each stopover site (Nolet *et al.* 2001; Green *et al.* 2002; Eichhorn *et al.* 2005). Plant forage availability and quality on these sites play a crucial role for these small herbivores, as the amount of body reserves accumulated by individuals prior to migration directly affects breeding success (Ankney and Macinnes 1978; Ebbs and Spaans 1995; Prop and Black 1998; Madsen 2001). At the breeding sites, food availability and quality influence final adult body size because of the impact on gosling growth rates (Cooch *et al.* 1991; Sedinger *et al.* 1995; Loonen *et al.* 1997; Larsson *et al.* 1998). Fledgling weight also influences post-fledgling survival (Loonen *et al.* 1997; Van der Jeugd and Larsson 1998) and the probability of breeding for individuals that survive (Sedinger *et al.* 2004). It is evident that food availability and quality shape fitness and life history parameters of these avian herbivores. However, the herbivores are faced with a dilemma on their migration; as an increase in plant biomass frequently corresponds with a decline in food quality (Lepage *et al.* 1998; Chapter 5). Several studies on foraging by avian herbivores suggest that the foragers may not maximise intake as such, but instead maximise nutrient intake (Lepage *et al.* 1998; Kristiansen *et al.* 2000; Hassall *et al.* 2001). A recent study with captive birds demonstrates experimentally that herbivorous waterfowl maximise digestible nitrogen intake rate rather than dry matter intake rate (Durant *et al.* 2004). Prop and Black (1998) showed that Barnacle Geese, *Branta leucopsis*, accumulated fat and protein reserves when feeding on natural vegetation during staging, whereas birds feeding on fertilised agricultural fields accumulated large amounts of fat but little protein. Birds foraging on natural salt-marsh vegetation showed a positive correlation between stored fat and breeding success, but for birds foraging in other habitats this relationship was lacking. These results suggest that protein intake plays an important role and we therefore hypothesise that small avian herbivores do not maximise food intake, but instead maximise protein intake. On the tested assumption that protein intake is a function of food intake and that food quality declines with the increasing aging of the flush of growth of spring forage, birds have two alternatives in order to obtain maximum protein intake: either forage on patches with high biomass and low quality and maximise total intake, or forage on patches of vegetation with a lower biomass but a higher quality. Based on the digestive constraints on intake rate (Sedinger and Raveling 1988; Prop and Vulink 1992) and time constraints of birds during migration, we hypothesise that the latter strategy will be followed.

In this study this hypothesis was tested using the Barnacle Goose. During their spring migration from staging sites in the European Wadden Sea to (sub-) Arctic breeding sites, Barnacle Geese follow consecutive waves of fresh spring growth of their forage plants as they migrate northwards (Drent *et al.* 1978; Owen 1980; Chapter 5). At each stopover site, goose arrival is timed to maximise the profit from increased spring production of the vegetation and the high initial nutritional quality of forage grasses. At the (sub-) Arctic breeding sites, the peak in spring growth and quality appears to coincide with gosling hatch and it is assumed to facilitate good growth conditions for goslings (Sedinger and Raveling 1986; Lepage *et al.* 1998; Chapter 5). We tested forage patch choice of migrating Barnacle Geese along the entire East-Atlantic flyway of this species (Ganter *et al.* 1999). On a temperate spring staging site in the Wadden Sea, a Baltic stopover site and a Russian sub-Arctic breeding site, tissue quality and biomass of the main forage species were experimentally manipulated and choice of forage patch of migrating geese was measured. Supplementary behavioural observations were conducted at the Baltic stopover site to validate the numerical responses of the geese, as measured through dropping densities at sites.

Methods

Study sites

The study was conducted at three sites representing staging, stopover and breeding areas along the East-Atlantic flyway of the Barnacle Goose during the spring of 2003 and 2004. The western-most study site is the island of Schiermonnikoog in the Dutch Wadden Sea (53°30'N, 6°10'E; Box 1). The island is used as a winter and spring staging site by up to 13,000 Barnacle Geese (Bos and Stahl 2003). The salt marsh of the island consists of an ungrazed area and an area that is grazed by livestock from early May until late November. Both areas are intensively used by wild geese prior to migration (Van der Graaf *et al.* 2002). We chose to conduct the experiment on the livestock-grazed salt marsh, because vegetation structure here is more similar to that of the other selected sites. On the ungrazed marsh accumulation of litter complicates the foraging choices of the geese (Summers and Critchley 1990; Riddington *et al.* 1997; Van der Wal *et al.* 1998b). The geese leave this site towards the end of April, each year.

The second study site is situated on the Swedish island of Gotland in the Baltic Sea (Box 2). Here, thousands of geese use the narrow bands of coastal salt marshes and adjacent agricultural pastures as a stopover site during a period of about four weeks in late April and May. These marshes are grazed by livestock from early June until late October. Our study site is a salt marsh on the peninsula Grötlingboud, in the south-east of Gotland, Sweden (57°07'N, 18°27'E).

The third study site represents a breeding site at the Barents Sea coast in northern Russia, at the Kolokolkova Bay, near the abandoned village of Tobseda (68°35'N, 52°20'E; chapter 2). Geese arrive here end of May and start breeding upon arrival. Large moulting flocks gather in this area from mid-July onwards, together with family birds and all geese leave the area at the end of September. This colony holds around 1,500 breeding pairs with peak hatch in early July (Van der Jeugd *et al.* 2003). No livestock grazing is currently taking place at this site, but the area has been grazed by horses until around 1995.

On the first two sites the main forage plant is Red Fescue, *Festuca rubra*, accounting for respectively 90% (Schiermonnikoog; Van der Wal *et al.* 1998b) and 45% (Gotland, own data based on epidermal counts of plant remains in goose faeces) of the goose diet. On the Russian site the diet consists of *Carex subspathacea* and *Puccinellia phryganodes* in equal proportions (own data).

Experimental set-up and measurements (Experiment 1)

Plant biomass was manipulated by placing temporary grazing exclosures on salt-marsh swards for 3-4 weeks, thereby creating a difference in plant biomass compared to continuously grazed, non-fenced control plots. At the same time, forage quality was manipulated by fertilising plots with commercial granular fertiliser (NPK, 12-10-18) resulting in an experimental addition of 10 grams of nitrogen per square metre. We used the same experimental design at the three sites, on every site an area was selected that was frequently used by foraging geese. Additionally we calculated total nitrogen in above-ground plant biomass, a combination of nitrogen per unit biomass multiplied by the amount of biomass and expressed in g N m^{-2} .

Within the experimental area at each site, we created six replicate, randomly located blocks, spaced about 50m apart from each other. Each block contained four plots (4 m x 4 m) representing the four treatments: naturally grazed, ungrazed, fertilised and ungrazed & fertilised. A treatment was randomly assigned to each plot within a block. Exclosures at the the Wadden Sea staging site, the Baltic Sea stopover site and the Russian breeding site respectively were set-up on 20 March 2004, 4 April 2003 and 1 July 2003. After three to four weeks exclosures were removed, forage biomass and quality were measured on all plots and all droppings were removed from previously grazed plots. Plots were now accessible for wild Barnacle Geese. For the Wadden Sea staging site, the Baltic Sea stopover site and the Russian breeding site respectively exclosures were removed on 13 April 2004, 5 May 2003 and 22 July 2003. This point in time is called start of the experiment throughout this chapter and coincided for all areas with the peak in utilisation of the area by the geese. Grazing intensity of geese was measured by dropping counts on all plots, which allowed an assessment of foraging choices of the geese. Droppings were counted as soon as all replicate blocks were visited by geese, in order to prevent differences being obscured by geese foraging on less favourite plots after the favourite plots had been depleted.

For the Wadden Sea staging site this was seven days, for the Baltic stopover site five days and for the Russian breeding site four days. Grazing intensity is determined by the number of droppings accumulated during this period.

At the start of the experiment, the status of forage biomass was determined from combined measures of tiller density and tiller weight of the main forage species. As destructive biomass sampling is connected with rather large measuring errors in this type of short grass swards (own experience), the following approach was adopted instead. This method combines measurements of tiller densities, leaf length and length-to-biomass ratios to obtain a measure of biomass. In each plot the number of tillers was counted in 20 randomly placed quadrats, each of 5.5 cm x 5.5 cm. Tiller weight was determined by clipping 50 individual tillers at ground level from each plot, drying them for 48 hours at 60°C and subsequently weighing them. In order to obtain a representative sample of tillers, a point was randomly selected within each quadrat and all tillers around this point were collected until a sample of 50 tillers was achieved. Forage biomass was calculated by multiplying tiller density by mean tiller weight. In order to determine forage quality, a sample of green leaf tips was collected at the start of the experiment. Samples were dried at 60°C for 48 hours, ground and analyzed for nitrogen content, using CNHS-automated elemental analysis (Interscience EA 1110).

Specific tests, including behavioural observations (Experiment 2)

In May 2004, the experiment was repeated with five replicates, similar to the design of 2003, at the Baltic stopover site only, with the objective of assessing forage patch choice by the geese based on direct behavioural observations, in addition to dropping counts. Experiment 2 was conducted close to the area used for Experiment 1 in 2003. Measurements on biomass were conducted by cutting a small turf (10 cm x 10 cm), removing all above-ground biomass and sorting it into grasses and other species. The material was then dried at 60°C for 48 hours and weighed. Biomass data, therefore, comprise the weight of all grasses present. This destructive method, as opposed to the detailed non-destructive method used in Experiment 1, was used because a mixed sward of several species occurred in the area of Experiment 2. Forage quality was measured following procedures used in 2003. Dropping counts to measure grazing intensity were performed in the same way as in 2003. Additionally, canopy height was measured randomly 20 times per plot to the nearest 0.5 cm using a polystyrene disc (20 cm diameter, 24 g), which slid along a graduated stick. The choice experiment was conducted in early May 2004 on Gotland. Corners of all experimental plots were marked by inconspicuous small plastic tubes in order to be able to distinguish plots from a distance. Observations were made from a hide at a distance of about 250 m, which was placed on a slightly elevated position. During the first five days after the start of the experiment, the number of geese present on each plot of the different treatments was noted every five minutes.

In addition, the number of aggressive encounters between geese on the plot and other flock members was recorded. For each plot, goose presence was calculated as the total time geese were present on a plot multiplied by the number of geese on the plot during the entire observation period. Goose presence is expressed as goose minutes. Interactions are given as the number of interactions per goose observed for each minute that geese were present on the plot. As a measure of forage intake, peck rates were collected for individual geese on all different treatments. Peck rates were measured as the time needed for 50 pecks; these data were later converted to pecks per minute.

Statistical analyses

All data were tested for normality using a Kolmogorov-Smirnov test (SPSS for Windows, version 12.0.1). When data were not normally distributed a non-parametrical Mann-Whitney U-test was used. To test whether grazing exclusion and fertilisation had an effect on plant biomass and quality, a multivariate ANOVA with biomass and quality as dependent variables and exclosure and fertilisation as fixed factors was used for each site. To test whether grazing exclusion and fertilisation influence grazing intensity, a univariate ANOVA was used, with site, grazing exclusion and fertilisation as fixed factors. Additionally, the same test was performed for each site. Univariate ANOVAs with grazing exclusion and fertilisation as fixed factors were used for the vegetation and observational data of 2004. Additionally, a Tukey LSD was performed to find differences in response of the geese to the individual treatments. All analyses were performed using the statistical package SPSS for Windows, version 12.0.1.

Table 3.1: Results of multivariate ANOVAs testing the effects of grazing exclusion and fertilisation (fixed factors) on tissue biomass and quality (measured as nitrogen content of the plant tissue as percentage) of forage species at the start of Experiment 1 at the Wadden Sea staging site, the Baltic Sea stopover site and the Russian breeding site (on 13 April 2004, 5 May 2003 and 22 July 2003 respectively).

Effect of :	On:	Wadden Sea staging site		Baltic Sea stopover site		Russian breeding site *	
		$F_{1,20} =$	P	$F_{1,20} =$	P	$F_{1,20} =$	P
Exclosure	Biomass	19.12	< 0.001	13.39	< 0.001	28.18	< 0.001
	Quality	0.97	= 0.337	3.11	= 0.093	0.00	= 0.985
Fertilisation	Biomass	1.54	= 0.229	2.89	= 0.104	0.14	= 0.710
	Quality	23.57	< 0.001	20.44	< 0.001	120.78	< 0.001

* with significant interaction of exclosure x fertilisation on biomass: $F_{1,20} = 6.83$, $P = 0.017$. All other interactions were not significant.

Results

Experimental manipulations and numerical response (Experiment 1)

On all sites, exclusion of grazing increased aboveground biomass of forage plants and fertilisation increased nitrogen content of the leaf tissue (Figure 3.1, Table 3.1). At the Russian breeding site there was a significant interaction between grazing exclusion and fertilisation with respect to forage biomass, with the ungrazed and fertilised combination plot showing a high biomass response as compared to solely ungrazed or fertilised plots. Because the treatments had the required effect on the vegetation from here on they will be referred to as increased quality (fertilised), increased biomass (exclosed) and increased quality and biomass (fertilised and exclosed).

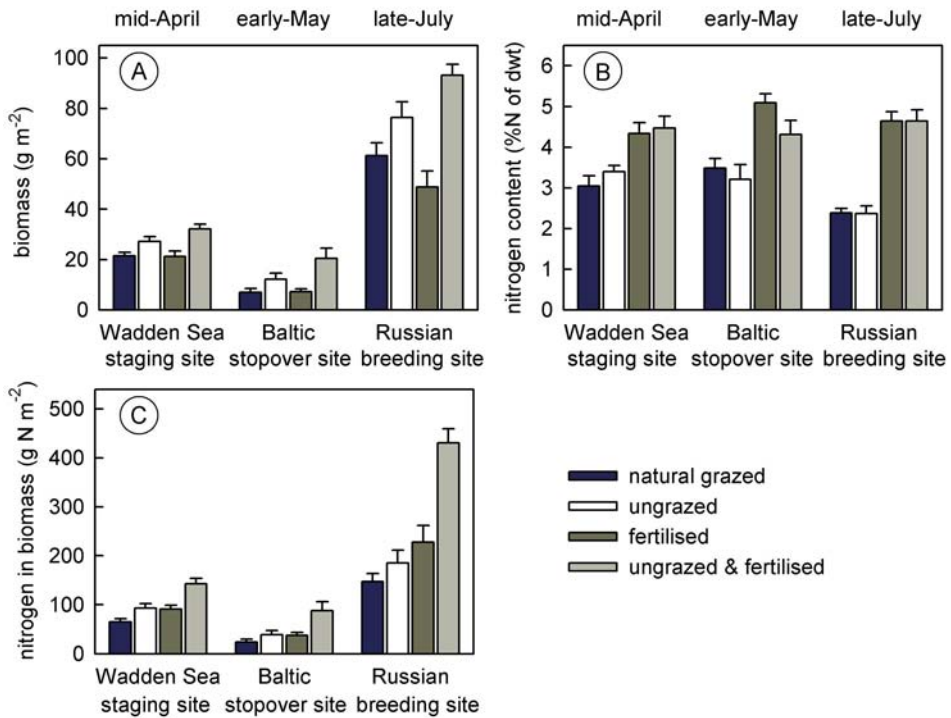


Figure 3.1: The effects of exclosure and fertilisation treatments at the start of the experiment on **A.** leaf tissue biomass (in g m⁻²), **B.** quality of forage species, measured as percentage nitrogen and **C.** the product of biomass and quality, nitrogen content of the vegetation per unit area (in g N m⁻²), at the Wadden Sea staging site, the Baltic Sea stopover site and the Russian breeding site (on 13 April 2004, 5 May 2003 and 22 July 2003 respectively), Experiment 1. Shown are means \pm standard error ($N=6$). Test results are shown in Table 3.1.

When effects of grazing exclusion and fertilisation on subsequent grazing intensity were tested for all sites in comparison, a strong three-way interaction was found between the two treatments and site. This interaction demonstrates that the treatments had a different effect on grazing intensity at each site. Further analyses were therefore performed for each site separately (Table 3.2). At all sites along the flyway, the geese showed a strong and significant numerical response to the experimental treatments. Figure 3.2 shows the response of the geese to the experimental treatments, values are expressed as the percentage of the total cumulative grazing intensity per unit area in order to compare sites; all statistical tests, however, were performed based on the original data. Highest grazing intensities occurred on plots that had been exclosed and fertilised (Figure 3.2). At the Wadden Sea staging site preference for plots with either increased quality only or increased biomass only was similar to the selection by the geese of naturally grazed plots. On the Baltic site both increased biomass and increased quality are preferentially selected, while on the Russian site increased biomass only is not selected above the naturally grazed situation, in contrast to plots of increased quality which are strongly preferred.

Combining data of all sites, there were strong correlations between forage plant biomass, forage quality and grazing intensity (Table 3.3). For the Wadden Sea staging site only a correlation of grazing intensity with forage quality was observed, while for the Baltic stopover site there was only a correlation of grazing intensity with biomass (Table 3.3). Finally, at the Russian breeding site grazing intensity was correlated with both biomass and quality. In addition, at all three sites, there was a very strong correlation between grazing intensity and the combined measure of nitrogen per unit area in green biomass, which explains 35-65 % of the observed variation in grazing intensities (Table 3.3).

Table 3.2: Results of a univariate ANOVA testing the response of cumulative goose grazing intensity 4-7 days after the start of the experiment, to experimentally increased tissue biomass and quality (measured as nitrogen content of the plant tissue as percentage) in Experiment 1, tested on all sites combined and for each site separately.

Effect of	All sites combined		Wadden Sea staging site		Baltic stopover site		Russian breeding site	
	<i>F</i>	<i>P</i>	<i>F</i> _{1,20} =	<i>P</i>	<i>F</i> _{1,20} =	<i>P</i>	<i>F</i> _{1,20} =	<i>P</i>
Site	<i>F</i> _{2,60} = 3.47	= 0.038						
Increased Biomass	<i>F</i> _{1,60} = 68.44	< 0.001	16.87	= 0.001	24.02	< 0.001	30.93	< 0.001
Increased Quality	<i>F</i> _{1,60} = 155.46	< 0.001	20.50	< 0.001	62.92	< 0.001	93.15	< 0.001
B * Q	<i>F</i> _{1,60} = 28.97	< 0.001	2.09	= 0.164	7.45	= 0.013	26.05	< 0.001
S * B	<i>F</i> _{2,60} = 1.88	= 0.161						
S * Q	<i>F</i> _{2,60} = 10.26	< 0.001						
S * B * Q	<i>F</i> _{2,60} = 5.28	= 0.008						

Table 3.3: Pearson correlation between grazing intensity on the different plots and forage plant characteristics such as nitrogen content of plant tissue as a percentage, biomass, and nitrogen content of the vegetation per unit area in Experiment 1 ($N=24$ for each site, $N=72$ for all sites combined). * $P \leq 0.05$ level, ** $P \leq 0.01$, *** $P \leq 0.001$

		All Sites	Wadden Sea staging site	Baltic stopover site	Russian breeding site
Nitrogen content (%)	R	0.54 ***	0.64 ***	0.36	0.68 ***
Biomass (g m^{-2})	R	0.33 **	0.31	0.72 **	0.46 *
Available N (g N m^{-2})	R	0.59 ***	0.64 ***	0.81 **	0.79 ***

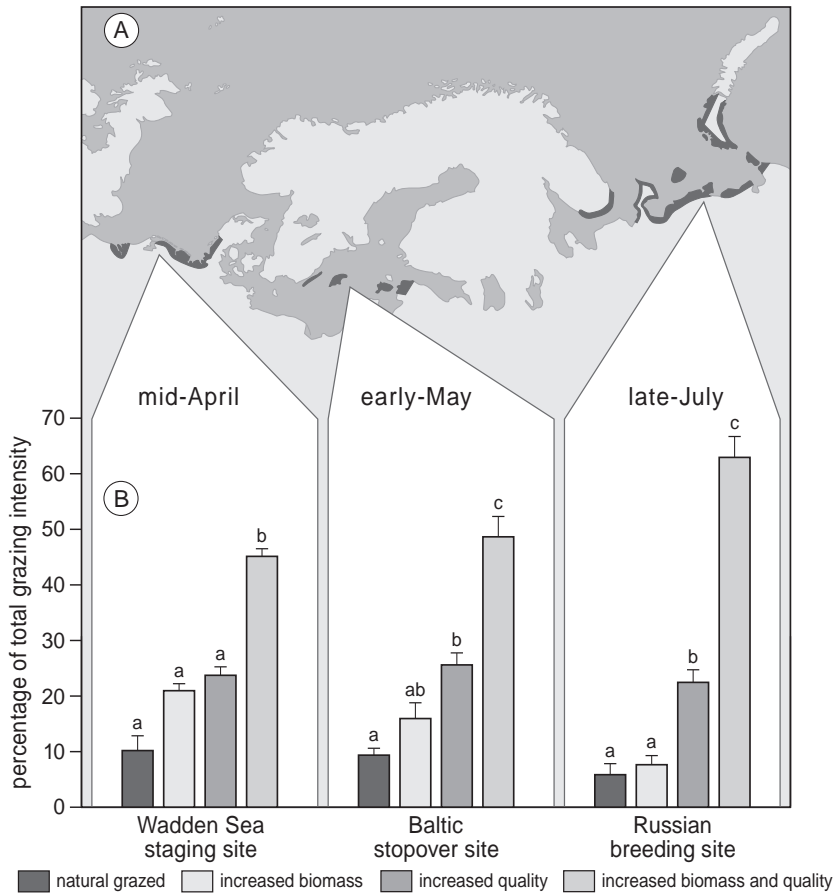


Figure 3.2: **A.** The flyway of the Barnacle Goose projected from left to right, with the three study sites. **B.** The effects of increased biomass and quality on the relative grazing intensity for each study site, Experiment 1. Shown are mean percentages + standard error ($N=6$). Different letters denote significant different values, $P < 0.05$ Tukey LSD test. Behavioural response (Experiment 2)

Table 3.4: Results of univariate ANOVAs testing the effects of grazing exclusion and fertilisation (fixed factors) on the vegetation parameters: aboveground-biomass (g m^{-2}), canopy height (cm) and tissue quality (%) and on behavioural observations: grazing intensity (# droppings m^{-2}), goose presence (gooseminutes), the number of interactions (# goose $^{-1}$ min $^{-1}$) and peck rate (pecks min $^{-1}$) on Gotland in 2004, Experiment 2. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Effects of:	Biomass	Height	Quality	Grazing intensity	Goose presence	Inter-actions	Peck rate
	$F_{1,16} =$	$F_{1,16} =$	$F_{1,16} =$	$F_{1,16} =$	$F_{1,16} =$	$U^{\#}$	$F_{1,205} =$
Exclosure	51.00 ***	115.98 ***	15.96 ***	10.13 **	61.89 ***	100.0 ***	90.54 ***
Fertilisation	4.69 *	4.54 *	35.70 ***	12.88 **	33.90 ***	39.0	2.56
E * F	4.85 *	5.33 *	0.36	7.10 *	13.67 **	-	0.14

Data are not normally distributed, a non-parametric Mann-Whitney U-test was used

In 2004 at Gotland, grazing exclusion significantly increased grass biomass (naturally grazed, ungrazed, fertilised, ungrazed and fertilised respectively 28.1 ± 4.5 , 75.1 ± 6.9 , 27.8 ± 6.5 and 116.6 ± 15.9 g dwt m^{-2}) as well as canopy height (naturally grazed, ungrazed, fertilised, ungrazed and fertilised respectively 2.1 ± 0.1 , 3.8 ± 0.1 , 2.0 ± 0.1 and 4.7 ± 0.3 cm) and experimental fertilisation increased grass quality (naturally grazed, ungrazed, fertilised, ungrazed and fertilised respectively 2.8 ± 0.1 , 2.1 ± 0.1 , 4.0 ± 0.3 and 3.2 ± 0.2 %) (Table 3.4). Dropping counts one week after start of the choice experiment gave similar results in 2003 and 2004 at this site (Figures 3.2 and 3.3); plots with a combined increase of biomass and quality were preferred above all other treatments. The data from 2004 reveal a non-significant trend of higher grazing intensities on plots with either increased quality or biomass, as compared to the naturally grazed plots. The behavioural observations indicate that geese preferred the treatment with combined high quality and high biomass (Figure 3.3). Here, goose presence was higher than on all other treatments and more aggressive interactions were observed (Table 3.4). Both goose presence and the number of aggressive interactions also were higher on the plots with high biomass compared to naturally grazed plots. There were no differences detected in these two parameters for plots with increased quality. Peck rate was lower on plots with increased biomass; this shows that either increased biomass or canopy height decreased peck rate.

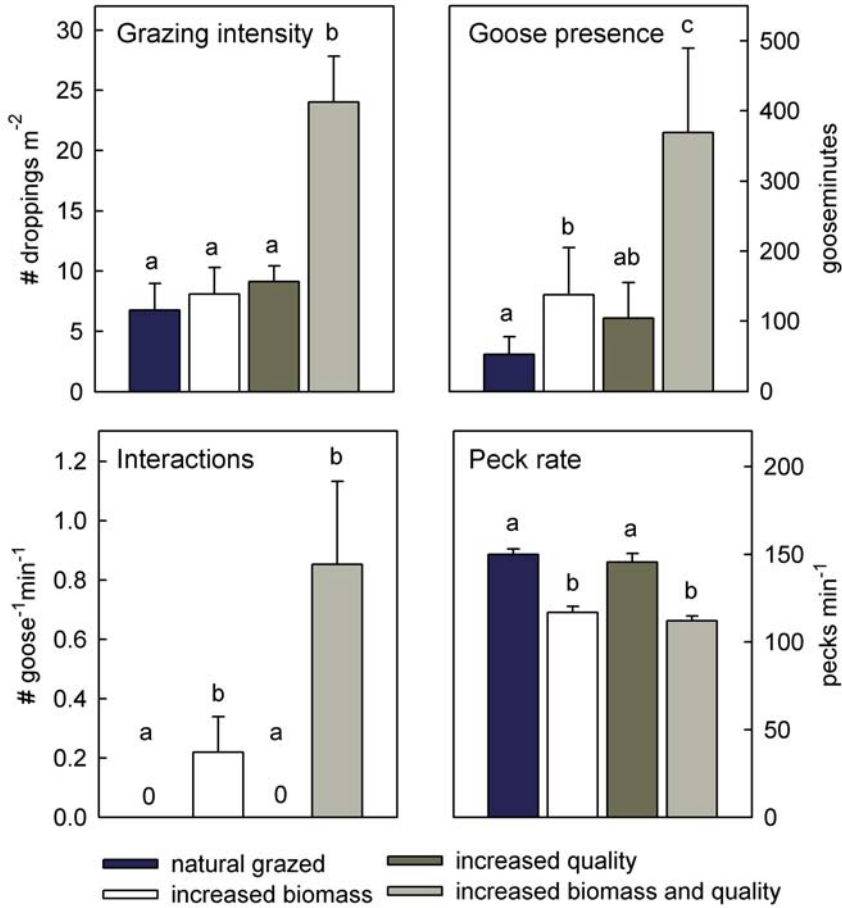


Figure 3.3: Behavioural observations on the use of experimental plots on the Baltic stopover site in 2004, Experiment 2. Shown are mean percentages + standard error ($N=5$). Different letters denote significant different values, $P < 0.05$ Tukey LSD test. For statistics see Table 3.4.



Top: Julia Stahl and Reinout Havinga on their way to apply the fertiliser treatment (Tobseda, July 2003).

Bottom: Effects of the fertiliser and exclosure treatments on Gotland, May 2003

Discussion

Geese maximise nutrient intake

When experimentally exploring the relationship of goose visitation with plant nitrogen content, forage biomass and the above-ground nitrogen content of plants per unit area of green biomass (Table 3.3) it becomes evident that the geese have a clear preference for plots with highest nitrogen content per unit area along the entire migration route. Our data support the recent findings on captive geese by Durant *et al.* (2004) and are also in agreement with an earlier study on Dark-bellied Brent Geese, *Branta bernicla bernicla* at a spring staging site in the Wadden Sea (Teunissen *et al.* 1985). Similar to the findings of these studies, we conclude that Barnacle Geese appear to maximise total nitrogen intake instead of total biomass intake along the entire flyway. Several studies have already pointed out the importance of a high-quality diet on the growth rate and final body size of goslings (Lindholm *et al.* 1994; Lepage *et al.* 1998).

The preference of geese for a combination of plant quality and biomass does not come as a surprise as these plots naturally provide the opportunity for the highest nitrogen intake per unit area. In nature, however, there is always a trade-off between forage quality and quantity: with increasing biomass plant quality decreases (Lepage *et al.* 1998; Chapter 5) and digestive constraints limit an increased intake of plant material to compensate for low forage quality (Prop and Vulink 1992). We, therefore, aimed to investigate the preference of geese between plots with high nutritional quality of the plant tissue and low biomass, as opposed to plots with low quality and high biomass. At all sites along the goose flyway we witness a similar trend; plots with increased quality and average biomass are preferred by herbivores above average quality and high biomass. This trend is consistent with our hypothesis that selecting high quality plants reduces the time necessary to collect sufficient reserves for breeding and thus potentially gives the birds the advantage of arriving earlier on the breeding sites. Several advantages of early breeding have been found in other studies: brood-size decreases seasonally in many geese and in other waterfowl species associated with late breeding (Toft *et al.* 1996; Dalhaug *et al.* 1996; Lepage *et al.* 1998; Béty *et al.* 2003), and several studies demonstrate a decline in growth rate and final adult body size of late-hatched goslings (Sedinger and Flint 1991; Williams *et al.* 1993; Lindholm *et al.* 1994).

Additionally, the correlation of goose visitation with nitrogen content of the vegetation per unit area and forage biomass (Table 3.3) indicates that patch choice differs between staging sites. We suggest that this is caused by differing limiting resources along the migration route. At the Russian breeding site overall levels of biomass are high due to low levels of goose grazing, but forage quality is low (this study; Chapter 2), here forage quality is the choice criterion. At the Baltic stopover sites where high grazing intensities during spring migration result in comparatively low levels of biomass (Chapter 5) and where overall tissue quality is high (this study), nitrogen content of the vegetation per unit area is

highest on previously ungrazed plots with a high standing biomass. Here, Barnacle Geese aggressively monopolise food patches with increased biomass as our behavioural data showed (Figure 3.3, Table 3.4). At the spring staging grounds in the Wadden Sea, neither biomass nor quality *per se* are limiting on the livestock-grazed salt marsh and a raised nutrient intake rate can be achieved by selecting sites with increased levels of these two parameters.

For the same flyway, we have shown that Barnacle Geese appear to follow peaks of nitrogen content of the vegetation per unit area along their spring migration route, the so-called “*Green wave*” (Chapter 5). This strategy provides them with sufficient levels of biomass intake to accumulate fat as well as an adequate protein intake for successful breeding (Prop and Black 1998).

Human land use and foraging perspectives for small herbivores – conclusions from the experiment

Our experiments demonstrate that nitrogen content of the vegetation per unit area is the best predictor for goose foraging choices along the entire flyway. This plant characteristic, however, included both forage biomass and forage nitrogen per unit mass of plant tissue in different proportions at the different sites along the flyway. Both parameters are under the influence of management practices, such as livestock grazing and the application of agricultural fertiliser. At staging sites in the Wadden Sea but also at stopover sites in the Baltic, summer grazing of salt marshes by livestock and the application of fertiliser on agriculturally-exploited coastal sites, both on salt marshes and on inland pastures, results in a high nitrogen content of plant forage (Vickery and Gill 1999; Hassall *et al.* 2001). In the absence of intensive land use at the sub-Arctic Russian breeding sites and with the naturally low soil nutrient levels of these sub-Arctic sandy soils (Chapter 2) forage quality remains low. Grazing by large herbivores not only increases the nitrogen content of plant forage (Singer 1995), but also the overall quality of the vegetation by preventing accumulation of litter (Coughenour 1991; Singer 1995; Hobbs *et al.* 1996) and the dominance of less palatable plant species (Olff *et al.* 1997; Jutila 1999) and by maintaining a short dense sward (Van der Graaf *et al.* 2002). Barnacle Geese have been shown to prefer grazed marshes with short, dense vegetation and a high live/dead ratio of above-ground plant tissue (Van der Wal *et al.* 1998b; Bos *et al.* 2005b). However, biomass levels in spring seem to be mainly limited by forage removal as a result of grazing by the geese themselves rather than by human activities, since no livestock grazing or mowing occurs at any of the sites along the entire flyway in spring. We presume that livestock grazing up to the end of the growing season (end of October for the Baltic stopover site and end of November for the Wadden Sea staging site) prevents the accumulation of litter during winter.

The bottlenecks in nitrogen availability for the small herbivores appear to lie in the limited biomass availability at the Baltic stopover site and the limited nutrient content of food in the sub-Arctic breeding site. Density dependent effects found in the Gotlandic breeding population of Barnacle Geese (Larsson *et al.* 1998) can be seen as a consequence of high grazing intensities, high levels of biomass removal and therefore comparably low food availability in the Baltic. However, there is currently no evidence of density dependence acting on the Barnacle Goose population that breeds in Russia. Since the early 1980s Barnacle Geese have continuously expanded their breeding areas from the traditional breeding range on Novaya Zembyla and Vaygach westwards along the Russian coast (Ganter *et al.* 1999). Along with this expansion in breeding sites, the number of staging sites in the Baltic that are used by geese in spring has increased (Stock and Hofeditz 2002; Leito and Truu 2004). However, the expansion of staging sites has resulted in a growing conflict with land use, since the goose populations expanded into inland agricultural fields at sites where they traditionally were restricted to salt marshes (Leito 1996; Vickery and Gill 1999). These inland fields are often fertilised or livestock grazed and therefore form ideal sites for small herbivores maximising nutrient intake rates (Bos *et al.* 2005a). At present there seems to be little limitation for a further expansion of the Barnacle Goose population with respect to the availability of preferred forage at sites during staging and stopover.

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Top: Hide for goose observations at the salt marsh of Grötlingbo-udd

Bottom: Barnacle Geese foraging in the vicinity of experimental plots, recognisable by small flags

Sward height and bite size affect the functional response of Barnacle Geese *Branta leucopsis*

Alexandra J. van der Graaf, Pieter Coehoorn and Julia Stahl

Summary

Intake rate, the rate in which herbivores can process their food, is presumed to be an important factor in habitat selection at the scale of the foraging patch. Much attention has been given to the selection of swards of high nutritional quality, but much less to the influences of sward structure on patch selection by small herbivores.

In this study, we test the effects of sward density and height on the functional foraging response of Barnacle Geese, *Branta leucopsis*. The functional response curve for herbivores describes how intake rate is affected by food availability. We conducted feeding trials in order to determine intake rate and bite size of Barnacle Geese on experimentally manipulated swards. Results indicate that intake rate is mainly dependent on sward height, and that there is a strong correlation between bite size and intake rate. Sward density does not influence the rate of food consumption; it is, however, a crucial parameter affecting potential total yield.

We conclude that bite size is the crucial parameter influencing intake rate. Bite size is explained both by sward height and individual differences in bill morphology. Intake rate appears to be dependent on the physical structure of the grass species consumed.

Introduction

Herbivore grazing creates a short, dense canopy of nutritious plant tissue. Small herbivores have been shown to prefer these sward properties (McNaughton 1984; Drent and Van der Wal 1999; Van der Graaf *et al.* 2002; Bos *et al.* 2005b). As a consequence, they often follow herds of larger herbivores (McNaughton 1984) or prefer fields grazed by livestock (Van der Graaf *et al.* 2002; Bos *et al.* 2005b). This process in which one herbivore improves foraging conditions for another, is called grazing facilitation. Not only larger herbivores can induce these profitable sward changes, recently it has been shown that small herbivores themselves can create and maintain grazing lawns (Bos *et al.* 2004; Chapter 7). Most studies focus on the increase in nutritional quality of grazed swards, which is measured as nitrogen or protein content of plant tissue. Little is known on the effect of structural properties of the sward, such as height and density, on forage preferences of small herbivores, though many investigations have examined this topic (Van de Koppel *et al.* 1996; Van der Wal *et al.* 1998b).

The functional response describes the relationship between the individual intake rate and food availability. For herbivores, food availability is expressed as biomass, which is a function of sward density and height. Intake rate (gram biomass per unit time) is the product of bite rate (number of pecks per unit time) and bite size (amount of biomass consumed per bite). The results of most studies indicate that the functional response curve initially increases with increasing biomass, but decreases or levels off as biomass increases (Fryxell 1991; Gross *et al.* 1993; Van de Koppel *et al.* 1996; Bos *et al.* 2004; Iason *et al.* 2002). For small herbivores, intake rate at low sward heights is limited because of a small bite size (Iason *et al.* 2002), while at high sward heights intake rate is believed to decrease because of handling problems associated with long leaves (Van der Wal *et al.* 1998b; Hassall *et al.* 2001), increased costs of locomotion and increased vigilance due to changes in the perception of predation risk (Van de Koppel *et al.* 1996).

In addition, sward density might be an important parameter influencing the functional response of small herbivores, but this factor has remained largely unstudied. It is hypothesised that an increased density of shoots in a sward will positively affect bite size, as it sustains the consumption of multiple leaves per bite, as well as the peck rate as searching time is reduced. We, therefore, expect a functional response curve in which intake rate will increase with increasing sward density. Here, we experimentally test the effects of sward density and height on the functional response of Barnacle Geese, *Branta leucopsis*. We conducted feeding trials with captive Barnacle Geese in order to determine intake rate and bite size on swards of different heights and densities. Based on recently published work on the functional response of different waterfowl species, we now are able to discuss the role and significance of the different sward parameters on their functional response and discuss implications for our understanding of habitat selection by wild geese.

Methods

Feeding trials

In order to determine the intake rate of Barnacle Geese on swards of different height and density, we conducted feeding trials in which three captive Barnacle Geese were offered turfs with different sward properties. During the feeding trials geese were taken from their holding pen at 5 p.m. daily and put separately in 1 m x 1 m cages, consisting of a wooden frame, with netting on the sides and top, and a hardboard floor. During the night the geese had access to water, but not to food. Trials were started shortly after sunrise the next morning. Since the geese were starved overnight, they always foraged on the turfs immediately. Each turf was put in the cage for 5 minutes. We chose this relatively short time period to make sure that the geese did not deplete turfs, within a feeding trial. In addition, we restricted the number of consecutive turfs a goose was offered each morning to three, in order to make sure that the geese did not become satiated. In total 55-57 turfs were presented to each goose in 22 days, between 10 February and 19 March 2004.

Observations were made by one observer from approximately 10 metres distance from the cages, which caused no disturbance, since the geese were tame and trained to the routine. During the 5 minutes of the feeding trial, foraging time (FT) was determined as the time each goose had its head down towards the turf and the total number of pecks on the turf was counted (P) using a hand counter. Peck rate (PR) was calculated as $PR = FT/P$, bite size (BS) as $BS = I/P$ and intake rate (IR) as $IR = I/FT$. After the feeding trials the geese were released from the cages and could graze freely in a small group of yearlings until they were caught again in the late afternoon.

Durant *et al.* (2003) showed that bill size and in particular bill width can have a large influence on bite size and therefore on intake rate. In addition, age and sex can be important factors determining intake rate (Lang and Black 2001). From a group of 15 yearlings we selected three geese that had similar bill size (width and length). All geese selected were males and accustomed to humans. The experimental routine was started two weeks before measurements began in order to habituate the geese to the situation.

Turf preparation

Nine months before the start of the experimental feeding trials *Festuca rubra* seeds were sown in trays of 40 cm x 40 cm; these trays were put inside a greenhouse that provided good growing conditions. Seeds were sown in two densities; however, measurements later revealed a continuous range of tiller densities rather than two density classes. Grass in all trays was regularly cut throughout this period. Prior to the trials the swards on the turfs were cut to a height of about 1, 3 or 6 cm, and allowed to regrow for several days so that fresh leaf tips formed for consumption by the geese. This procedure created a range of sward heights from 2 - 8 cm. Each turf was sub-divided into eight turfs of 10 cm x 20 cm.

Turfs were put in a plastic container of similar size in order to prevent soil loss. Of each four turfs, one turf was offered to each individual goose and one was used as an evaporation control. On each turf all tillers were counted and sward height was measured to the nearest 0.5 cm using a sward stick on the afternoon, prior to the feeding trial. At the start of the feeding trial, each turf and the control turf were weighed (W1 and WC1, respectively); weighing was repeated immediately after the feeding trial (W2 and WC2). All weighing was conducted on an analytical balance (Mettler Toledo AG204) to the nearest 0.1 mg.

Evaporation (E) was calculated from the weight loss of the control turf:

$$E = 1 - (WC_2/WC_1).$$

Intake (I) was calculated as

$$I = W_2 - W_1 - (E * W_1).$$

Two instances when the calculations resulted in a negative intake were discarded. After the feeding trials a total of 40 randomly selected turfs were clipped and material was sorted into live *Festuca* tillers and other material. *Festuca* tillers were weighed, dried for 48 hours at 60°C and weighed again afterwards in order to determine the conversion factor of wet weight (WW) to dry weight (DW). The resulting conversion $DW = 0.54 * WW$ was used to convert all weights to dry weights. Additionally biomass (B) of the turfs is characterised by the product of canopy height (H) and density (D), in which W is constant and represents the weight per grass length.

$$B = H * D * W$$

Average weight per grass length was calculated from the weighed *Festuca* tillers, divided by the number of tillers and the height, $W = 0.59 \text{ mg/cm}$.

Statistical procedures

Intake rate and bite size were squareroot-transformed to obtain normality. To test whether peck rate, bite size and intake rate were affected by sward density and height we used a multivariate ANOVA with individual geese ($N=3$) as a fixed factor and sward density and height as covariates. Additionally we used a Pearson correlation to test for a relationship between bite size and intake rate.

Results

Table 4.1 shows test results of a multivariate ANOVA, testing for effects of sward density and height on peck rate, bite size and intake rate, this test also incorporated the three individual geese. We found no differences between the individual geese nor any significant interactions between individual geese and sward parameters, suggesting that all geese responded in a similar way to changes in sward densities and heights. We found no effect of sward density on either peck rate, bite size or intake rate of the geese (Table 4.1). There was no significant interaction between sward height and sward density. We found an effect of sward height on both bite size and intake rate (Table 4.1, Figure 4.1); our results thus indicate that intake rate and bite size are only influenced by sward height, not by density. Bite size and intake rate were strongly correlated ($R^2 = 0.92$, $P < 0.001$, $N = 167$, Figure 4.2).

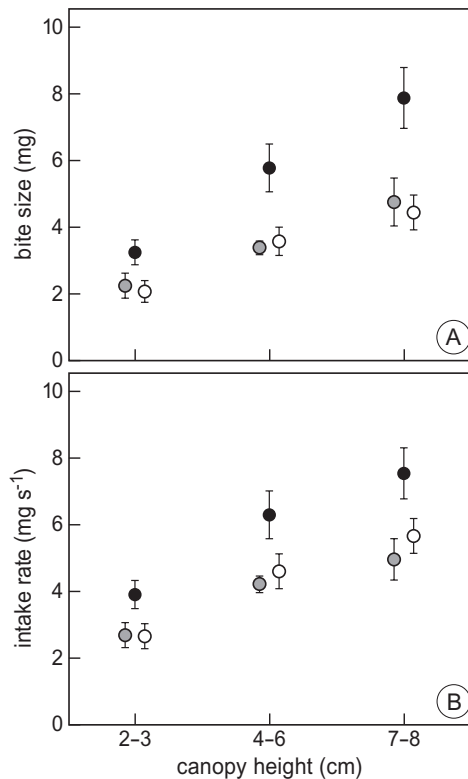


Figure 4.1: Relationships between sward height (divided in three height classes) and (A) Bite size and (B) Intake rate. Shown are means \pm standard error, differently shaded symbols represent the three individual geese. Analyses were performed on the raw data, but mean values are presented for clarity. See Table 4.1 for test results.

Table 4.1: Test results of a multivariate ANOVA testing for the effects of individual goose (as fixed factor) and sward density and height (as covariates) on (a) Peck rate, (b) Bite size, and (c) intake rate. (a) $R^2=0.205$, (b) $R^2=0.460$, (c) $R^2=0.358$. Significant results are printed bold.

Source	<i>df</i>	(a) Peck rate		(b) Bite size		(c) Intake rate	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Corrected Model	11	3.632	0.000	12.017	0.000	7.874	0.000
Intercept	1	120.665	0.000	36.002	0.000	41.812	0.000
Individual goose	2	0.219	0.804	0.624	0.537	0.447	0.640
Sward density	1	1.876	0.173	1.061	0.305	0.431	0.512
Sward height	1	1.168	0.282	10.333	0.002	7.011	0.009
density x height	1	0.299	0.585	0.663	0.417	0.577	0.449
goose x density	2	0.255	0.776	0.411	0.664	0.262	0.770
goose x height	2	0.043	0.958	0.104	0.901	0.058	0.943
goose x density x height	2	0.192	0.826	0.491	0.613	0.328	0.721
Error	155						
Total	167						

Discussion

Effect of sward density and height on bite size and intake rate

Though other studies tested the effects of sward height or biomass on goose intake rate, no previous study addressed the effects of sward density on goose intake rate. From our results we conclude that sward density mainly affects the food availability for the geese, i.e. yield to grazers (Chapter 7), not the rate at which the geese can consume the food. Average sward density in our study was $13.67 \cdot 10^3$ tillers m^{-2} ($se = 0.51 \cdot 10^3$, $N = 167$) which is similar to a long-term ungrazed natural salt marsh in the wintering areas of the Russian Barnacle Goose population in the Wadden Sea ($16.36 \cdot 10^3$ tillers m^{-2} , Van der Graaf *et al.* 2002), and closely similar to the sward density at the wintering area of the Spitsbergen population of Barnacle Geese in Caerlaverock, Scotland ($12.67 \cdot 10^3$ tillers m^{-2} , Lang and Black 2001).

Since biomass is the product of tiller density and height it is represented in the analysis by the interaction between these two factors. This interaction was not significant and we therefore conclude that there is no effect of biomass *per se* on intake rate or bite size in these small avian herbivores. In contrast, the functional response of mammalian herbivores is most often based on biomass (Gross *et al.* 1993). However, most of these studies do not include sward height in their analyses. Since sward height and biomass are often closely linked, we expect that even in these studies sward height could turn out to be of prime importance. We detected a strong effect of sward height on bite size and intake rate, plus a strong correlation between those parameters in the sward (Figure 4.2). A similarly close relationship between intake rate and bite size was found for several species of mammalian herbivores by Gross *et al.* (1993), as well as for waterfowl (Rowcliffe *et al.* 1998; Lang and Black 2001; Durant *et al.* 2003).

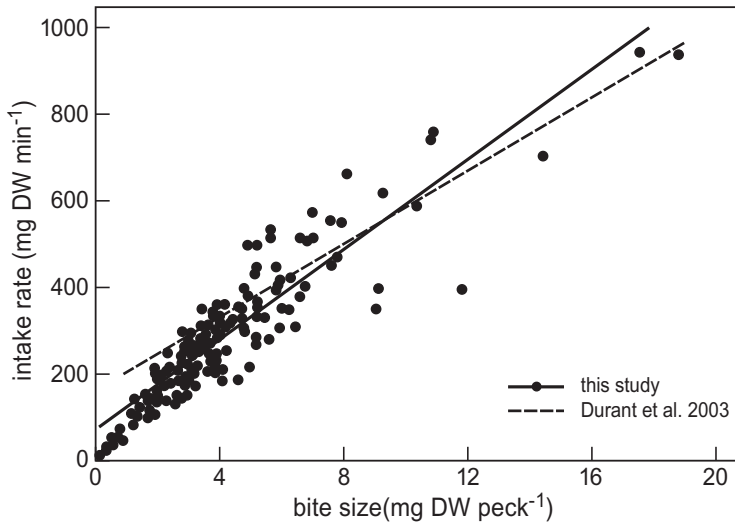


Figure 4.2: Relationship between bite size and intake rate for Barnacle Geese found in our study on swards of *Festuca rubra* (dots and solid line, $R^2=0.92$, $P<0.001$, $N=167$) and that found by Durant *et al.* 2003 on swards of *Lolium perenne* (dotted line, $R^2=0.76$, $P<0.001$, $N=53$).

Comparing recent studies

The results of our study correspond with those of other recent studies on intake rate in herbivorous wildfowl. There are three other studies on the effects of sward height on intake rate in geese. In three of the four studies, bite size increases with increasing sward height (Lang and Black 2001; Durant *et al.* 2003; this study). Cope *et al.* (2005) employed the same methods as in our study but failed to detect a significant relationship between sward height and bite size. However, they comment on the large between-individual variation in bite size, which appears to be related to the wide array in bill length of their geese. Two studies demonstrate a decreasing peck rate with increasing sward height, a relationship also found for other waterfowl i.e. Wigeon, *Anas penelope* (Jacobsen 1992), and Cackling Canada Geese, *Branta canadensis minima* (Sedinger and Raveling 1986), whereas we did not encounter this relationship in our own data based on the restricted range of sward heights used (Table 4.2). Finally, intake rate is shown either to increase with increasing sward height (this study), or to increase to a certain level and subsequently decline (Lang and Black 2001), or to remain constant throughout the treatments (Durant *et al.* 2003).

Table 4.2 provides an overview of the relationships found in the aforementioned studies; also shown are the forage grass species and the sward height range under study. It becomes evident that previous studies used agricultural grasses, mainly *Lolium perenne*, for the feeding trials, whereas we used *Festuca rubra*, a grass growing in natural salt marshes which are the traditional feeding ground of Barnacle Geese. Structural differences between the forage grass species may account for some of the differences indicated above. *Lolium* has broad leaves; whereas *Festuca* leaves are very narrow (Illius *et al.* 1995). *Lolium* in agricultural meadows grows taller than *Festuca*. With our experimentally grown turfs, it turned out to be impossible to create a *Festuca* sward with a sward height above 10 cm, since the individual shoots would start to bend and lay flat.

Similar bite sizes on *Lolium* and *Festuca* swards suggest that the geese take more leaves of the narrower *Festuca* leaves per bite to reach a similar bite size. The lower peck rate on *Festuca* swards, as found in our study, could then be explained by prolonged handling, while, concurrently, the lack of relationship between peck rate and sward height may be attributed to a generally long handling time, even on short swards of *Festuca*. We here refer to a study by Iason *et al.* (2002) who contrasted the functional response in Rabbits, *Oryctolagus cuniculus*, foraging on swards of *Festuca ovina* and *Lolium perenne*. In contrast to the asymptotic function in *Lolium*, the response to *Festuca* was characterised by peak values at a much lower sward height and there tended to be a negative relationship at higher sward heights. Iason explained that this result was due to the structural complexity of the *Festuca* sward and the increased handling time, as compared to swards of *Lolium*.

Table 4.2: Between-study comparison of the effect of sward height on intake parameters in Barnacle Geese.

	<u>Relation between sward height and</u>			<u>Grass properties</u>	
	Peck rate	Bite size	Intake rate	Grass species	Height range
Lang & Black 2001	-	+	+	<i>Lolium perenne</i>	3.5 - 12 cm
Durant <i>et al.</i> 2003	-	+	0	<i>Lolium perenne</i>	1 - 12 cm
Cope <i>et al.</i> 2005	no data	0 (+)	no data	<i>Poa</i> spp./ <i>Lolium perenne</i>	1.5 - 23 cm
This study	0	+	+	<i>Festuca rubra</i>	2 - 8 cm

Do feeding trials explain foraging choices?

In close agreement with Lang and Black (2001), our results indicate that intake rate increases with sward height up to a threshold value of about 8 cm. We would thus expect that geese confronted with a choice will select swards of about that height. However, a study by Durant *et al.* (2003) reveals that Barnacle Geese prefer foraging on swards of 2-3 cm, rather than on 5-6 cm or 10-12 cm. Concurrently, field studies indicate a preference of wild geese for swards lower than 8 cm in height (Summers and Critchley 1990; Hassall *et al.* 2001; own unpublished data).

A similar discrepancy was found in a study on European rabbits, where in feeding trials intake rate increased with forage biomass, while the rabbits selected swards of low biomass and thus of a low potential intake rate when they were given a free choice (Iason *et al.* 2002). For rabbits it was argued that the rate of predator detection is highest in short grasslands and that the animals naturally prefer these open habitats. For geese we do not expect that swards within the height ranges studied will influence the perception of predation risk. However, there is substantial evidence that shorter swards are of higher nutritional quality as forage quality of grasses declines with increasing sward height (Summers and Critchley 1990; Hassall *et al.* 2001; Durant *et al.* 2004; Bos *et al.* 2005a). For small avian herbivores this might be more important than the physical structure of the sward. The digestive system of avian herbivores is characterised by a short retention time and fast passage through the gut. Their digestion is, therefore, rather inefficient and they need to consume high quality food (Prop and Vulink 1992). Future studies should model the combination of intake rate and nutritional quality, i.e. the nutrient intake rate, taking into account different sward structures and forage species.

Conclusions

We conclude that bite size is the most important parameter influencing intake rate. Bite size is explained both by sward height as well as by individual differences in bill size. Moreover, peck rate and the negative relationship between peck rate and sward height is most likely influenced by the choice of forage grass species, both by geese in natural habitats and when they are feeding in feeding trials.

Acknowledgements

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Captive Barnacle Goose foraging on a *Festuca* turf in one of the experimental feeding trials.

Surfing on a green wave - how plant growth drives spring migration in the Barnacle Goose

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Summary

The nutritional quality of forage plants varies in space and time. This variation is presumed to drive the annual migration of herbivore species which follow peaks in the availability of high quality forage between sites. The green-wave hypothesis predicts that during spring migration to northern breeding sites, geese and other herbivorous waterfowl travel along a climatic gradient, taking advantage of the flush of spring growth of forage plants at each stopover site along the gradient.

Here, we explore a basic assumption of the green wave hypothesis which states that there are successive waves of forage availability along the East-Atlantic Flyway from temperate to Arctic sites, as spring advances. We use one of the migration routes of the Barnacle Goose as a model to compare data on food quality and quantity of forage plants with the timing of migration along its migratory corridor. We collected data on forage biomass and quality at three salt-marsh sites along the traditional migration route of the Barnacle Goose: a temperate staging site in the Wadden Sea, a Baltic stopover site and a Russian sub-Arctic breeding site. In all areas forage biomass increased in spring, while the nutritional quality peaked early in the season and declined with increasing biomass. We combined data on forage biomass and nutritional quality as grams of nitrogen per unit area. For all sites, nitrogen in biomass per unit area showed a peak in early spring.

We used observations on goose migration to examine whether the geese utilise these peaks in nutrient biomass, as is predicted by the green wave hypothesis. Our data show that the geese utilise the Wadden Sea staging site and the Baltic stopover site at the moments of peak availability of nitrogen in biomass per unit area. At the Russian breeding site, geese arrive prior to the flush of spring growth of forage plants and profit from the peak in nitrogen when the goslings hatch and adult birds start moulting. We conclude that the spring increase of nitrogen in biomass at the successive sites along the flyway is a key factor driving the timing of the annual northern migration of avian herbivores

Introduction

Although large parts of our world look green, plant tissues are often of poor nutritional-quality and represent unpredictable resources for herbivores. The availability of forage plants and their nutritional quality varies heterogeneously in space and in time (Hartley and Jones 1997), particularly in response to seasonal changes. Herbivores frequently migrate between sites following local peaks in the nutritional quality of forage plants, as exemplified by the annual migration of the Wildebeest, *Connochaetes taurines*, in the Serengeti in East Africa (McNaughton 1979). Wildebeest migrate in the wet season from the northern woodlands to the southern plains where seasonal rains initiate the growth of green swards, returning after the wet season to the woodlands where overall precipitation is higher (Maddock 1979). Changes in plant phenology account for migratory shifts of herbivores along altitudinal gradients. For example, several species of deer migrate along an altitudinal gradient to gain access to newly emergent, high-quality forage represented by spring growth, e.g. Red Deer, *Cervus elaphus*, (Albon and Langvatn 1992; Mysterud *et al.* 2001), Roe Deer, *Capreolus capreolus*, (Mysterud 1999), Sika Deer, *Cervus nippon*, (Sakuragi *et al.* 2003) and Reindeer, *Rangifer tarandus*, (Skogland 1980).

The “green wave hypothesis” was proposed in the late 1970’s (Drent *et al.* 1978, Owen 1980) to account for the northerly migration of herbivorous waterfowl from temperate latitudes. The green wave hypothesis predicts that avian herbivores travel along a climatic gradient during their spring migration from temperate staging sites to Arctic breeding areas, taking advantage of the successively delayed spring flush of plants at each staging site, hence surfing a wave of forage availability as they move along the migration corridor. Figure 5.1 shows a schematic view of the movements of the Russian breeding Barnacle Geese, *Branta leucopsis*, “riding the crest of the green wave” (Drent *et al.* 1978), along their traditional flyway.

Barnacle Geese use Dutch and German Wadden Sea salt marshes as spring staging areas. They depart temperate salt marshes around mid-April and move north, making short stop-overs at coastal sites in areas of the Baltic and White Seas, en route to the breeding grounds along the Barents Sea coast in northern Russia (Ganter *et al.* 1999). Traditionally, breeding sites were restricted to Novaya Zemlya and Vaygach islands, but in recent decades their breeding range has expanded west to the Archangelsk region (Filchagov and Leonovich 1992; Syroechkovsky Jr. 1995; Van der Jeugd *et al.* 2003), coastal regions of the Baltic Sea (Larsson *et al.* 1988; Leito 1991) and in the delta region of the south-west Netherlands (Ouweneel 2001). Barnacle Geese are highly selective herbivores, depending on forage of high nutritional quality (Prop and Vulink 1992). Foraging mainly on monocotyledonous plants, their main food source changes from Red Fescue, *Festuca rubra*, on salt marshes of the Wadden Sea and Baltic to Creeping Saltmarsh Grass, *Puccinellia*

phryganodes, and Hoppner's Sedge, *Carex subspathacea*, at the Russian stopover and breeding sites. However, in temperate regions the geese also have started to feed in agricultural fields, where they forage mainly on Perennial Ryegrass, *Lolium perenne*, (Wadden Sea) and Timothy, *Phleum pratense*, (Baltic Sea). Nomenclature follows Van der Meijden and Weeda (1990). Monocotyledonous plants grow from a basal meristem, enabling sequential harvests within one season. At the start of the growing season, early spring in temperate areas and just after snowmelt for more northern areas, monocot tissues have high protein contents and, therefore, high nutritional quality. When growth continues and biomass increases, tissues become more fibrous, with lower protein contents, hence, nutritional quality decreases (Sedinger and Raveling 1986; Van Soest 1994; Hassal *et al.* 2001; Bos *et al.* 2004). Moreover, as the plants continue to grow, the structurally tall swards become increasingly difficult for the geese to graze. Many studies have

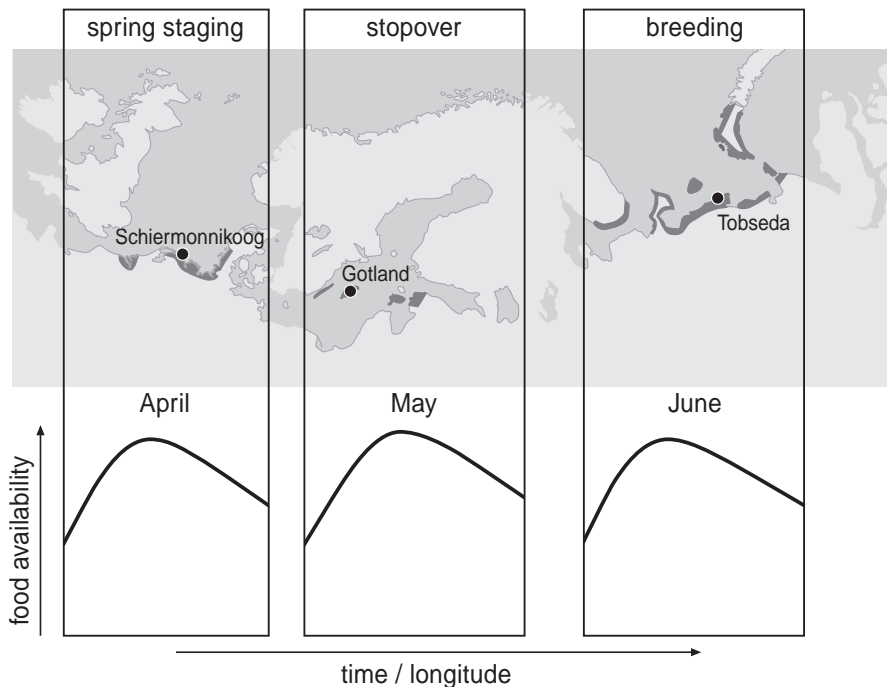


Figure 5.1: A schematic overview of the green-wave hypothesis (Drent *et al.* 1978, Owen 1980), modified for the flyway of the Russian population of Barnacle Geese. Breeding sites are given with dark grey shading. The three study sites are indicated on the map; Schiermonnikoog - a Wadden Sea staging site, Gotland - a Baltic Stopover site and Tobsseda - a Russian breeding site.

demonstrated that geese and other small herbivores prefer vegetation of low or intermediate heights (Van de Koppel *et al.* 1996; Van der Wal *et al.* 1998; Lang and Black 2001; Durant *et al.* 2003). There is thus a subtle interplay between forage biomass and nutritional quality, as an increase in biomass results in a decrease in nutritional quality. Several studies have shown that foraging Barnacle Geese maximise nutrient intake, instead of total biomass intake (Teunissen *et al.* 1985; Durant *et al.* 2004). We will combine the separate measures of biomass (g dry weight of green leaves m⁻²) and nutritional quality (measured as the nitrogen content of leaf tips as a percentage of their dry weight) to provide a measure of the total amount of nitrogen in biomass per unit area (measured as g N m⁻²) in this study.

Here, we explore an underlying assumption of the green wave hypothesis, namely the occurrence of sequential “waves” of forage availability along the migratory route. Following the above reasoning that forage decisions in small herbivores are based on a combined parameter of plant quality and biomass, we adjust the hypothesis to predict that there are waves of nutrient-rich biomass along the flyway and that Barnacle Geese adjust their travel itinerary to take advantage of the peaks in nutritional quality. To examine this assumption, we collected vegetation data from three salt-marsh sites along the flyway (Figure 5.1): a spring staging site in the Wadden Sea (the Dutch island of Schiermonnikoog), a Baltic stopover site (the Swedish island of Gotland), and a sub-Arctic breeding site (the Russian Tobseda peninsula on the west coast of the Pechora delta). We determined forage biomass and its nutritional quality at the sites. This data-set enables us to correlate the timing of migration to the production of high-quality forage during the flush of spring growth. First, we will investigate whether this occurs in distinct successive waves at progressively distant points along the spring migration route. Subsequently, we compare temporal patterns in the availability of high-quality forage with the migration pattern of Barnacle Geese as recorded at these sites.

Methods

Study sites

The study was conducted at three sites constituting spring staging, stopover and breeding areas along the North-Atlantic flyway of the Barnacle Goose during the springs of 2003 and 2004. The first study site are the salt marshes on the island of Schiermonnikoog (Box 1) in the Dutch Wadden Sea (53°30'N, 6°10'E). The island is used as a winter and spring staging site by up to 13,000 Barnacle Geese (Bos and Stahl 2003), some salt marshes are grazed by cattle in summer that maintains a low canopy. The second study site is on the island of Gotland (57°07'N, 18°27'E) in the Swedish Baltic Sea, where, thousands of geese use the narrow bands of salt marshes and adjacent agricultural pastures as a stop-over (Box 2).

The third study site is a breeding site in the Pechora Delta in northern Russia next to the abandoned village of Tobседа (68°35'N, 52°20'E). Geese arrive here in late May and start nest initiation upon arrival. Large moulting flocks gather in this area from mid-July onwards, and all geese leave the area by the end of September. The colony consists of about 1,500 breeding pairs of geese (Van der Jeugd *et al.* 2003; Chapter 2). Vegetation structure at all three sites is similar; canopy is low, due to summer-grazing by livestock in the Wadden Sea and Baltic Sea sites, whereas canopy remains low at the Russian breeding grounds because of environmental constraints.

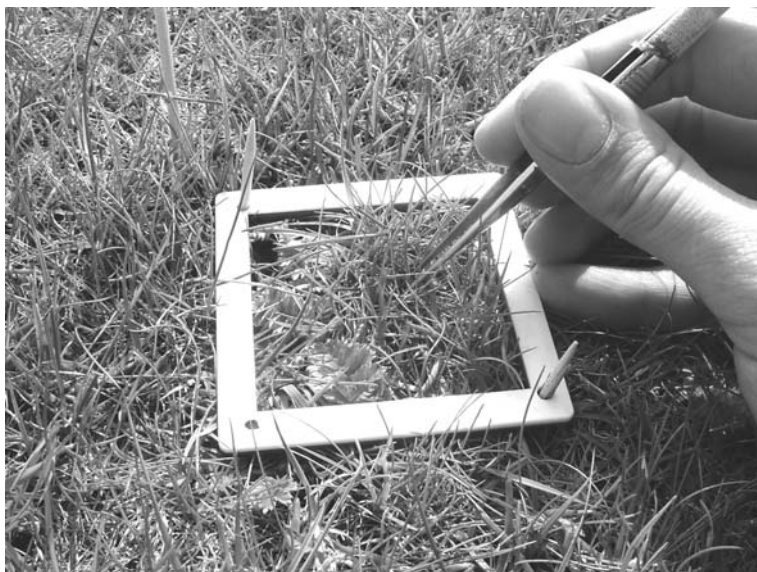
Migration dynamics

At the Wadden Sea staging site and the Baltic stopover site in 2004 and on the Russian breeding site in 2003, we assessed goose grazing pressure, based on faecal counts. Goose droppings were counted along transects consisting of 5 inconspicuous marked sticks at intervals of 10 m. At the Wadden Sea, Baltic Sea and Russian sites, we established 10, 10 and 7 replicated transects respectively. The transects were randomly placed in areas with suitable vegetation. Every 10 days droppings were counted and removed in a 4 m² area around each stick. Grazing pressure (expressed in droppings m⁻² day⁻¹) for the period between two consecutive dates was then calculated by dividing the number of droppings per square metre by the number of days between the two counts.

Published information on the migratory timetable of birds along the flyway is patchy, and there are not many detailed reports of arrival and departure of our study species at the staging sites. Detailed observations were available on the timing of departure from the Wadden Sea and timing of departure from the Baltic Sea. Departure dates from the Wadden Sea were taken from the Hamburger Hallig, Germany (1988-1997; Stock and Hofeditz 2002) and from Eemshaven, The Netherlands (1999-2002, data Kees Koffijberg –SOVON), data from both sites were combined to represent departure date from the Wadden Sea. Data on peak migration days over southern Finland were obtained from Lintukymi, the annual reports of the Kymenlaakso Birding Society (1990-2004). For both data sets, the date at which 75% of the observed Barnacle Geese had passed over that site (75% of total migration) was used. These data form the basis for Figure 5.2B. Data on peak hatch and nest initiation were obtained from Gotland, Sweden (1985-2004, pers. comm. Henk van der Jeugd and Kjell Larsson) and Tobседа, Russia (2002-2004, pers. comm. Henk van der Jeugd and Götz Eichhorn).

Forage biomass and quality

We collected data on forage biomass its nutritional quality at the three main study sites, on the Wadden Sea staging site March 6th and April 29th (2003 and 2004), on the Baltic Sea stopover site between April 1st and June 18th (2003 and 2004), and on the Russian breeding site between June 14th and July 22nd (2003). We measured tiller density on ten marked quadrats of 5 cm x 5 cm. To measure biomass, we sampled 50 tillers from either swards of Red Fescue (Wadden Sea staging site, Baltic stopover site) or swards of both Creeping Saltmarsh Grass and Hoppner's Sedge, that grew together on the Russian breeding site. These tillers were dried at 60°C for 48 hours and weighed. By multiplying the average tiller weight with the average tiller density we obtained a measure of aboveground biomass (in g m⁻²). Samples of leaf-tips of Red Fescue or entire shoots of Creeping Saltmarsh Grass and Hoppner's Sedge were taken around the same time in order to obtain a measure of nutritional quality. Samples were dried at 60°C for 48 hours and thereafter ground to a fine powder. Ground samples were analysed for nitrogen content, using an automated CHNS-analyser (automated element analysis, Interscience EA 1110, New York, USA). Nitrogen content (as a percentage of dry weight), from here on is referred to as N-content, was used as an indicator of the protein content of the plant material and thus as a measure of plant nutritional quality. Measurements of tiller densities and weight and N-content were taken approximately every ten days.



Counting tillers of *Festuca rubra* on Gotland in a 5 cm x 5 cm quadrat.

To control for biomass removed by grazing, we set up a number of small exclosures at each site (Wadden Sea staging site $N=8$ in 2004, Baltic stopover site $N=10$ in 2004, Russian breeding site $N=7$ in 2003). The circular exclosures were constructed from chicken wire and bamboo sticks and had a diameter of about 50 cm. In the exclosures as well as on an adjacent grazed control plot, biomass was measured initially and ten days later. The exclosures were then moved to a different spot where the procedure was repeated (4, 5 and 3 repeats on the Wadden Sea, Baltic and Russian sites respectively). At the Baltic stopover site the first exclosure which was set up in early April was measured one month later, in early May. Thereafter, the growth of plants in exclosures was measured approximately every 10 days. Biomass was estimated by counting and collecting tillers as described above. The difference in tiller biomass between the establishment and removal of the exclosures provides an estimate of biomass production. We tested whether there were differences in estimated biomass between control and exclosed plots after 10 days, using a one-way ANOVA with exclosure as fixed factor and date as random factor.

We fitted both linear and quadratic regressions through our data on forage biomass, nutritional quality and nutrient biomass, when both fits were significant we chose the quadratic fit if this had a higher R^2 value (by at least 0.01) than the linear fit. Residuals were tested for a normal distribution. To compare forage biomass and nutritional quality between staging sites, we performed an independent sample t -test for specified time periods. Nutrient biomass (g N m^{-2}), was calculated as the product of the regression lines of time with forage biomass (g m^{-2}) and N-content (%). All data were tested for normal distribution and equality of variances. When data did not match variance criteria, we used a t -test assuming unequal variances. All analyses were performed using SPSS, version 12.0.1 for Windows.

Results

Migration Dynamics

At the Wadden Sea staging site, grazing pressure peaked in mid-April. At the same time geese started to arrive at the Baltic stopover site where peak grazing pressure occurred in early May (Figure 5.2A). Grazing pressure at the Baltic stopover site was consistently higher than that at the Wadden Sea staging site which can partly be explained by the smaller total surface area of coastal sites used by the geese in the Baltic area and by the fact that the total flyway population passes through the Baltic area on spring migration (Ganter *et al.* 1999). Grazing pressure at the Russian breeding site remained low during the first weeks after arrival of the geese. Only later in the season, after peak hatch, grazing pressure increased, as the site attracted moulting birds and families from other local breeding islands and shorelines. For our story, however, the trends within each site, i.e. the occurrence of peaks of utilisation by the geese are more interesting than the comparison between sites. Figure 5.2B shows average arrival and departure dates of the geese for the different sites.

Green wave

At all study sites, forage biomass increased after the onset of spring growth, while N-content decreased (Figures 5.3 A and B). Biomass increased linearly as spring progressed in all areas. N-content for both the Baltic stopover site and the Russian breeding site showed a quadratic curve with a peak early in the season. For the Wadden Sea staging site, we did not find a peak within the measuring period. Table 5.1 gives the regression models for the plant parameters versus time. All residuals showed a normal distribution. The regression lines on forage biomass and N-content were combined into a measurement of nutrient biomass (g N m^{-2}). Figure 5.4 shows that, for each site, this results in a quadratic function with a maximum nutrient biomass within the period the geese utilise the sites.

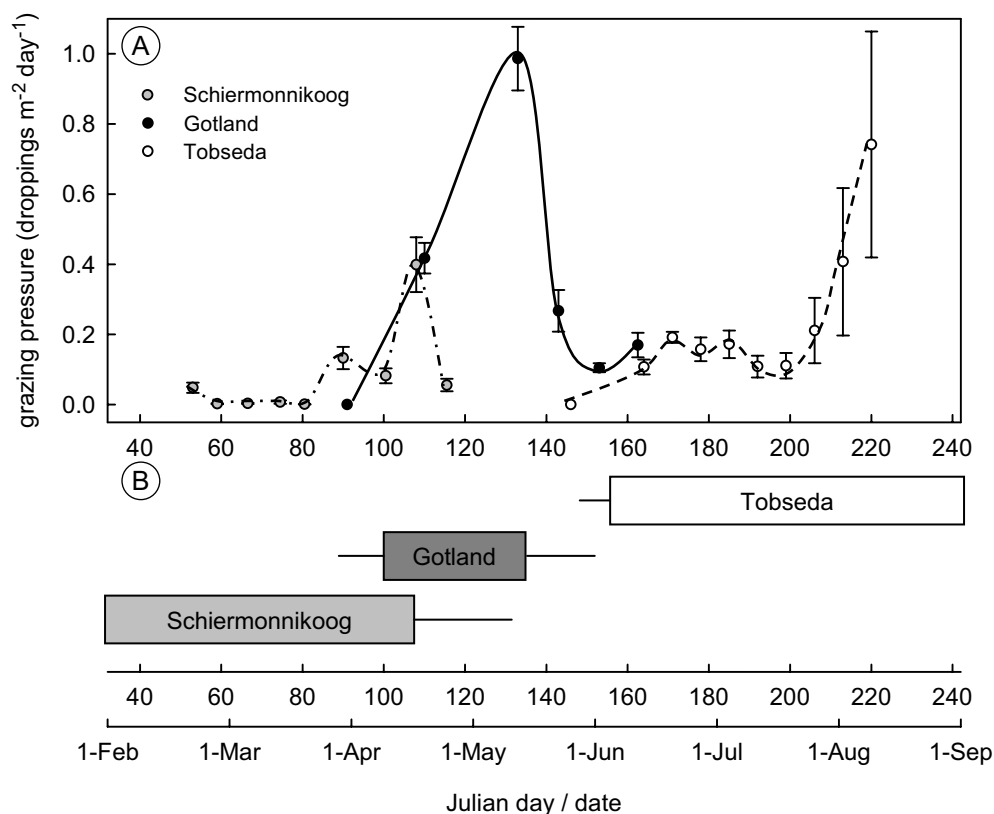


Figure 5.2: Timing of goose migration; (A) grazing pressure in the years 2003/2004 expressed as the number of droppings per m^2 per day for each area over the staging season (mean \pm se) and (B) staging periods as derived from observations (Schiermonnikoog, pers obs. D. Bos and J. Stahl; Gotland, pers obs. HP. van der Jeugd and K. Larsson; Tobседа, pers. obs. K. Litvin and R.H. Drent). Horizontal bars on the x-axis mark the time period when the majority of the migrating geese use the site; lines indicate early arrival or late departure.

Table 5.1: Regression parameters of vegetation biomass and nutritional quality over time (Julian day) for three sites along the flyway of the Barnacle Goose; a Wadden Sea staging site, Baltic Stopover site and a Russian breeding site. Equations for the linear and quadratic regressions are respectively, $Y=a + b t$ and $Y=a + b t + c t^2$.

Biomass (Linear)	R^2	df	F	P	a	b	
Wadden Sea staging site	0.241	65	20.60	< 0.001	-0.284	0.220	
Baltic stopover site	0.089	129	12.62	0.001	1.779	0.100	
Russian breeding site	0.803	49	199.74	< 0.001	-230.45	1.419	
Quality (Quadratic)	R^2	df	F	P	a	b	c
Wadden Sea staging site	0.520	68	36.79	< 0.001	4.734	-0.005	-0.0001
Baltic stopover site	0.224	148	21.32	< 0.001	-0.856	0.063	-0.0003
Russian breeding site	0.513	76	40.10	< 0.001	-29.001	0.376	-0.0011

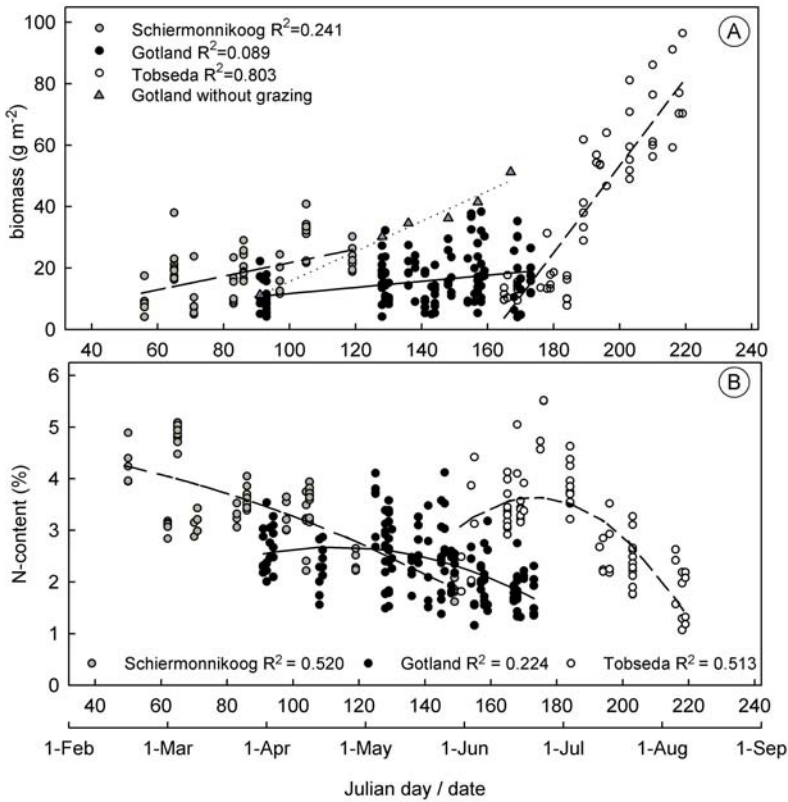


Figure 5.3: Forage biomass (g m^{-2}) (A) and N-content (% of dry weight of above-ground biomass) (B) between day 40 and day 220, at three sites along the flyway of the Barnacle Goose; Schiermonnikoog - a Wadden Sea staging site, Gotland - a Baltic Stopover site and Tobseida - a Russian breeding site. For all regression lines $P \leq 0.001$.

On the Wadden Sea staging site and on the Russian breeding site we found no differences between biomass inside the temporary exclosures and that in control plots (Wadden Sea staging site $F_{1,52}=0.484$, $P=0.450$; Russian breeding site $F_{1,60}=0.596$, $P=0.443$; in both tests date did have a significant influence on biomass at the level of $P<0.001$). At the Baltic stopover site there were large differences in estimated biomass between grazed and ungrazed plots (exclosure $F_{1,94}=4.257$, $P=0.042$; date $F_{4,94}=4.035$, $P=0.005$). These were most pronounced at the start of the season: biomass almost doubled inside the exclosures (ungrazed plot: 30.2 g m^{-2} , grazed plot: 18.7 g m^{-2}). This high impact of grazing was caused by high densities of staging Arctic Barnacle Geese early in the season. Only for the first interval, at the start of the season, could a significant difference between ungrazed and grazed plots be detected ($F_{1,18}=6.639$, $P=0.019$). Cumulative biomass was calculated for ungrazed swards at the Baltic stopover site by adding the average biomass production per week to the biomass in this first exclosure. These results are plotted as dotted line in Figure 5.3B.

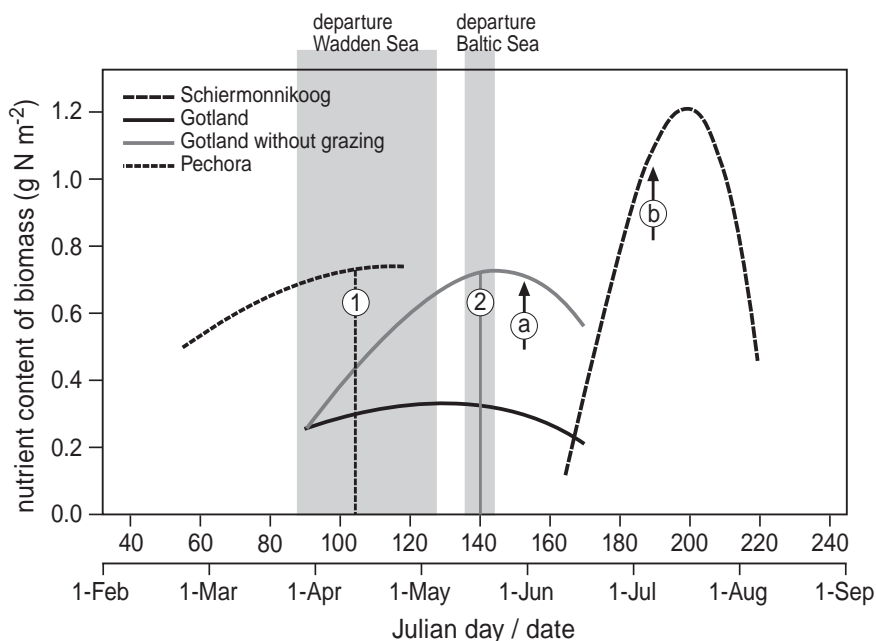


Figure 5.4: Nitrogen content in biomass per unit area (g N m^{-2}) as a combined measure of forage biomass (g m^{-2}) and N-content (%) at three sites along the flyway of the Barnacle Goose; Schiermonnikoog - a Wadden Sea staging site, Gotland - a Baltic Stopover site and Tobseba - a Russian breeding site. Shaded areas indicate timing of departure from the Wadden Sea (1) and Baltic Sea (2) respectively; dotted vertical lines indicate the average departure date. Arrows indicate peak hatch date at the Baltic Sea (a) and the Russian breeding ground (b) respectively.

Comparisons between sites

Forage biomass and N-content at the Wadden Sea staging site and the Baltic stopover site were compared for the 10-day period from 1 April (day 91) to 12 April (day 100) when most geese arrived in the Baltic (Figure 5.2B), although some birds still remained on their staging sites in the Wadden Sea region. A similar comparison was made for the main stopover period of the geese in the Baltic, from 12 April (day 102) until 15 May (day 135). The tests showed that for both periods, biomass and N-content were higher at the Wadden Sea staging site than at the Baltic stopover site (Table 5.2, comparisons 1 and 2 respectively).

Biomass and N-content at the Baltic stopover site and at the Russian breeding site were compared during the period the geese leave the Baltic (15 May until 3 June, day 154) and arrive on the breeding grounds (27 May until 10 June, day 147-161). The comparison showed that at the Russian breeding site estimated biomass was similar to that at the Baltic stopover site at the time of departure, but that the N-content of the vegetation was higher (Table 5.2, comparison 3). We also compared the estimated forage biomass and the N-content of leaves at peak hatch at the Baltic stopover site (30 May; Loonen *et al.* 1998) and on the Russian breeding grounds (10 July, day 191, pers. obs. H. van der Jeugd). At the time of peak hatch, plant biomass on the Russian breeding grounds was much higher than that at the Baltic stopover site, but N-content of the vegetation was similar (Table 5.2, comparison 4).

Table 5.2: Mean plant biomass and quality for three study sites at different times in spring ($\pm se$) and results of statistical comparison between sites: 1 – arrival Baltic vs. staging in Wadden Sea (1-10 April), 2 – staging Baltic vs. Wadden Sea (12 April – 15 May), 3-leaving Baltic vs. arriving Russia (15 May – 3 June vs. 27 May – 10 June), 4 – peak hatch Baltic vs. peak hatch Russia (30 May vs. 10 July).

Biomass comparison	Wadden Sea staging site	Baltic Sea stopover site	Russian breeding site	Equal variances assumed	Test results		
					<i>t</i>	<i>df</i>	<i>P</i>
1	15.68 \pm 1.61	10.66 \pm 1.15		Y	2.433	25	0.022
2	27.21 \pm 1.50	15.25 \pm 1.22		Y	6.181	44	<0.001
3		14.67 \pm 1.02	12.47 \pm 0.89	N	1.623	34.74	0.114
4		20.25 \pm 2.45	48.42 \pm 3.51	Y	-6.807	25	<0.001
Quality comparison	staging site	stopover site	breeding site		<i>t</i>	<i>df</i>	<i>P</i>
1	3.61 \pm 0.12	2.63 \pm 0.10		Y	6.277	34	<0.001
2	2.85 \pm 0.04	2.63 \pm 0.10		N	1.939	54.41	0.058
3		2.43 \pm 0.09	3.38 \pm 0.13	Y	-6.130	68	<0.001
4		2.35 \pm 0.12	2.592 \pm 0.14	Y	-1.135	41	0.263

Discussion

A green wave?

This study demonstrates that maximum values of N in biomass occurred in successive waves along the spring flyway of herbivorous waterfowl as they migrated northwards. This may help to explain the timing of spring migration of the birds to Arctic sites. At the three study sites, a quadratic function best described the N-content of the vegetation. At the spring staging site in the Wadden Sea highest values of N per unit of biomass must have been well before measurements started. Estimated biomass increased linearly throughout the spring at all sites. Plant biomass did not reach peak standing crop within the recording period which was based on site-use by the geese. We expect forage biomass to peak later in the season as above-ground tissues mature, or as the plants invest more in reproductive tissue. At each site we found a maximum value of nutrient content of biomass per unit area, g N m^{-2} , during spring (Figure 5.4). We expect the same holds for other stopover sites along the migration route of the geese; additional important stopover sites between the Baltic stop-over site and the Russian breeding grounds are in Estonia (Leito 1996) and on the coast of the White Sea (Ganter *et al.* 1999).

Timing of migration and breeding

Geese left their winter and spring staging sites in the Wadden Sea when the nutrient biomass (g N m^{-2}) reached a peak (Figures 5.2 and 5.4), with biomass still increasing but N-content (%) decreasing. When the geese arrived at Gotland both the N-content (%) and the amount of biomass (g m^{-2}) were lower than at the previous site, and remained at a very low level. At our study site in Gotland, above-ground biomass was heavily grazed by large numbers of staging Barnacle Geese in spring, resulting in an extremely short sward that remained low throughout the period. The comparison of short-term exclosures with adjacent grazed plots demonstrated that high grazing pressure by geese at the beginning of the growing season (see Figure 5.2) prevented biomass accumulation. The dotted line in Figure 5.4 represents the N available in biomass per m^2 at Gotland, assuming no grazers and it gives an indication of the amount of harvestable forage available to small herbivores at that site. A similar significant impact of staging geese on forage biomass (g m^{-2}) and total N available in biomass (g N m^{-2}) was not detected either at the Wadden Sea staging site or at the Russian breeding site.

When the geese arrived at the Russian breeding sites above-ground biomass was very low as snow melt had just occurred. Estimates of biomass were comparable with estimates at the Baltic site at the time of departure of the geese; however, the N-content of the forage was high. At the time of peak hatch in this Arctic breeding colony, forage quality remained high and comparable to that at peak hatch at the temperate breeding colonies in Gotland.

However, the biomass available to goslings and moulting adult birds was much higher at the Russian breeding site compared to that in Gotland. Total N in biomass (g N m^{-2}), as a result, was much higher on the Russian breeding site after peak hatch than in Gotland. It thus seems that on the last leg of migration the geese jump ahead of the green wave that benefits gosling-rearing later in the season.

Acknowledgements

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Julia Stahl and Ciska Veen on their way to work at the salt marsh of Grötlingbo-udd



Jan Bakker and students of the Community and conservation Ecology course 2004, studying the vegetation on Grötlingbo-udd (Top) and cattle studying the students during their lunch break (Bottom).

Part 2

Flexible migrants in a changing world



Subtle interplay of competition and facilitation among small herbivores in coastal grasslands.

Julia Stahl, Alexandra J. van der Graaf, Rudolf H. Drent and Jan P. Bakker

Summary

1. Overlap in habitat use between herbivores can result in facilitative interactions, through enhancement of forage quality, as well as competitive interactions. The latter result from either interference or indirectly from resource depletion.
2. We investigated competitive and facilitative interactions between wild Barnacle and Brent Geese and European Brown Hares on a salt marsh in the Dutch Wadden Sea. In a multifactorial experimental design we manipulated biomass and quality of grass swards and determined foraging preferences of the wild herbivores.
3. We found that both Brent and Barnacle Geese select plots with plants which have a higher nitrogen content. Barnacle Geese avoid plots with high plant biomass.
4. Grazing increases the quality of the vegetation within a season. Geese mainly select plots that have been previously grazed by either geese or hare within the same season.
5. Hares prefer the combination of high biomass with high plant quality, when geese are absent. However, in the natural situation with geese present, hares select high biomass swards.
6. We conclude that indirect competition through forage depletion by large numbers of geese in spring plays a significant role determining the foraging choices of hares, while Barnacle Geese profit from grazing facilitation by other small herbivores which prevents the maturation of forage tissues.

Introduction

In terrestrial ecosystems, herbivores consume, on average, only 10-20% of annual net primary production (Cyr and Pace 1993). Explaining why so much of the terrestrial plant biomass is left uneaten, remains a major challenge in studies of plant-animal interactions (Polis and Strong 1996; Polis 1999). It has been argued that herbivore numbers are controlled partly by predators, parasites and diseases (Hairston *et al.* 1960). In addition, potential food plants show many characteristics that deter herbivores, e.g. low nutritional quality and chemical defences (Cameron *et al.* 1993). These plant characteristics are intrinsically heterogeneous in space and time, rendering plants a patchy and unpredictable food source (Hartley and Jones 1997).

Two constraints on rates of nutrient uptake in herbivores are the short-term rate of food intake, mainly influenced by forage availability, and the long-term rate of energy assimilation, mainly characterised by processing constraints that reflect forage quality (Wilmschurst *et al.* 1995). Besides plant phenological changes, food plant availability and nutritional quality also depend on the manipulation of the foraging environment by the herbivores themselves (Drent and Van der Wal 1999). The maintenance of grazing lawns brought about by cyclic grazing (McNaughton 1979; Prins *et al.* 1980; McNaughton 1984) is one example of maximising intake per unit time (reviewed in Drent and Van der Wal 1999). Foraging herbivores can either physically change the structure of a plant community (trampling or selective grazing) or can modify plant phenology as a consequence of consumption, which often changes indirectly the chemical composition of tissues (Arsenault and Owen-Smith 2002). We use the term herbivore facilitation when the foraging opportunities of one species are enhanced indirectly by the feeding activities of another. In contrast, depletion of resources, interference and resource competition between consumer species negatively affect resource acquisition by a particular herbivore species, potentially influencing foraging choices, and inducing resource partitioning by different herbivores (Belovsky 1984; Gordon and Illius 1989; Edwards *et al.* 1996; Murray and Illius 2000).

The close interplay of facilitative and competitive interactions between herbivores has long been neglected and experimental field studies remain scarce (Van der Wal *et al.* 1998a; Van der Wal *et al.* 2000b). Overlap in habitat use, sharing of food plants and limited food supply, which are generally described as necessary prerequisites for resource competition (De Boer and Prins 1990), are also prerequisites for facilitation in a system where one herbivore species has a beneficial effect upon another. We suggest that the timing of overlap in plant use by different herbivores in connection with seasonal patterns of plant phenology can lead to either competition or facilitation. The African savannahs with their collection of large, mainly migratory, ungulate grazers are an example of a system where both competitive and

facilitative interactions between herbivores occur (Maddock 1979; De Boer and Prins 1990; Sinclair 1995; Van de Koppel and Prins 1998; Prins and Olff 1999).

In the present study we report on temperate salt marshes, where there is the potential for interactions between three herbivore species with strong temporal and spatial overlaps. Barnacle Geese, *Branta leucopsis*, and Dark-bellied Brent Geese, *Branta bernicla bernicla*, use coastal salt marshes in the Dutch, German and Danish Wadden Sea during spring fattening, accumulating energy reserves essential for successful migration and subsequent reproduction at Arctic breeding sites (Ebbinge and Spaans 1995). On natural salt marshes European brown hares, *Lepus europaeus*, are the only other important vertebrate herbivore, which, in contrast to staging geese, use the salt marsh year round. Migratory geese are among those herbivores, for which the terrestrial green world is far from being universally edible or universally nutritious (Keddy 1989), and the birds show a high degree of dependency on forage of superior quality (e.g. Prop and Deerenberg 1991). For this reason, geese are particularly selective in their habitat choices (Owen 1980), and we predict that they are sensitive to alterations in food availability and quality imposed by interactions with other herbivores using the same forage. Recent studies provide evidence for direct interference and food competition between brown hares and Brent Geese during spring (Van der Wal *et al.* 1998a), as well as for indirect, long-term facilitation by hares for Brent Geese through selective removal of woody plant material in winter (Van der Wal *et al.* 2000b). In this study we focus both on competitive (i.e. removal of potential forage by preceding grazers) and facilitative (i.e. grazing lawns maintained by predecessors) interactions.

With a multifactorial experimental approach, we manipulated biomass and quality of forage grass swards in the field. Subsequently we monitored the use of these plots by wild geese and hares. The experiments allowed us to investigate the reaction of small herbivores to the main forage parameters which are biomass availability and forage quality. We expect that geese prefer plots with high quality. For hares, we hypothesise that they will select a combination of high biomass and high forage quality. In particular, we aimed to gain insights into the interactions of geese and hares on a common food source in the spring period. We expect the relationship between these vertebrate herbivores to be competitive when resident hares and staging geese jointly use *Festuca rubra* as forage, especially during March, April and May, the spring staging period of the migratory geese. These competitive interactions may result in one of the herbivores accepting sub-optimal foraging conditions.

Methods

Study Area

The field experiments were performed on the salt marsh of the island of Schiermonnikoog (Box 1), in the eastern part of the Dutch Wadden Sea (53°30'N, 6°10'E). As cattle are excluded from the study area, Brown Hares and Rabbits, *Oryctolagus cuniculus*, are the only resident vertebrate herbivores, but Brent and Barnacle Geese are transient grazers during winter and spring. Grazing by rabbits was considered to be insignificant, as rabbits stayed close to the dunes beyond the experimental area. There are no voles (*Microtus sp.*) on this island and other rodent folivores are absent. Numbers of hares counted in November 1996, 2001 and 2002 preceding the experiments in spring, were respectively 550, 350 and 300 in the 550 ha marsh and dune area (Van der Wal *et al.* 1998a; Kuijper 2004). Maximum Barnacle Goose numbers in the same area varied between 2500 in March and 900 in April (own observations). Maximum Brent Goose numbers on the salt marsh rose from 850 in February to 910 in April and 1500 in May (own observations).

Three experimental studies were conducted during the spring of 1997, 2002 and 2003. The study area on the higher marsh was approximately 30 years of age (as described by Van der Wal *et al.* 1998a) and is one of the salt-marsh areas most intensively grazed by small herbivores in spring (Van de Koppel *et al.* 1996). The vegetation was dominated by dense swards of *Festuca rubra* (average cover value 72%), *Juncus gerardi* was present in shallow depressions (average cover value 18%). Emerging stems of the shrub *Artemisia maritima*, can locally dominate the plant community during summer, but average cover was only 2% during spring. Nomenclature of plants follows Van der Meijden and Weeda (1990). *Festuca rubra* accounts for 90% of the diet in staging Barnacle Geese (Van der Wal *et al.* 1998b), 53% of the diet in staging Brent Geese (Van der Wal *et al.* 2000a) and 51% of the estimated spring diet of hares in the study area (Van der Wal *et al.* 1998a).

In this study we concentrated on the *Festuca* meadows of the upper marsh where the three herbivores occur together, with peak usage from mid March to late April. In this period the majority of the geese grazing on the *Festuca* meadows are Barnacle Geese. By early May the Barnacle Geese have left the island on migration to the breeding areas, and the Brent Geese shift to the lower marsh where they select a more varied diet (Prop and Deerenberg 1991), but still exploit *Festuca* until they depart from mid- to late May. We can profit, therefore, from a study system where resident and migratory herbivores use a joint food source during the period of rapid spring plant growth within partially overlapping time windows: hares and Barnacle Geese in March/April, hares and Brent Geese in April/May.

Testing forage choices in relation to different competitive scenarios (main experiment)

In mid-February, in early-March and at the beginning of April 2003 respectively, a set of ten replicates consisting of four experimental plots was created on homogeneous swards of *Festuca rubra*. Each replicate consisted of an untreated control plot (called bq from now on), a plot with increased biomass (subsequently called Bq), a plot with increased quality (subsequently called bQ) and a plot with increased quality and increased biomass (subsequently called BQ), each plot measuring 4 m x 4 m.. The experimental biomass increase was obtained by setting up exclosures, consisting of 50 cm high chicken wire, screened from above by thin ropes (called full exclosure from now on). The corners of the control areas were marked with short plastic pegs. The experimental increase in quality was obtained by applying a commercial granular fertiliser (NPK 12-10-18, 12% N, resulting in an addition of 100 kg nitrogen ha⁻¹).

The exclosures were established for two weeks and then removed. This event is called start of the experiment. Upon removal, we imposed two different competitive scenarios: Five replicates (each containing four plots representing the four treatments) were completely opened for herbivore access, so both geese and hares could graze in these plots. On the other five replicates selective goose exclosures were erected. The goose exclosures allowed hares to graze the plot but effectively excluded geese. The exclosures were constructed from bamboo sticks connected by horizontal ropes at different heights (10 cm and 50 cm). The four treatments within one replicate were separated by approximately three metres and replicates were spaced approximately 150 m apart. As an indicator of grazing pressure, we counted the number of droppings of both hares and geese on the plots. Droppings were counted before opening the treatments to grazing, as a measure of grazing pressure before the start of the experiment, and again three weeks after the start of the experiment.

At the start of the experiment biomass and forage quality were measured. In order to leave the sward undisturbed we applied a non-destructive technique to measure biomass by multiplying average tiller weight with average tiller density. Tiller density was measured on twenty squares of 5 cm x 5 cm on each individual plot. In these quadrats we counted all tillers of *Festuca rubra*. Tiller weight was determined by collecting 50 tillers of *Festuca rubra* on each plot. These tillers were dried at 60°C for 48 hours and weighed. In addition, samples of approximately 4 grams of fresh *Festuca* tips (2 cm) were collected on each plot. Plant material was washed, dried at 60°C for 48 hours and ground to a fine powder. As a measure of forage quality, total nitrogen content of the plant tissue was determined using an automated CHNS-analyser (automated element analysis, Interscience EA 1110, New York, US).

Additional experiments

Additional experiments were conducted during spring 1997 and spring 2002 at a salt-marsh site in the surroundings of the main experiment. In both studies food availability and quality of *Festuca rubra* were manipulated and foraging choices of geese and hares were monitored through dropping counts. In these years, hares and geese were jointly using the plots and, therefore, interactions between the herbivores could not be tested in detail.

In 1997, we applied differently scheduled exclosure treatments in combination with fertilisation (in total 48 plots of 4 m x 4 m) to create a range of amounts of plant biomass and of tissues with different N-contents on *Festuca* swards, which was offered to wild Brent Geese and hares at the start of the experiment in the first week of May. At that time in spring, Barnacle Geese had already left on migration.

In 2002 we created ten replicates, each consisting of four experimental plots. Each replicate consisted of a natural control plot (grazed by wild geese and hares), a plot on which grazing by geese was excluded (goose exclosure), a plot on which grazing by both geese and hares was excluded (full exclosure) and a plot on which grazing by captive geese was applied (two geese in a holding pen for 24 hours). Grazing pressure applied by the captive geese, closely mimicked the natural cumulative grazing pressure of the site during that period in spring (natural vs. experimental grazing pressure, mean \pm se: 2.85 ± 0.54 vs. 3.06 ± 0.29). These treatments created a range of amounts of plant biomass and of tissues with different N-contents on *Festuca* swards (in total 40 plots of 2 m x 4 m). The plots were opened to wild Barnacle Geese and Brown Hares at the start of the experiment in the first week of April, 2002. At that time in spring, Brent Geese rarely forage on *Festuca* swards and the measured response of goose grazing pressure, therefore, represents the grazing pressure of Barnacle Geese only. Plot selection, exclosure design and fertiliser application followed the same protocol as described in the previous paragraph for the main experiment. Grazing with captive geese was conducted under licence of the ethical committee for use of experimental animals of the University of Groningen (DEC RuG, licence number 2734).

In the additional experiments, forage biomass and quality were measured at the start of the experiment following the protocol described for the main experiment. At the start of both additional experiments, goose and hare droppings were counted on all plots and removed. The foraging choice of wild geese and hares was monitored, based on weekly dropping counts for a period of three weeks after the start of the experiment. For the analyses, cumulative dropping numbers for three weeks were linked to values of biomass and forage quality of each individual plot. In our analyses we do not examine the experimental history of the plots, since this was merely the means of creating a range of biomass and forage quality values. We will relate directly grazing pressure to differences in biomass and forage quality that were created from the different treatments. Replicates (N=48 for 1997 and N=40 for 2002) and date (first week of May and first week of April for 1997 and 2002, respectively) were included as factors in the statistical model, given below.

Statistics

In all analyses, we log-transformed ($\log(x+1)$) data of the dropping counts to meet normality. In the analysis of the data from the main experiment in 2003, we used a univariate ANOVA with fertilisation and exclosure as fixed factors, and replicate nested within the starting date of the experiment as a random factor. From now all we will refer to the set of ten replicates started on the same date as set. To test the effects of the treatments on *Festuca* biomass and its nitrogen content we used a multivariate ANOVA with the same factors as mentioned above.

Data from all years were used to correlate *Festuca* biomass, nitrogen content and the reaction of the herbivores. The reaction of hares to the different levels of biomass and forage quality on offer was tested using the full data set (1997, 2002, 2003). In the case of Brent Geese, only data from 1997 and for Barnacle Geese data from both 2002 and 2003 were used. The plots that were only opened to hares in 2003 were analysed separately. We used univariate ANOVAs with *Festuca* biomass and nitrogen content as covariates and replica nested within date nested within year as a random factor.

For the comparison of goose and hare droppings before (preceding grazing pressure) and after (foraging choice) the start of the experiments we used a Pearson correlation coefficient.

Table 6.1: Quantity and nitrogen content of biomass of *Festuca rubra* as created by the different treatments (fertiliser application and exclosed from grazing by geese and hares), at the start of the main experiment, given as mean \pm se for each treatment and summarised for three sets in mid-February, early-March and early-April 2003 on the salt marsh of Schiermonnikoog. **A.**; results of a multivariate ANOVA in **B.** Treatments: bq – low biomass, low quality, Bq – high biomass, low quality, bQ – low biomass, high quality, BQ – high biomass, high quality.

A.		Biomass		Quality	
treatment	<i>N</i>	(g dryweight m ⁻¹)		(% N)	
bq	30	24.2 \pm 1.3		3.38 \pm 0.68	
Bq	30	26.7 \pm 1.3		3.35 \pm 0.69	
bQ	30	24.3 \pm 0.9		4.66 \pm 1.09	
BQ	30	27.2 \pm 1.4		4.66 \pm 1.08	

B.		Biomass		Quality	
	<i>df</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Fertilisation	1	0.011	0.917	187.633	< 0.001
Exclosure	1	6.520	0.012	0.074	0.786
Fert.*Excl.	1	0.000	0.997	0.080	0.778
Replicate (Set)	29	1.939	0.010	6.197	< 0.001
Error	86				

Results

Testing forage choices in relation to different competitive scenarios (main experiment)

Our results of the vegetation measurements clearly indicate that the enclosure treatment created a sward with increased biomass and that the fertilisation treatment increased quality of the forage plants (Table 6.1). Fertilisation did not increase biomass, nor did enclosures affect forage quality. These data from our main experiment in 2003 demonstrated clear foraging choices by the Barnacle Geese: they preferred fertilised plots above non-fertilised plots, and they avoided previously ungrazed (exclosed) plots (Figure 6.1A, Table 6.2). We conclude that the geese prefer forage of high N-content in combination with low or moderate above-ground biomass levels.

Hares showed no preference for any treatment when plots were simultaneously used by geese (Figure 6.1B), which simulates the natural spring grazing situation. However, we detected a non-significant trend ($P=0.160$) towards a preference of previously exclosed plots with higher levels of biomass (Table 6.2). When geese were excluded and hares were the only grazers on the plots, hares preferentially foraged on plots with high biomass and shoots of high nutritional quality (Figure 6.1C, Table 6.2). Forage choices of the hares thus shifted in the absence of direct competition with geese as shown in Figure 6.2 which depicts the relative preference of the herbivores for plants subject to the different treatments.

Reaction on other herbivores measured via droppings

We used a Pearson correlation to relate goose and hare grazing pressure at the start of the three experiments with cumulative grazing pressure. Hares avoided plots that had been grazed previously by either hares or Barnacle Geese, while Barnacle Geese preferred these plots (Table 6.4). Combined results of all experiments indicate that quality of a plot increased with increased goose grazing (univariate ANOVA, goose droppings: $F_{1,58} = 12.026$, $P=0.001$; hare droppings: $F_{1,58} = 0.511$, n.s.; Replicate(day(year)) $F_{42,58} = 10.730$, $P<0.001$), while biomass declined with previous grazing (univariate ANOVA, goose droppings: $F_{1,74} = 7.810$, $P=0.007$; hare droppings: $F_{1,74} = 4.371$, $P=0.040$; Replicate (day (year)) $F_{47,74} = 3.039$, $P<0.001$). This again demonstrates that, within a given biomass range, the Barnacle Geese selectively chose plots with low biomass, which had been grazed previously, but which offered forage tissue of increased quality. Hares avoided previously grazed plots and we conclude that biomass per se is a more powerful determinant of forage choices than quality in the case of this herbivore.

Table 6.2: Results of a univariate ANOVA testing the response of (A.) Barnacle Geese (with hares present), (B.) Brown Hares (with geese present) and (C.) Brown Hares (with geese absent) to the treatments applied to swards of *Festuca rubra* in the main experiment in 2003 (fertiliser application and exclosed from grazing by geese and hares) on the salt marsh of Schiermonnikoog, $N=60$. Sets 1-3 were opened respectively in mid-February, early-March and early-April 2003.

A. Goose droppings – with hares present				
	Parameter estimate	<i>df</i>	<i>F</i>	<i>P</i>
Fertilisation	+ 0.214	1	15.283	<0.001
Exclosure	- 0.123	1	5.011	0.030
Replica (Set)		14	15.951	<0.001
Error		43		

B. Hare droppings - with geese present				
	Parameter estimate	<i>df</i>	<i>F</i>	<i>P</i>
Fertilisation	n.s.	1	0.123	0.728
Exclosure	n.s.	1	2.049	0.160
Replica (Set)		14	15.868	<0.001
Error		43		

C. Hare droppings - without geese				
	Parameter estimate	<i>df</i>	<i>F</i>	<i>P</i>
Fertilisation	+ 0.247	1	24.884	<0.001
Exclosure	+ 0.137	1	7.698	0.008
Replica (Set)		14	7.555	<0.001
Error		43		

Table 6.3: Response of geese and hares to the manipulation of biomass and quality on plots of *Festuca rubra* on the salt marsh of Schiermonnikoog for all experiments combined: in early-May 1997 (Brent Geese, Hares – geese present), early-April 2002 (Barnacle Geese, Hares – geese present) and (Barnacle Geese, Hares – geese present, Hares – geese absent). N is lower than the actual number of experimental plots for ‘Barnacle Geese’ and ‘Hares – geese present’ as quality samples were collected for only part of the plots in 2002.

	Brent Geese			Barnacle Geese			Hares – geese present			Hares – geese absent		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Biomass	1	0.549	0.463	1	0.140	0.709	1	19.888	< 0.001	1	6.064	0.017
Quality	1	4.290	0.045	1	12.185	0.001	1	0.092	0.763	1	9.359	0.004
Replicate (Set(Year))	7	13.311	< 0.001	19	8.707	< 0.001	27	9.348	< 0.001	4	0.572	0.684
Error	38			58			98			52		

Table 6.4: Pearson Correlation between grazing pressure of Brown Hares and Brent and Barnacle Geese before the start of the experiments and grazing pressure three weeks after the start of the experiments on the salt marsh of Schiermonnikoog, for all experiments combined: early-May 1997 (Brent Geese, Hares), early-April 2002 (Barnacle Geese, Hares) and (Barnacle Geese, Hares). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Response during experiment	N	Accumulated grazing pressure at the start of the experiment	
		Barnacle Goose	Hare
Hare	148	-0.384 ***	-0.233 **
Barnacle Goose	100	0.210 *	0.344 ***
Brent Goose	48	-0.054	-0.312 *

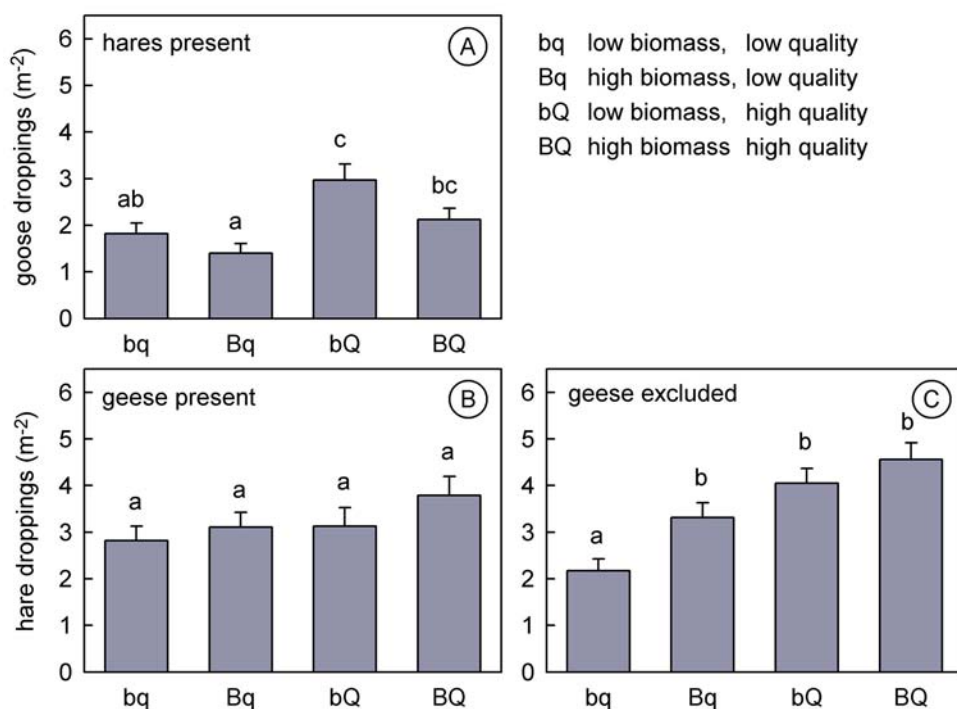


Figure 6.1: Use of the different treatments, created in the main experiment, by either geese (A.), hares in a natural situation where geese are present (B.) and in a situation where geese are excluded (C.) on the salt marsh of Schiermonnikoog. Shown is the mean \pm se, summarised for three sets in mid-February, early-March and early-April 2003. Different letters denote significantly different values (Tukey LSD test).

Discussion

Forage choice by geese

All our experimental data indicate that both Brent and Barnacle Geese prefer plots with a nutrient-rich sward (Figures 1 and 2, Tables 2 and 3). Additionally, we found that Barnacle Geese avoid plots with high biomass. This finding is supported by the significant positive correlation between the grazing pressure of Barnacle Geese during the experiment and the previous history of grazing by Brown Hares and Barnacle Geese on the experimental plots (Table 6.4). Forage quality in our salt-marsh system is generally highest in the beginning of the growing season and decreases rapidly as the season progresses (Chapter 5). However, continuous grazing can retard this seasonal decline (Stahl *et al.* 2001b). Grazing by either hares or geese apparently improves the quality of the vegetation relative to an ungrazed area and makes these plots particularly attractive for foraging geese (Ydenberg and Prins 1981, this study). Brent Geese prefer high-quality plots (Table 6.3), although, unlike the Barnacle Geese, they do not favour previously grazed vegetation (Table 6.4).

Brent and Barnacle Geese use the salt marsh during spring fattening. In this period they need to accumulate energy reserves essential for successful migration and subsequent reproduction at Arctic breeding sites (Ebbinge and Spaans 1995). Since their digestive system combines rapid passage of plant food through the gut with low digestive efficiency (Prop and Vulink 1992), the birds show a high degree of dependency on forage of superior quality (e.g. Prop and Deerenberg 1991).

Forage choice by hares

For hares, we detected a subtle interplay of foraging choice with concurrent goose grazing. When given a free choice in the absence of goose grazing, hares chose to forage on plots which combine biomass of a high quality and quantity. However, when geese are present, as in the spring situation at our study site, hares chose high biomass plots, which are avoided by geese (Table 6.3, Figure 6.2).

Van der Wal *et al.* (1998a) provided descriptive and experimental evidence that hares avoid salt-marsh sites that have been previously grazed by Brent Geese. Van der Wal argued against the occurrence of direct competition between geese and hares, since both species forage at different times within a day (i.e. hares feed mainly at dawn and dusk and geese during the daylight period). We witnessed a strong negative correlation between hare foraging choices and previous grazing by either geese or hares in our study (Table 6.4). Based on these experimental data, we conclude that resource competition as a result of depletion of favourable plots by large numbers of spring staging geese is driving forage patch choice in hares on the salt marsh.

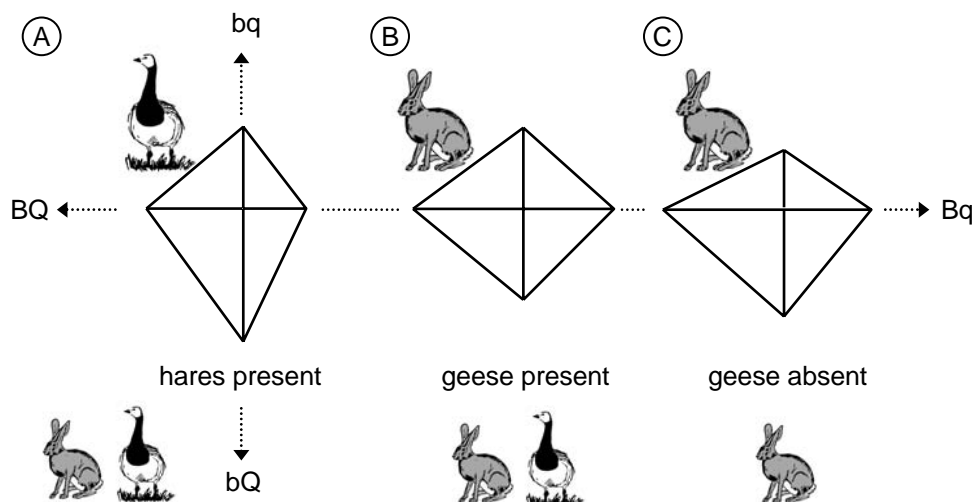


Figure 6.2: Relative grazing pressure of Barnacle Geese (left), Brown Hares with geese present (middle) and Brown Hares with geese absent (right) on the different treatments of the main experiment, summarised for three sets in mid-February, early-March and early-April 2003 on the salt marsh of Schiermonnikoog (mean values of Figure 6.1), given as profile plots; the lengths of each arm of the cross inside the polygon represents the contribution of each treatments to the total grazing pressure. The total length of all arms represents the total grazing pressure accumulated on all treatments, set at 100%.

A subtle balance between resource competition and grazing facilitation

Grazing by both geese and hares leads to an increased quality of vegetation. This facilitative process in which grazing of one herbivore induces a subsequent increase in quality of forage tissue through the production of new tissue within one season has been found in previous studies at our salt-marsh site (Ydenberg and Prins 1981; Chapter 7), and has been demonstrated for herbivore-plant interactions in a variety of ecosystems (McNaughton 1984; Gordon 1988; Hobbs *et al.* 1996; Ruess *et al.* 1997; Fox *et al.* 1998; Green and Detling 2000). Under these circumstances, herbivores profit from the increased tissue quality as a result of an elevated rate of nutrient intake.

However, when the forage resource is used concurrently by more than one herbivore species, we expect a shift towards less preferred plots by one species to avoid resource competition. In our experimental study, hares avoided plots that were favoured by geese. A distinct foraging choice of hares manifested itself only in a situation where concurrent goose grazing had been excluded experimentally. We interpret this as an indication of resource competition with geese. It was suggested by Van der Wal *et al.* (1998a) that large flocks of socially foraging geese rapidly deplete preferred salt-marsh sites in spring and evict hares to alternative, less favourable foraging sites.

We can explain the observed pattern of forage choices in the small herbivores with a species-specific functional response. For smaller herbivores, several studies demonstrate a dome-shaped functional response of food intake rate versus forage biomass (Fryxell 1991; Gross *et al.* 1993; Van de Koppel *et al.* 1996; Iason *et al.* 2002; Durant *et al.* 2003; Bos *et al.* 2004; Chapter 4), i.e. the intake rate of the herbivore increases with increasing biomass availability, beyond which intake rate declines at even higher levels of biomass. This decrease in the functional response is usually explained as a response to the handling problems associated with long leaves which decreases intake rate (Van der Wal *et al.* 1998b; Hassall *et al.* 2001; Durant *et al.* 2003; Bos *et al.* 2004), increased costs of locomotion and increased vigilance due to changes in the perception of predation risks (Van de Koppel *et al.* 1996). We conclude that hares are able to cope with swards of higher biomass, while geese show a preferred grazing response for swards which have low biomass levels.

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Jan Bakker and Sandra van der Graaf making a detailed vegetation description inside an enclosure on the salt marsh of Gotland (June 2004).

Compensatory growth of *Festuca rubra* after grazing – Can migratory herbivores increase their own harvest during staging?

Alexandra J. van der Graaf, Julia Stahl and Jan P. Bakker

Summary

1. The grazing optimisation hypothesis predicts an increased production and quality of plants grazed at intermediate grazing pressures. Following this hypothesis, herbivores will be able to increase their own harvest by repeated grazing. We tested the predictions of this hypothesis for Barnacle Geese, *Branta leucopsis*.
2. We manipulated grazing intensity of *Festuca rubra* swards through trials with captive geese in early spring. Levels of experimental grazing matched levels of natural grazing pressure. Growth response of individually marked tillers was measured over six weeks.
3. Aboveground biomass production of individual tillers was not different among different grazing intensities. Lost biomass in grazed tillers was compensated by a lower senescence.
4. Grazing significantly affected sward characteristics; the proportion of dead biomass in the vegetation was reduced and production of additional axillary tillers increased.
5. When extrapolating the experimental findings to foraging opportunities for staging geese, we calculate an increase in potential harvest for grazed as compared to ungrazed swards at levels of natural spring grazing.
6. The experiment demonstrates an increase in carrying capacity of the staging site for migratory geese through grazing. When comparing the experiment with grazing levels of wild Barnacle Geese, it is obvious that current goose densities maximise potential harvest.

Introduction

In the 1970s, Dyer (1975) and McNaughton (1979) postulated the grazing optimisation hypothesis (GOH). This hypothesis describes the reaction of plants to increasing herbivory. It predicts that grazing at intermediate intensities stimulates plant production and enhances the net primary production of grazed plants above that of ungrazed plants. Several studies demonstrated a positive response of plant tissue production on grazing (Cargill and Jefferies 1984b; Frank and McNaughton 1993), but evidence is limited to certain ecosystems and re-mains controversial (Belsky 1986; Belsky *et al.* 1993). Responses of various plant traits like total production, final biomass, root biomass and relative growth rate differ among species (Ferraro and Oesterheld 2002). In general, relative growth rate increased under defoliation. It is important to note that grazing facilitation is not caused solely by increased tissue production and biomass (i.e. grazing optimisation). Further reactions of vegetation to grazing comprise an increased nutrient concentration, denser sward and decreased cover of standing dead material. Sites which are repeatedly grazed by herbivores, often referred to as grazing lawns (McNaughton 1984; Drent and Van der Wal 1999), are characterised by these traits.

McNaughton (1979) developed the theoretical framework of grazing optimisation in view of the large-scale movements of herbivores in the Serengeti (e.g. wildebeest, *Connochaetes taurinus*). In ecosystems periodically visited by many migratory herbivores, grazing facilitation can be of great importance. Here, plant regrowth might counteract forage depletion and thereby allowing repeated usage of forage by passing herbivores within one season. In the Northern Hemisphere, avian herbivores (mainly geese and swans) commute between tundra sites in the High Arctic and coastal sites in the temperate zone. At different staging sites, forage plants repeatedly experience short periods of heavy grazing, mostly during the start of the growing season when different waves of migratory birds pass through.

At the Dutch island of Schiermonnikoog, about 3,000 Barnacle Geese and 1,500 Brent Geese forage on the salt marsh during the months of March, April and May (Bos and Stahl 2003). During these months, both goose species accumulate body reserves prior to their migration to the Arctic (e.g. Prop and Deerenberg 1991). The salt-marsh grass *Festuca rubra* is an important component of the diet of both species. For long-distance migrating geese, consequences of foraging performance at a staging site are far-reaching: improved foraging opportunities during spring translate into improved body condition and subsequently into successful reproduction at the Arctic breeding grounds (Ebbinge and Spaans 1995). It was suggested earlier that Brent Geese, *Branta bernicla bernicla*, adopt a cyclic grazing pattern by which they optimise their protein intake (Ydenberg and Prins 1981; Drent and Van der Wal 1999). We argue that the potential importance of grazing facilitation of large numbers of avian herbivores concentrating at coastal sites during short periods of spring migration has been largely ignored in literature.

We present here an experimental field test to interpret the consequences of successive waves of grazing on biomass production at a major staging site of Arctic geese. In a field experiment, we tested the predictions of the grazing optimisation hypothesis on a temperate salt marsh in North-Western Europe. Using captive geese, different grazing schemes were applied to the grass sward and the growth response of individual tillers of *Festuca rubra* was followed for six weeks. Our aim was to explore the scope for grazing optimisation on a temperate salt marsh that is a key site for staging migratory geese and to examine consequences for the carrying capacity of these sites.

Methods

Study area

Our study area was located at the eastern salt marsh of the island of Schiermonnikoog in the Dutch Wadden Sea (53°30'N, 6°10'E) which is an area unaffected by livestock grazing throughout the year (Box 1). At these salt-marsh sites, about 2,500 Barnacle Geese were present during the experiments (pers. obs. – goose count March/April 2002). At the same time, about a 1000 Brent Geese (pers. obs.) along with 350 brown hares (D.P.J. Kuijper, pers. comm.) used the 1,350 ha study area on the salt marsh. With regard to the grazing of small herbivores, our study area is one of the most intensively used salt-marsh areas on the island in spring (Van de Koppel *et al.* 1996). We conducted the grazing experiment on the high salt marsh (for description see Olff *et al.* 1997; Van der Wal *et al.* 1998b) in the *Festuca* community, where the vegetation mainly consists of Red Fescue, *Festuca rubra*, combined with the Salt-marsh Rush, *Juncus gerardi*, and sparsely distributed rosettes of Sea Plantain, *Plantago maritima*. On our study site (1350 ha), the *Festuca* community (De Jong *et al.* 1998; Kers *et al.* 1998) covers 262 ha, which amounts to about 20% of the total area. *Festuca* forms about 90% of the diet of Barnacle Geese (Van Dinteren 1988) and about 50% of the diet of Brent Geese (Van der Wal *et al.* 2000a). The diet of resident Brown Hares, *Lepus europaeus*, contains about 70% *Festuca* in early spring (Van der Wal *et al.* 1998b).

Grazing treatments

In 1998, fresh droppings were counted weekly on 30 plots of 4 m² marked by a PVC tube, to allow for repeated counts on the same places. Grazing intensity was calculated by multiplying these field measures of dropping densities with field observations on dropping intervals of Barnacle Geese. Prop and Vulink (1992) recorded dropping intervals of 4.4 min for Barnacle Geese foraging on *Festuca* at this site in spring. Cumulative grazing intensity of wild Barnacle Geese amounted to $13.9 \pm 1.5 \text{ min m}^{-2}$ (mean \pm SE, $N=30$) for two weeks in mid March.

In 2002, five replicate sites were selected and matched for homogeneity of the *Festuca* sward. Sites were about 100 m apart from each other. At each site, an area of 2 by 12 m was fenced with chicken wire in order to exclude grazing by wild geese and hares. Other herbivores are virtually absent on these marshes. Fences were erected in mid-March 2002 prior to arrival of wild geese on the salt marsh and were maintained throughout the measuring period. Within these fences, we randomly appointed one plot of 4 m² to each treatment. Five treatments characterised by different grazing intensities were created through controlled grazing with two captive Barnacle Geese for a fixed time period. This experimental design was adopted from a study by Hik and Jefferies (1990), studying growth stimulation through grazing in a sub-Arctic salt marsh.

For the experimental grazing with captive geese, five different treatments were created: 0, 7, 14, 21 or 28 min grazing m⁻². The grazing intensity recorded for wild geese at that site (14 min m⁻²) was represented within the range of experimentally chosen grazing bouts. Natural grazing pressure on *Festuca* swards is based on measurements at the same site during a two-week period in mid March 1998. The timing of these measurements corresponds with the time period between erection of the enclosures and experimental grazing in our experiments.

On the day prior to experimental grazing, a holding pen was erected surrounding the treatments. During the night preceding the experiment, two geese stayed on a depleted plot adjacent to the trial plots to increase feeding susceptibility of the geese. In the morning of the grazing trials the geese were allowed to enter the first plot. Grazing time of both geese was recorded to the nearest second and trials stopped when the amount of grazing time specified for a treatment was reached cumulatively by both geese. Then the geese had to graze an adjacent plot until plots of all treatments had received grazing. By arranging plots in a line, the geese could be driven to the next plot without catching, and stress was reduced to a minimum. The grazing took place on five consecutive days (25-29 of March 2002) for the five replicates. Experimental grazing with captive geese was conducted under licence of the ethical committee for use of experimental animals of the University of Groningen (DEC RuG, licence number 2734). The Barnacle Geese were born in captivity and kept on a grass diet for more than two weeks prior to the experiment.

Measurements on *Festuca rubra*

The biomass response of the *Festuca* sward to the different treatments is a crucial parameter in our analyses. As destructive biomass sampling is connected with rather large measuring errors in this type of short grass swards with high proportions of litter, we instead adopted a detailed approach which combines measurements of tiller densities, leaf length and length-to-biomass calibrations to a fine-tuned measure of biomass. Directly after experimental grazing tiller density was counted within 3 square frames of 5.5 x 5.5 cm in every replicate of the treatments. All 15 counts were grouped per replicate and the average tiller density at the start of the experiment was calculated from the averages of the five replicates.

At the same time, 20 tillers of *Festuca rubra* were marked individually in each plot. In each of two sections of 10 cm x 25 cm, ten tillers were selected close to the centre of each plot to prevent edge effects. For the grazed treatments we selected tillers of which at least one leaf had been grazed, for the 'no grazing' treatment we selected ungrazed tillers. The leaves of every tiller were measured to the nearest millimetre and marked with Indian ink for subsequent identification in the following week. With this method, we were able to follow individual leaves from their emergence until their death. For all leaves, we measured the length of the living and the dead parts. Following the first marking, tillers were measured six times with intervals of one week.

We started out with 20 marked tillers in each replicate of the treatments. Mortality accounted for approximately 5% of the loss in tillers and was not significantly different between treatments (Univariate ANOVA $F_{4,20} = 0.229$, $P = 0.919$). Reasons other than mortality accounted for a loss in tillers of 16% and did not differ between treatments (Univariate ANOVA $F_{4,20} = 0.449$, $P = 0.772$). Therefore, sample sizes decreased to about 15 tillers per plot at the end of the season. To avoid pseudo-replication measurements of the individual tillers were averaged per replicate per treatment. Only tillers that were still present at the last measurement were taken into account. On three occasions covering the whole period of the experiment leaf material of *Festuca rubra* was collected in order to establish a conversion between leaf length and leaf biomass. On each occasion, about 100 leaves were measured, dried and weighed (in total about 2.5 m). Average dry-weight of *Festuca* leaves was 0.034 mg mm^{-1} (± 0.0007).

Additionally samples of green leaf tips for chemical analysis were collected two, four and six weeks after grazing. Samples were oven-dried at 60°C for at least 48 hours and ground in a planetary micro mill (Pulverisette 7, Fritsch GmbH, Idar-Oberstein Germany), on a rotational speed of 750 rpm, for 3 x 3 minutes. Ground samples were analysed for total nitrogen and carbon contents using an automated CNHS-analyser (automated element analysis, Interscience EA 1110, New York, USA).

Calculations and Statistics

Tiller growth was calculated in the following ways (see Bakker and Loonen 1998): Increment in standing crop (ISC); aboveground biomass production (ABP) including both ISC and senescence; and number of leaf births and deaths. Increment in standing crop is a frequently used measure (e.g. McNaughton 1979; Hik and Jefferies 1990; Frank and McNaughton 1993), however Bakker and Loonen (1998) suggested ABP as a more specific measure of plant response.

Yield to grazers was calculated as the harvestable biomass at the end of the experiment (6 weeks after experimental grazing) plus the harvest during experimental grazing. Harvestable biomass at the end of the experiment was calculated per tiller, assuming a maximum bite size of 3 cm per leaf. This means that for every leaf on a tiller the harvestable biomass was set at either 3 cm or the entire length of the leaf if the leaf was shorter than 3 cm. The harvestable biomass of all leaves on a tiller was summed to calculate the harvestable biomass per tiller. This was multiplied by the tiller density at the start of the experiment (2574 m^{-2}) and the dry-weight of *Festuca rubra* (0.034 mg mm^{-1}) to convert the measure of leaf length into yield to grazers as g dwt m^{-2} . Nitrogen yield (g N m^{-2}) was calculated by multiplying yield to grazers with the nitrogen concentration ($\text{g N g}^{-1} \text{ dwt}$) of leaves of the different treatments.

Finally, carrying capacity of the area (262 ha of mid-marsh dominated by *Festuca rubra*) was calculated, using published data on intake rate and feeding time. For Barnacle Geese feeding on *Festuca* in spring, intake rate was measured as 0.19 g min^{-1} (Prop *et al.* 1998) and feeding time as 907 min day^{-1} (Black *et al.* 1991). From these data total biomass removal by the geese during 8 weeks was calculated, a period corresponding with the interval between the establishment of the exclosures and the last measurement.

To test for trends over time, a repeated measures ANOVA was used with week as the repeated factor, treatment as the fixed factor and replicate as the random factor; a post-hoc Tukey test was used to test for differences between treatments. Since we were interested in the yield to grazers after specific periods, the tests were subsequently performed separately for every measurement date. For all tests a Randomised block design was used with treatment as fixed factor, and replicate as random factor with additional Tukey post-hoc test to test for differences between treatments. All analyses were performed using the SPSS for Windows, version 12.0.1.

Results

Growth after grazing

Average live biomass per tiller was reduced after the experimental grazing bouts by approximately 13 mm in all grazed treatments. A repeated measurement ANOVA showed significant differences between the treatments for both live aboveground biomass (Figure 7.1; Treatment: $F_{4,16}=6.153$, $P=0.002$; Replicate: $F_{4,16}=6.659$, $P=0.001$) and dead biomass (Treatment: $F_{4,16}=4.782$, $P=0.010$; Replicate: $F_{4,16}=17.322$, $P<0.001$). For dead biomass the ungrazed treatment was higher than all grazed treatment for live aboveground biomass the 14-min grazing treatment did not differ significantly from either the other grazed or the ungrazed treatments, while the ungrazed treatment differed significantly from the grazed treatments.

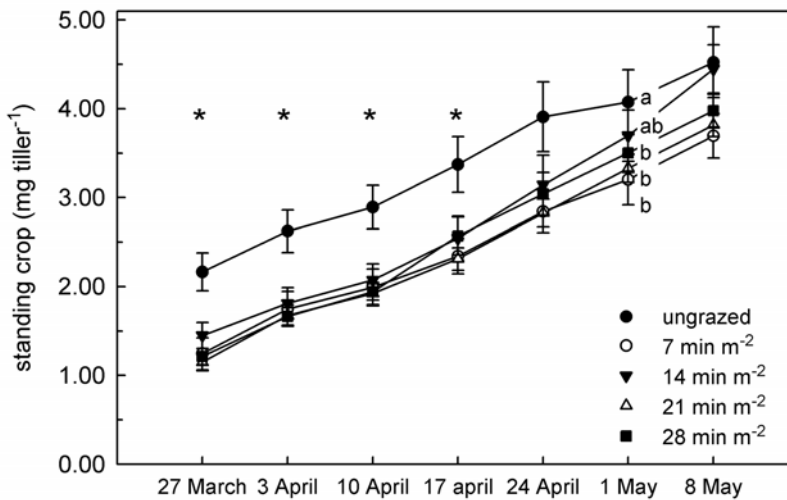


Figure 7.1: Seasonal change in standing crop for the different grazing intensities. Values represent means with SE (n=5). Asterisks denote significant differences ($P<0.05$) between the ungrazed and all grazed treatments. Different letters denote significant differences between treatments ($P<0.05$).

When analysed per measuring date, aboveground biomass of the ungrazed treatment exceeded that of all grazed treatments during the first three weeks after experimental grazing (Treatment $P<0.005$; Replicate $P<0.005$). In the fourth week, the 14 min-grazing treatment was not significantly different from the ungrazed (Treatment: $F_{4,16}=4.635$, $P=0.011$; Replicate: $F_{4,16}=5.613$, $P=0.005$) and in the fifth and sixth weeks, there were no differences between any of the grazed treatments and the ungrazed treatment (Treatment: $F_{4,16}=2.533$ n.s. and $F_{4,16}=2.780$ n.s. for week 5 and 6 respectively and Replicate: $F_{4,16}=4.716$, $P=0.010$ and $F_{4,16}=2.860$ n.s.). This implies a greater increase in live biomass (increment in standing crop – ISC) in the grazed treatments. We found a significant effect of grazing treatment on ISC in week six after grazing (Treatment: $F_{4,16}=3.029$, $P=0.049$; Replicate: $F_{4,16}=0.827$ n.s.; Figure 7.2A), caused by the difference between the ungrazed and the treatment receiving 14-min grazing (post hoc Tukey).

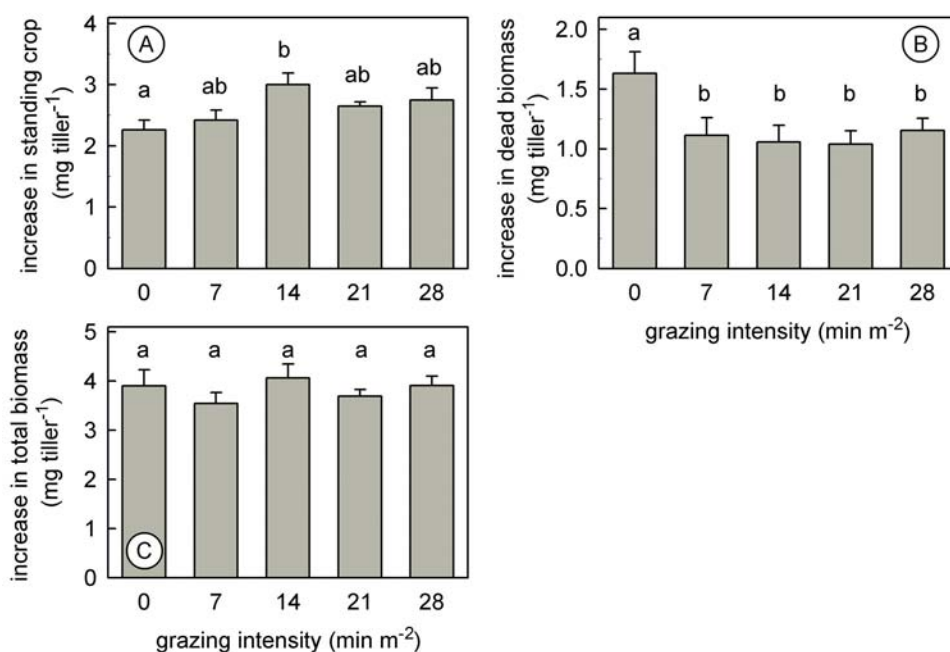


Figure 7.2: Increment of standing crop (A), increase in dead biomass (B) and total biomass production (C) over six weeks, given as mean + SE ($N=5$) for the different treatments. Different letters denote significant differences with $P<0.05$.

Tiller senescence differed significantly between treatments: In the ungrazed treatment more material died than in each of the grazed treatments (Treatment: $F_{4,16}=7.224$, $P=0.002$; Replicate: $F_{4,16}=7.557$, $P=0.001$; Figure 7.2B). When combining the measures of increment of standing crop and tiller senescence to the parameter of total aboveground biomass production (ABP), we found no effect of treatment ($F_{4,16}=0.871$, $P=0.503$; Figure 7.2C) or replicate ($F_{4,16}=2.230$ n.s.). This implies that the growth of tillers in all treatments was equal, but more biomass died in the ungrazed treatment. Interestingly, the amount of biomass that died in the ungrazed treatment equals the amount of biomass that was eaten in the grazed treatments. At the end of the experiment this resulted in a significantly lower percentage of live biomass in the ungrazed treatment as compared to the 14 and 21 min-grazing treatments (live biomass 70% versus 79 and 77%; Treatment $F_{4,16}=4.905$, $P=0.009$; Replicate $F_{4,16}=0.760$, n.s., Figure 7.3A).

Increased tillering after grazing

At the beginning of the experiment tiller density was 2574 ± 303 tillers m^{-2} . At the beginning of the experiment the number of leaves per tiller was equal for all treatments (Treatment $F_{4,16}=0.690$, n.s.; Replicate $F_{4,16}=21.526$, $P<0.001$). When comparing the number of new axillary shoots between different treatments at the end of the measuring period (first week of May) it is obvious that grazing at an intermediate intensity increased the number of axillary shoots (Figure 7.3B Treatment $F_{4,16}=3.493$ $P=0.031$; Replicate $F_{4,16}=1.276$, n.s.). The number of leaves of the main shoot (Treatment $F_{4,16}=0.842$, n.s.; Replicate $F_{4,16}=5.104$, $P=0.008$) and the number of leaves per axillary shoot did not differ significantly between treatments (Treatment $F_{4,13}=0.274$, n.s.; Replicate $F_{4,13}=1.719$, n.s.).

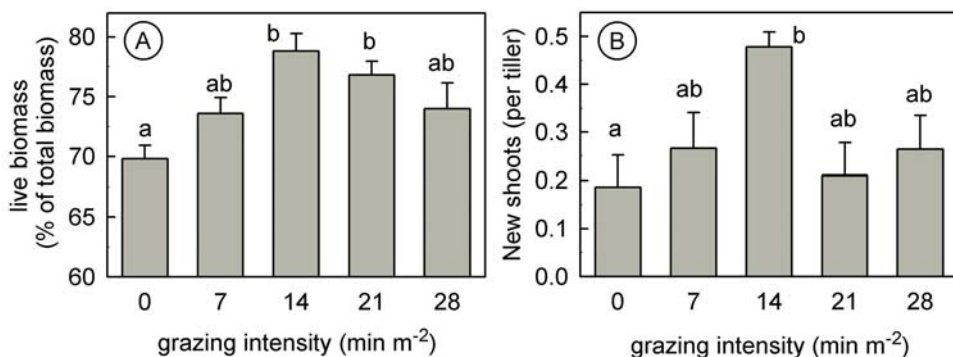


Figure 7.3: The effects of grazing intensity on sward characteristics: (A) The percentage of live biomass in the vegetation. (B) The number of new shoots per tiller six weeks after experimental-grazing treatment. Bars represent overall mean + SE ($N=5$).

Increased quality after grazing

For nitrogen concentration, taken as a measure of forage quality, we found a significant difference between treatments (Repeated measurements ANOVA, Treatment $F_{4,16}=4.316$, $P=0.015$; Replicate $F_{4,16}=12.852$, $P<0.001$). A post-hoc Tukey test revealed that nitrogen concentration of leaf material in the ungrazed treatment was significantly lower than in the 21 min- and 28 min- grazed treatments. Quality in all treatments decreased throughout the measuring period, but the decline in the ungrazed treatment was distinctly stronger than in the grazed treatments. Five weeks after grazing the 28 min-grazing treatment was significantly different from the ungrazed treatments (Treatment $F_{4,16}=3.266$, $P=0.039$; Replicate $F_{4,16}=4.115$, $P=0.018$). Twelve weeks after grazing all differences between treatments had disappeared and nitrogen contents were similar (Treatment $F_{4,16}=1.180$, n.s.; Replicate $F_{4,16}=0.275$, n.s.).

Yield to grazers

Figure 7.4A shows that yield to grazers increased by approximately 20% in the intermediate, 14-min grazing treatment (Treatment $F_{4,16}=3.420$, $P=0.033$; Replicate $F_{4,16}=1.518$, n.s.). Also in the intermediate, 14-min grazing treatment we found an increase of about 40% in nitrogen yield, and of about 25% in all other grazed treatments as compared to the ungrazed treatment (Treatment $F_{4,16}=5.936$, $P=0.004$; Replicate $F_{4,16}=0.568$, n.s.; Figure 7.4B). Subsequently, carrying capacity also showed an optimum at the 14-min grazing treatment (Figure 7.5).

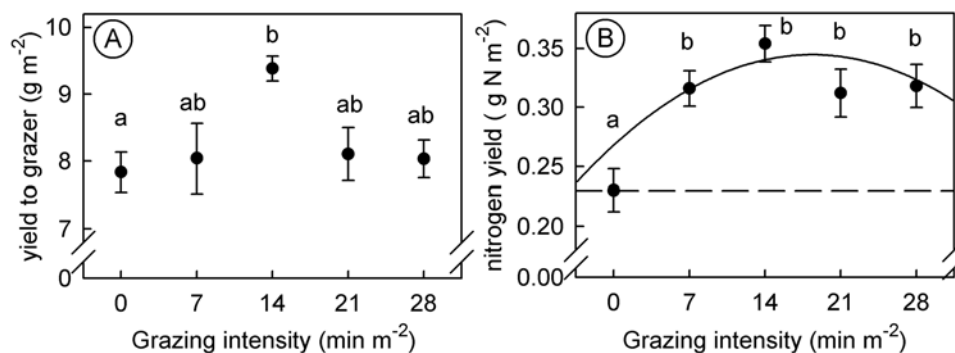


Figure 7.4: (A) Yield to grazers and (B) Nitrogen yield 6 weeks after experimental grazing for all grazing intensities (mean + SE). Different letters in (A) denote significant differences between treatments ($P<0.05$). The curve in (B) shows the quadratic regression: $y=0.2373+0.0123x-0.0003x^2$ ($F_{2,22}=10.5031$, $P=0.0006$, $R^2=0.488$), the dashed reference line gives the potential harvest for ungrazed swards.

Discussion

We can distinguish four ways in which herbivores might positively alter availability and quality of plant resources through grazing: (1) the maintenance of phenologically young stages of plants leading to a high nutrient concentration in leaf material; (2) the stimulation of growth leading to increased biomass; (3) the stimulation of tillering which increases shoot density; and (4) a shift in vegetation composition which can increase plant cover and reduce that of standing dead biomass, through selective foraging and a reduction of senescing tissue. The second point has received most attention and the controversy about the mechanism has produced evidence for (Ydenberg and Prins 1981; Hik and Jefferies 1990; Pandey and Singh 1992; Frank and McNaughton 1993; Nolet 2004) and against it (Belsky 1986; Zellmer *et al.* 1993; Beaulieu *et al.* 1996). An increase of the nutrient concentration in previously grazed tissue is a well-reported effect of grazing in many different ecosystems (Ydenberg and Prins 1981; Gauthier *et al.* 1995; Ruess *et al.* 1997; Fox *et al.* 1998; Green and Detling 2000; but see also Piedboeuf and Gauthier 1999; Leriche *et al.* 2003). Alterations in shoot densities or live/dead ratios are often reported as side-effects in grazing studies (Coughenour 1991; Van de Koppel *et al.* 1996; Loonen and Solheim 1998; Zacheis *et al.* 2001), but usually do not receive much attention.

In our study, grazing did not increase biomass production, yet we found effects on sward characteristics like tiller density (increase in tillering, Figure 7.3B) and composition of the vegetation (increased percentage of live biomass, Figure 7.3A). When considering the increment of standing crop alone, we found evidence of overcompensation in grazed plants (Figure 7.2A). However, when correcting for senescence of leaf tissue through the measure of aboveground biomass production, the difference between grazing treatments disappeared (Figure 7.2C). At the end of the experiment, the biomass in the grazed treatments had recovered to that of the ungrazed treatment (Figure 7.1). Therefore, we conclude that *Festuca rubra* did compensate, but not overcompensate, for biomass lost through grazing. We stress the importance of incorporating leaf senescence in all measurements and to avoid measuring increment in standing crop alone. Single measurements of increment in standing crop overestimate plant production, increasing the risk of making erroneous conclusions about overcompensation under grazing. Bakker and Loonen (1998) already stressed this point and depict studies where proof of overcompensation disappeared when senescence was incorporated in the calculations.

We acknowledge that in all grazing treatments the individual tillers that we measured were grazed to the same extent. However, the sward received different grazing intensities and our results show that this has effects on the growth response of the individual tiller. Different treatment responses concerning the increase in standing crop (Figure 7.1A) and increase in new shoots (Figure 7.3B) suggest that these growth differences have repercussions for the total yield to grazers.

Grazing facilitation through increased (nitrogen) yield

Although experimental grazing did not increase biomass production of *Festuca rubra* in our study, we argue that goose grazing increased harvestable biomass and nitrogen. We have shown that yield to grazers was increased by approximately 20% in the intermediate, 14-min grazing treatment (Figure 7.4A). Because of their limited digestive volume, geese and other small herbivores are restricted to high quality diets (Demment and Van Soest 1985). Therefore we used nitrogen yield, the amount of nitrogen per square meter, as a measure of forage quality (Figure 7.4B). In line with the grazing optimisation hypothesis by McNaughton (1979) we fitted a quadratic curve to our data (Figure 7.4B); the curve shows an optimum of nitrogen yield at an intermediate grazing pressure (14-min m⁻²). It is important to note that this intermediate grazing pressure corresponds with the natural grazing pressure of wild Barnacle Geese at this site.

The carrying capacity of this salt-marsh area is increased by grazing, with an optimum at the natural grazing intensity. Interestingly, the current number of wild Barnacle Geese that rely on *Festuca* swards as spring forage (on average 2540 Barnacle Geese, annual counts for the period 2000-2002, own observations) matches the maximum carrying capacity as calculated from our experiment (Figure 7.5).

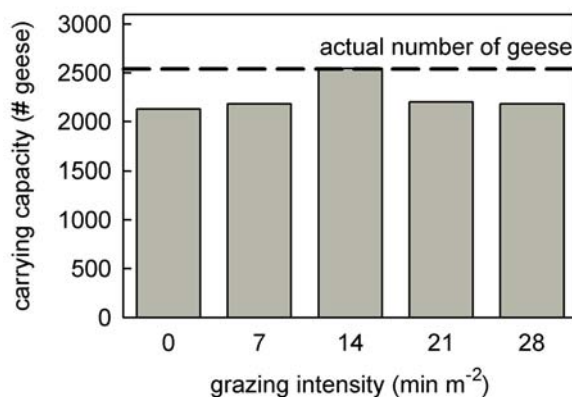


Figure 7.5: Estimate of the carrying capacity in response to grazing intensities and average number of geese observed in the area (dashed line).

Mechanisms for (over)compensatory growth

In the literature, two mechanisms of how plants can profit from grazing are generally discussed. The first, and most studied focuses on the interaction of grazing and an increased nutrient availability through nutrient input by faeces or urine. The second mechanism relates to the effects of shading by taller neighbouring species, by standing dead biomass or by the plant itself (self-shading) and the removal of competition for light through grazing.

Combined effects of grazing and nutrient input through droppings on the growth of forage plants have been found in many studies in various ecosystems. These studies often report increased nitrogen concentration of grazed tissue as well as increased growth rates and increased tiller densities (Ruess *et al.* 1983; Cargill and Jefferies 1984b; Ruess *et al.* 1997; Frank *et al.* 2002; but also see Zacheis *et al.* 2002). It is assumed that nutrient limitation of the vegetation and the ability of the plants to profit directly from the released nutrients are important prerequisites for the occurrence of enhanced growth of plants following grazing (Yamauchi and Yamamura 2004). Hik and Jefferies (1990) tested the predictions of the grazing optimisation hypothesis in a sub-Arctic ecosystem characterised by extensive but periodic grazing by large numbers of breeding Lesser Snow Geese, *Chen caerulescens caerulescens*, during summer. At their study site, the salt marsh of La Pérouse Bay, Canada, the vegetation is dominated by the graminoids *Puccinellia phryganodes* and *Carex subspathacea*. Hik and Jefferies demonstrated that goose grazing enhanced productivity of these species. However, the increase of aboveground production of grazed swards of *P. phryganodes* depended entirely upon the input of goose faeces (Hik and Jefferies 1990). As the sub-Arctic marsh at that site is primarily nitrogen-limited (Cargill and Jefferies 1984a), the increase in biomass production in grazed swards was explained by an acceleration of the nitrogen cycle caused by a combination of grazing and subsequent deposition of droppings. In several studies on temperate salt marshes in the Wadden Sea, addition of nitrogen and phosphorus had no effects on the biomass of *F. rubra* (Kiehl *et al.* 1997; Van Wijnen and Bakker 1999). Additionally, Van Wijnen *et al.* (1999) demonstrated that the total nitrogen input from droppings on a temperate salt marsh is negligible when compared to the inorganic nitrogen released by mineralisation. We therefore argue that fertilisation by droppings is an unlikely cause of increased tillering of grazed plants at our temperate site.

The second mechanism, a reduction of shading through removal of other taller species (McNaughton 1979), through reduction in standing dead biomass (Frank and McNaughton 1993) or through reduction of self-shading (Wegener and Odasz 1997; Nolet 2004) has received less attention. McNaughton (1976) first reported the higher productivity of vegetation on grazed sites compared to non-grazed sites in the Serengeti short-plains. These grasslands were dominated by the grass *Andropogon greenwayi*, which disappeared when a site remained ungrazed (McNaughton 1979). Belsky (1986) demonstrated that *A. greenwayi* profits from grazing which opens up the dense canopy, and facilitates the production of new tillers. The grass takes advantage of the intolerance of neighbouring plant species to grazing and trampling.

In the case of *Festuca rubra*, nutrient stores are maintained mainly below-ground, which reduces nitrogen-loss to aboveground grazing (Berendse *et al.* 1992). This can be interpreted as an adaptation to grazing. Kiehl *et al.* (1997) suggested that self-shading may decrease tillering in *Festuca* swards. In an experimental set-up non-shaded *Festuca* clones produced significantly more tillers than artificially shaded clones, resulting in a denser sward of the non-shaded clones (Skalova and Krahulec 1992). If *Festuca* reacts with increased tillering to improved light-conditions after grazing, this can explain the increased sward density found in our grazing experiment. We call for further experimental field studies on the mechanism behind plant responses to grazing in non-nutrient limited systems.



Julia Stahl conducting detailed measurements on the vegetation.

Conclusions

Although the mechanism is not entirely understood yet, our data demonstrate that geese can increase their harvest and the quality of their forage through grazing. This can have far-reaching consequences for their survival and breeding performance, as improved foraging opportunities during spring translate into improved body condition and subsequently into successful reproduction at the Arctic breeding grounds (Ebbinge and Spaans 1995). We conclude that the geese optimise grazing of the area, thereby ensuring a maximum carrying capacity. This is an interesting finding contrasting that of McNaughton (1979) who showed that natural grazing intensities of wildebeest in his savannah study system are higher than optimal. Two studies that experimentally manipulated grazing frequency in disparate ecosystems such as a mixed-grass prairie in the USA grazed mainly by bison, *Bison bison*, (Green and Detling 2000) and hayfields on Iceland grazed by Greenland White-fronted Geese, *Anser albifrons flavirostris* (Fox *et al.* 1998) found comparable results; an increase in nitrogen yield at grazing frequencies that corresponded to natural levels. Other experimental field tests did generally not apply multiple levels of grazing intensity (for example: Frank and McNaughton 1993; Gauthier *et al.* 1995; Ruess *et al.* 1997; Fox *et al.* 1998) or do not provide the natural level of grazing intensity (Hik and Jefferies 1990). For our study, we suppose that the observed optimal level of grazing intensity results from a decline of foraging intake of the geese at non-optimal grazing intensities; at low grazing intensity the vegetation will eventually become too tall for the geese and intake rate will decline (Van der Wal *et al.* 1998b); at high grazing intensities intake rate will also decline because of lower food availability and higher levels of interference competition. This so-called dome-shaped functional response was recently described for Dark-bellied Brent Geese (*Branta bernicla bernicla*) by Bos *et al.* (2004).

Acknowledgements

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Holding pen on the the salt marsh of Schiermonnikoog with two captive Barnacle Geese in the night pen (top) and grazing on one of the plots (bottom).

Forage enhancement through dropping deposition by migratory Barnacle Geese? - Experimental tests along the East Atlantic flyway.

Alexandra J. van der Graaf, Robert Buitenwerf and Julia Stahl

Summary

Herbivores can increase significantly biomass availability and quality of the vegetation as a consequence of grazing and fertilisation by faeces. In systems with low plant productivity, these enhancing effects can be significant for the herbivores themselves. Migrating Barnacle Geese are dependent on coastal salt marshes which have a low plant productivity along their entire flyway. Using field experiments, we investigated the effects of goose droppings on biomass production of the main forage species of the geese and its nutritional quality, at three sites along the migration route; a Wadden Sea spring staging site (the Netherlands), a Baltic Sea stopover site (Sweden) and a Barents Sea breeding site (Russia). We expected that fertilisation from droppings would have a significant effect on the forage species because of low nutrient availability in the soil and the inputs of droppings from high numbers of migrating geese. However, at all sites, addition of droppings did not have any effect on the biomass, production or nutritional quality of the main forage species. At the Dutch and Baltic sites this lack of effect can be explained by the fact that the growth of *Festuca rubra* is not nutrient-limited and that nitrogen input of droppings is negligible in comparison to inorganic nitrogen released through mineralisation. The Arctic species, *Puccinellia phryganodes* and *Carex subspathacea*, are frequently nutrient-limited in their growth and have been shown to react to addition of droppings at a Canadian intertidal site. An overview of studies on the effect of goose droppings on vegetation reveals that the combination of a high grazing intensity and a very low natural availability of nutrients is a prerequisite for this reaction.

We conclude from our experimental evidence that fertilisation by droppings does not affect forage plant biomass, production, nutritional quality or tillering at the main staging sites of Barnacle Geese along the East Atlantic Flyway.

Submitted

Introduction

Herbivores can significantly alter their own forage resources as a result of enhancement of growth conditions by fertilisation with faeces or urine (Ruess and McNaughton 1984, Day and Detling 1990). Several studies have shown that this natural fertilisation, in combination with grazing, can increase plant production, aboveground and belowground biomass as well as the nutritional quality of plant tissue (Ruess and McNaughton 1984, Day and Detling 1990, Frank and McNaughton 1993, Frank *et al.* 2002). Remarkable effects were demonstrated for the salt marsh of La Pérouse Bay, Canada, where faeces of Lesser Snow Geese, *Anser caerulescens caerulescens*, significantly increased aboveground primary production of the two main forage species of the geese: *Puccinellia phryganodes* and *Carex subspathacea* (Cargill and Jefferies 1984, Bazely and Jefferies 1985, Hik and Jefferies 1990). The increase of plant production by deposition of faeces in combination with plant growth responses to grazing ranged from 35-80%. An increase in plant production of this magnitude, especially in a low-productive system (Jefferies *et al.* 1994, Gauthier *et al.* 1997) can have large consequences for the use of the area by herbivores and even affect herbivore population numbers (Bazely and Jefferies 1989).

Not only Lesser Snow Geese, but in fact almost all migratory species of herbivorous waterfowl, such as geese and swans, depend on salt marshes for food resources along the major part of their migration route between temperate wintering and Arctic breeding sites. Many studies have documented that plant growth in temperate as well as Arctic salt marshes is limited by nutrients, in particular by nitrogen (Jefferies *et al.* 1994, Gauthier *et al.* 1997, Kiehl *et al.* 1997, Van Wijnen and Bakker 1999, Ngai and Jefferies 2004). Increased production of the vegetation through fertilisation by faeces may therefore significantly affect the herbivore carrying capacity of these salt marshes and consequently even maximum population size of these herbivore species.

The Barnacle Goose, *Branta leucopsis*, is one of the species that mainly depends on salt marshes for food resources along its migration route. They migrate from their traditional wintering sites, salt marshes in the temperate Wadden Sea, via a few stopover sites on salt marshes along the coasts of the Baltic and White Sea to their breeding grounds in Russia, where they also rely on salt marshes for forage (Ganter *et al.* 1999). Fertilisation of the sward by droppings potentially is an important factor influencing the food availability for Barnacle Geese along the flyway. An increase in plant production within a short time-span can significantly increase the potential harvest for the geese and thereby the carrying capacity of the site. Field experiments at a Dutch salt-marsh site demonstrated an increase of potential harvest and carrying capacity through the plant responses to the mechanical act of grazing alone, when the effect of droppings was excluded from the experimental setting (Chapter 7).

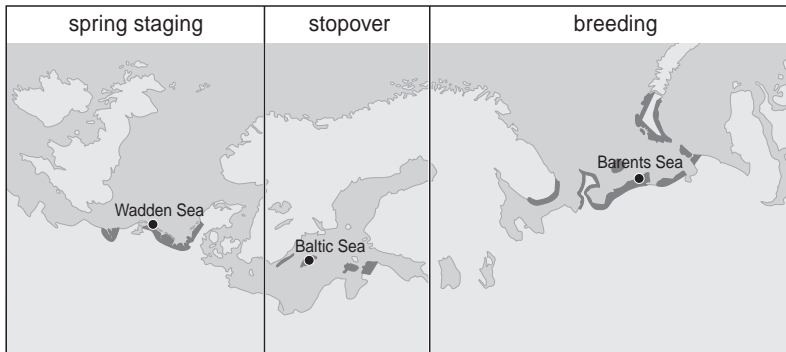


Figure 8.1: Map of the East Atlantic Flyway of the Barnacle Goose with the study sites indicated.

Besides forage biomass, tissue quality is an important parameter determining forage decisions in geese (Sedinger and Raveling 1986, Riddington *et al.* 1997, Hassall *et al.* 2001, Bos *et al.* 2005, Chapter 3). Accumulation of proteins is very important for the reproductive performance of geese (Prop and Black 1998). However, since geese possess a relatively inefficient digestive system with a rapid throughput, they are forced to select forage of high nutritional quality in order to be able to absorb enough nutrients (Prop and Vulink 1992). An increase in nutritional quality of the forage species will increase the attractiveness of the area for the small herbivores, since they can potentially accumulate more protein stores with no increase in the foraging effort.

In this study, we test the effects of fertilisation by goose droppings on salt-marsh swards along the flyway. We will compare our findings with other studies on the effects of droppings and grazing of geese on vegetation characteristics.

Methods

We experimentally examined the effect of goose droppings on forage biomass and nutritional quality on three sites along the East Atlantic flyway of the Barnacle Goose; a staging site in the Dutch Wadden Sea used from mid-March to end of April for spring fattening (Box 1), a stopover site in the Baltic Sea used from mid-April to end of May as a short stop during migration (Box 2), and a Russian breeding site (Chapter 2) used from early June to early September as a breeding and brood-rearing site (Figure 8.1; see Chapter 5, for detailed descriptions of the study sites). At the Dutch and Baltic sites the main forage species of the Barnacle Goose is the grass, *Festuca rubra*; at the Russian site, the goose diet

during incubation and brood rearing consists of the grass, *Puccinellia phryganodes*, and the sedge, *Carex subspathacea*, in equal proportions (own data). Grazing intensity of geese was measured throughout the experimental period on 5 transects. The length of each transects was approximately 40 m, and consisted of 5 short plastic sticks placed about 10 metres apart. On a surface area of 4 m² around each stick, droppings were counted and removed weekly.

At each site, 10 exclosures of 4 m x 4 m were constructed early in the growing season (Wadden Sea -21 March 2005; Baltic Sea -4 May 2005; Russia -21 June 2005), chicken wire prevented geese and hares from grazing. Inside the exclosures a grid was established of 12 plots of 15 cm x 15 cm, spaced 1 metre apart from each other. Hence, all plots within one exclosure were spaced close together to minimise variation in vegetation or soil properties which might potentially obscure our results, but far enough apart not to affect each other. On half of the plots three fresh goose droppings were added in a 5 cm x 5 cm quadrat around a marking stick in the centre of the plot. This experimental treatment mimics the occurrence of small dropping piles on the salt-marsh sward which mark plots where geese rested; therefore the treatment represents a maximal dropping addition within the range naturally observed at our sites within one season. The droppings added were not older than one hour and collected adjacent to the experimental site. Droppings were removed from the experimental plots after 10 days to prevent effects of shading or sheltering which might interfere with the fertilising effect. As an indication of the amount of nitrogen in the droppings at the start of the experiment and the nitrogen that had leached out within this 10-day period, we collected five bags with fresh droppings at the beginning of the experiment and 10 bags of droppings that were removed from the plots after 10 days from our study sites in the Wadden Sea and in Russia, one from each replicate exclosure. Droppings were dried at 60° C for 48 hours and subsequently ground and analysed for nitrogen content, using an automated CHNS-analyser (automated element analysis, Interscience EA 1110, New York, USA).

We obtained biomass data by combining tiller counts with tiller weights. From the 12 plots within a single exclosure, two were used as fixed plots for tiller counts, one with droppings and one without. The other 10 plots were harvested in five consecutive weeks to determine tiller weights and nitrogen content. In each exclosure ($N=10$) one plot with and one plot without experimentally added droppings was harvested each week. Each plot was never used more than once for harvesting tiller weights and quality in order to prevent effects from the tiller/leaf removal on biomass/quality. Net aboveground primary production (NAPP) was calculated as the difference in biomass between two consecutive harvests. Cumulative NAPP was calculated as the difference between the first and the last harvest (approximately 40 days for each study site).

On the two fixed plots we marked four small squares of 5cm x 5cm with toothpicks, immediately adjacent to the square on which droppings were added, or which was left empty in the control situation. In these squares tiller counts were conducted weekly. Tiller counts of the four squares were averaged per week and the number of tillers was multiplied by mean tiller weight. To determine tiller weight, samples of 50 tillers were collected from plots with and without added droppings within an enclosure. Samples were dried at 60°C for 48 hours and weighed on an analytical balance (Mettler Toledo AG204) to the nearest 0.1 mg. Samples of leaf tips (for *Festuca*) or whole shoots (for *Puccinellia* and *Carex*) were collected in order to determine nutritional quality as nitrogen content (%). Samples were dried at 60°C for 48 hours and thereafter ground to a fine powder. Samples were analysed for nitrogen content, using an automated CHNS-analyser (automated element analysis, Interscience EA 1110, New York, USA).

All data were tested for normal distribution. Nitrogen contents of the droppings at the start of the experiment and after 10 days were compared using an independent sample t-test. In order to compare plots with and without droppings, we used a repeated measurement ANOVA per site (and for the Russian site, per species) with biomass, production, quality or tiller density as dependent variables, measurement date as repeated factor and treatment as fixed factor. In order to analyse the effects of dropping additions on sward parameters for each measurement date, we used a multivariate ANOVA with treatment as a fixed factor.

Results

All data were normally distributed. There was a significant difference in the nitrogen content of the droppings that were added and the droppings that were collected after 10 days, both at the Wadden Sea site (3.20 ± 0.27 vs. 2.05 ± 0.13 , $t_{13} = 4.43$, $P < 0.001$) and at the Russian site (4.10 ± 0.76 vs. 2.64 ± 0.37 , $t_{13} = 2.28$, $P = 0.04$), unfortunately the relevant data for the Baltic site were incomplete. Our measurements revealed no significant effects of addition of droppings on biomass, production, tiller density or quality of the forage species at any of the three sites along the flyway over the entire measuring period (Table 8.1, Figure 8.2). Moreover, we did not find any significant differences for each measurement date ($P > 0.1$ in all cases).

Table 8.1: Results of a repeated measurement ANOVA testing the effect of added Barnacle Goose droppings on sward biomass (4 repeated measures), production (3 repeated measures), quality (4 repeated measures) and tiller density (4 repeated measures) of the main forage species, at three sites along the flyway: a staging site in the Wadden Sea, a stopover site in the Baltic Sea and a breeding site in Russia. Starting dates of the experiment were 21 March, 4 May and 21 June 2005, for the three sites, respectively.

Area	Species	Biomass		Production		Quality		Tillers	
		$F_{1,18}$	P	$F_{1,18}$	P	$F_{1,18}$	P	$F_{1,18}$	P
Wadden Sea	<i>Festuca rubra</i>	0.018	0.895	0.010	0.923	0.145	0.708	1.704	0.208
Baltic Sea	<i>Festuca rubra</i>	0.658	0.428	1.355	0.260	0.994	0.332	0.627	0.439
Russia	<i>Puccinellia phryganodes</i>	0.050	0.826	0.285	0.600	0.689	0.418	0.395	0.537
	<i>Carex subspathacea</i>	0.004	0.951	0.025	0.876	0.164	0.691	0.006	0.937

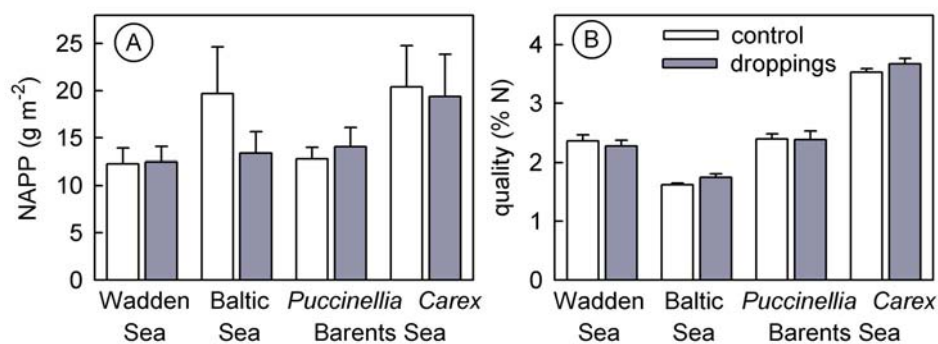


Figure 8.2: (A) Cumulative Net Aboveground Primary Production (NAPP in g m^{-2}) over the study period (4 weeks) and (B) Nutritional quality of the forage (% N per unit plant weight) at the end of the study period, for plots with and without droppings added on all study sites ($n=10$ in all sites). All differences are not significant.

Discussion

There are three conditions that must be fulfilled to induce an increased growth response in grasses fertilised by droppings; (1) growth is limited by nutrient availability (2) a rapid turnover of nutrients occurs in the rooting zone and (3) the plants can respond rapidly to increased nutrient availability (Jefferies 1994). On coastal Arctic locations, Bylot Island and Svalbard, no effect of goose grazing or droppings on plant production was found for several grass species (Gauthier *et al.* 1995, Beaulieu *et al.* 1996, Bakker and Loonen 1998). All three teams suggest that this is due to the thick moss layer in Arctic plant communities, which absorbs the nutrients from the faeces, preventing them from leaching to the soil. Similarly, Zellmer *et al.* (1993) suggested that the tufted growth form of the studied species prevented rapid turnover of nutrients. On our study sites in the Wadden Sea and the Baltic Sea no thick moss layer occurs, however, *Festuca rubra* forms a dense turf which might prevent droppings from making direct contact with the soil and nitrogen may be lost from the droppings as a result of the volatilisation of ammonia (Zellmer *et al.* 1993). Several studies on temperate salt marshes in the Wadden Sea show that addition of nitrogen and phosphorus had no effects on the biomass of *Festuca rubra* (Kiehl *et al.* 1997, Van Wijnen *et al.* 1999, Stahl *et al.* 2001, Chapter 3). Van Wijnen *et al.* (Van Wijnen *et al.* 1999) demonstrated that the total nitrogen input from goose droppings at our study site in the Wadden Sea is negligible when compared to the inorganic nitrogen released by mineralisation. From these studies, we conclude that *growth*, i.e. biomass accumulation, of *Festuca rubra* is not nutrient-limited at our Wadden Sea site. However, some studies show that fertilisation, either by gull droppings near a colony (Bazely *et al.* 1991) or by artificial fertiliser (Stahl *et al.* 2001, Chapter 3), can have an effect on the *nitrogen content* of *Festuca rubra*. Either the amount of nitrogen (and other nutrients) added to the vegetation in these studies was much higher than our experimental addition of droppings or (dissolved) fertilisers are more easily leached into the soil and made available for rapid recycling. Summarising, in our study the lack of growth response of *Festuca rubra* to experimentally added droppings can be explained by the absence of nitrogen limitation on the growth of this species, and by a lack of fast nutrient turnover enabling a rapid growth response.

Since there is no moss layer in the plant communities that were investigated at our Russian breeding site, we can exclude an interaction of moss and grass swards (Chapter 2). Earlier studies on the same site demonstrated that the growth of forage plants is enhanced by nutrient addition via artificial fertiliser, and we, therefore, conclude that growth is nutrient-limited (Stahl *et al.* 2001, Chapter 3). Moreover, since *Puccinellia phryganodes* and *Carex subspatheacea* were found to increase their production after fertilisation by droppings in the Canadian habitat of Lesser Snow Geese, we are aware of the capability of these plant species to respond rapidly to the addition of nutrients (Cargill and Jefferies 1984,

Bazely and Jefferies 1985, Hik and Jefferies 1990). A lack of response to fertilisation by droppings on our Russian study site may be explained by a difference in soil properties with the Canadian site that prevents rapid nutrient cycling.

We established an overview of studies on the effects of droppings and grazing on forage plants of different species of geese (Table 8.2). In La Pérouse Bay, Canada, Lesser Snow Geese were found to significantly enhance the production of *Puccinellia phryganodes* and *Carex subspathacea* by means of enhancing nitrogen cycling because of fertilisation from droppings (Cargill and Jefferies 1984, Bazely and Jefferies 1985, Hik and Jefferies 1990). Besides the studies in La Pérouse Bay there is only one other study that demonstrates a positive effect of faeces deposition (in combination with grazing) on biomass and productivity of the sward (Madsen 1989). A closer look reveals that the average cumulative grazing pressure (depicted as droppings $\text{m}^{-2} \text{day}^{-1}$) at these sites is much higher than on any other site, probably resulting in a higher total input of nitrogen from droppings as compared to all other sites. Additionally, nitrogen mineralisation rate, an indirect measure of productivity, in La Pérouse Bay is very low compared to other studies in which mineralisation has been measured (Table 8.2). Hik *et al.* (1991) showed that without addition of faeces *Puccinellia phryganodes* did not recover from biomass removal from grazing resulting in decreased biomass production. In comparison to the low natural availability of nitrogen on the marsh of La Pérouse Bay which limits plant (re)growth, and where the input of nitrogen from droppings is highly significant, the Wadden Sea study site receives significantly more input of nitrogen (Van Wijnen *et al.* 1999). Moreover, on the salt marsh of La Pérouse Bay the recycling of nitrogen in grazed patches, is facilitated by cyanobacteria that colonise bare, litter-free, patches of sediment (Bazely and Jefferies 1989). We have no data on mineralisation processes for our Russian study site or the presence and activity of cyanobacteria. The combination of abiotic and biotic properties in the salt marsh of La Pérouse Bay allows rapid recycling of the nutrients from goose droppings and their re-use by the vegetation within one season (Jefferies 1999). Our Russian study site apparently does not provide the right conditions for the forage species to be able to profit from fertilisation from droppings within one season.

A few other studies find positive effects of clipping or grazing on sward biomass, production and tillering. These studies indicate that the mechanical process of grazing can affect the growth of grasses even in the absence of a fertilising effect by droppings (Ruess *et al.* 1997, Fox *et al.* 1998). At our study site in the Wadden Sea, *Festuca rubra* increased tillering at a grazing intensity close to the natural grazing intensity on the marsh, which led to an increased potential harvest of plant material for the geese (Chapter 7). Increased nitrogen content of grazed, clipped or fertilised vegetation has been demonstrated in many studies (Table 8.2). The removal of leaves retards senescence, resulting in a higher nitrogen content in grazed plants, as compared to ungrazed plants.

We conclude from our experimental evidence that fertilisation by droppings does not affect forage plant biomass, production, tillering or nitrogen content at the main staging sites of Barnacle Geese along the East Atlantic Flyway.

Acknowledgements

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One of the fixed plots, repeatedly used for counting tillers, just after dropping addition. (Schiermonnikoog).

Table 8.2: Compilation of studies on the effects of droppings and grazing together and separately by geese on vegetation properties. Effects on: B – Biomass, P–NAPP, N– Nitrogen content, T– Tillering. Grazing and vegetation characteristics of the study sites are given. Grazing characteristics: Int. – grazing intensity (# droppings m⁻² d⁻¹), Per. – grazing period (days). Vegetation characteristics (all for an ungrazed sward): B – Peak biomass (g m⁻²), P – NAPP (g m⁻² d⁻¹), N – Peak Nitrogen content (%), M – Net Mineralisation Rate (g N m⁻² d⁻¹).

Plant species	Latitude		Grazing			Vegetation:			Effect on:			
	Site	(°N)	Int.	Per.	B	P	N	M	B	P	N	T
Combined effect of droppings and grazing												
<i>Calamagrostis deschampsii</i>	La Pérouse Bay, Ca ¹⁹	58	0.6 ⁵	100	160	0.7	2.2	1 ¹⁷	0	0	0	
<i>Carex subspathacea</i>	La Pérouse Bay, Ca ⁵	58	0.6 ⁵	100	69 ⁵	0.5 ⁵	4 ⁵	3-6 ¹⁷	-	+	+	0 ¹⁰
<i>C. subspathacea</i>	La Pérouse Bay, Ca ¹⁹	58	0.6 ⁵	100	80	0.5	2.8	1 ¹⁷	0	0	0	
<i>Dupontia fisheri</i>	Bylot Island, NWT, Ca ⁷	73	0.03-0.2	60	25	0.3	3		-	-	+	
<i>Eriophorum scheuchzeri</i>	Bylot Island, NWT, Ca ⁷	73	0.03-0.2	60	15	0.2	3.7		-	0	+	
<i>Festuca rubra</i>	La Pérouse Bay, Ca ¹⁹	58	0.6 ⁵	100	80	0.8	1.9	1 ¹⁷	0	0	0	
<i>Poa Arctica</i>	Ny Ålesund, Svalbard ¹	78	0.3 ¹⁵	90	3.4	0.06	2.7		-	0		0
<i>Puccinellia phryganodes</i>	La Pérouse Bay, Ca ^{5,8}	58	0.6 ⁵	100	92 ⁵	0.6 ⁵	2.5 ⁵	3-6 ¹⁷	-	+	+	+ ³
Grazing experiment: effects of droppings/grazing												
<i>Carex ramenskii</i>	Cook Inlet, Alaska ¹⁸	61	0.1	15	80	-	2	10	0/0		0/0	
<i>D. fisheri</i>	Bylot Island, NWT, Ca ⁴	73	0.03-0.2 ⁷	60	25 ⁷	0.3 ⁷	3 ⁷		0/0	0/0	0/+	0/0
<i>E. scheuchzeri</i>	Bylot Island, NWT, Ca ⁴	73	0.03-0.2 ⁷	60	15 ⁷	0.2 ⁷	3.7 ⁷		0/0	0/0	0/+	0/0
<i>P. phryganodes</i>	La Pérouse Bay, Ca ⁸	58	0.6 ⁵	100	92 ⁵	0.6 ⁵	2.5 ⁵	3-6 ¹⁷	0/0	+ /0	+ /-	
<i>Triglochin maritima</i>	Cook Inlet, Alaska ¹⁸	61	0.1	15	120	-	2.6	10	0/0		0/0	

Table 8.2 continued

Plant species	Latitude		(^N)	Grazing		Vegetation:				Effect on:			
	Site			Int.	Per.	B	P	N	M	B	P	N	T
Fertilising studies: effect of droppings													
<i>C. subspathacea</i>		La Pérouse Bay, Ca ²	58 ¹	0.6 ⁵	100	69 ⁵	0.5 ⁵	4 ⁵	3-6 ¹⁷	+	+	+	
<i>C. subspathacea</i>		Tobseada, Russia ²⁰	68	0.37	90	28	0.8	3.6		0	0	0	0
<i>F. rubra</i>		Gotland, Sweden ²⁰	57	0.15	40	40	0.9	2		0	0	0	0
<i>F. rubra</i>		Schiernonnik-oog, Nl ²⁰	53	0.07	40	23	0.33	3	60 ¹⁷	0	0	0	0
<i>Puccinellia maritima</i>		Langli, Dk ¹¹	55	0.4-0.9	70	30	0.8-1.6	5		+	+		
<i>P. phryganodes</i>		La Pérouse Bay, Ca ²	58 ¹	0.6	100	92 ⁵	0.6 ⁵	2.5 ⁵	3-6 ¹⁷	+	+	+	
<i>P. phryganodes</i>		Tobseada, Russia ²⁰	68	0.37	90	23	0.5	3.4		0	0	0	0
Clipping/Only grazing: effects of grazing													
<i>C. ramenskii</i>		Yukon-Kuskokwim River Delta, Alaska ¹³	61	0.2	60	250	3	0.8		+	+	+	0
<i>C. subspathacea</i>		La Pérouse Bay, Ca ⁹	58	0.6 ⁵	100	69 ⁵	0.5 ⁵	4 ⁵	3-6 ¹⁷	-	-	-	-
<i>F. rubra</i>		Schiernonnik-oog, Nl ¹⁴	53	0.07	40	23	0.33	3	30 ¹⁶	+	+	0	+
<i>Phleum pratense</i>		Borgarfjörður, Iceland ⁶	64		25							+	
<i>P. phryganodes</i>		La Pérouse Bay, Ca ⁹	58	0.6 ⁵	100	92 ⁵	0.6 ⁵	2.5 ⁵	3-6 ¹⁷	-	-	-	+

(1) Bakker and Loonen 1998; (2) Bazely and Jeffries 1985; (3) Bazely and Jeffries 1989; (4) Beaulieu *et al.* 1996; (5) Cargill and Jeffries 1984b; (6) Fox *et al.* 1998; (7) Gauthier *et al.* 1995; (8) Hik and Jeffries 1990; (9) Hik *et al.* 1991; (10) Kotanen and Jeffries 1987; (11) Madsen 1989; (12) Mulder and Ruess 1998; (13) Ruess *et al.* 1997; (14) Van der Graaf *et al.* 2005 *Chapter 7*; (15) Van der Wal and Loonen 1998; (16) Van Wijnen *et al.* 1999; (17) Wilson and Jeffries; (18) Zacheis *et al.* 2002; (19) Zellmer *et al.* 1993; (20) this study



Measurements on Gotland: Robert Buitenwerf, Julia Stahl and Sandra van der Graaf

Changing tides through climate change: Can migratory herbivores keep up with an advancing green wave of spring growth?

Alexandra J. van der Graaf and Julia Stahl

Abstract

The influence of climate change on the life histories of many species in temperate and Arctic regions is inevitably becoming more severe. Through trophic cascades, a changing phenology of plants affects primary and secondary consumers. Barnacle Geese, *Branta leucopsis*, are migratory herbivores, following consecutive waves of fresh spring growth of forage plants on their journey from temperate wintering to arctic breeding sites. At each stopover they time their staging to profit maximally from the spring production and the temporarily high quality of forage grasses. Temperature rise will advance the onset of spring growth. But can these migratory herbivores keep up with advancing food peaks?

Here we analyse weather data along the East Atlantic flyway during the past 30 years. We compare weather patterns of the traditional staging sites in order to assess the predictability of spring temperatures and food availability en route. We report on field experiments with portable green houses at three important staging sites along the flyway, in which a small temperature rise was induced in early spring and the growth responses of forage plant species were measured.

We show a correlation in weather patterns between sites. Plant growth is significantly advanced by small increases of spring temperatures and is closely related to cumulative spring temperatures. This allows predicting circumstances at the following migratory destination. An analysis of migration patterns of the geese demonstrates that timing of migration is advanced in warmer years; however this advancement does not match the advancement of plant growth at all staging sites. We discuss the capability of geese to keep up with the advancing green wave and other temperature induced changes and review alternative migration strategies that recently developed in this migratory species.

Submitted

Introduction

Temperature rise has become evident during the last century (IPCC 2001). The temperature increase is reflected in changes in phenology, in plants as well as in animals. Long-term phenological records show advancement in leaf appearance, flowering and first appearance dates of birds, butterflies and amphibians over the past century (Sparks and Carey 1995; Sparks *et al.* 2005b). Onset of spring growth of plants in cool and temperate areas mainly depends on spring temperatures (Botta *et al.* 2000). Plant growth at northern latitudes increased during the 1980's (Myneni *et al.* 1997), most likely related to the earlier disappearance of snow. At both Arctic and temperate latitudes, advancements in the start of spring has affected leaf appearance, flowering dates and fruit ripening as well as the length of the growing seasons, all of which have been related to the increased spring temperatures (Schwartz 1994; Sparks and Carey 1995; Myneni *et al.* 1997; Post and Stenseth 1999; Menzel and Fabian 1999; Menzel *et al.* 2001; Fitter and Fitter 2002; Menzel 2003).

When spring growth of plants is advanced, herbivores that depend on peaks of spring growth and quality of their forage will be forced to advance their life cycles also, as will the predators that feed on these herbivores. An example is given by Buse *et al.* (1999); winter moths (*Operophtera brumata*) feed on the young leaves of the pendunculate oak (*Quercus robur*) and are themselves the main food for great and blue tits (*Parus major* and *Parus caeruleus*) during chick rearing. With increasing spring temperatures bud burst advanced in oak, and winter moths advanced their hatching dates simultaneously, which forced the birds to advance their laying dates. A lack of synchrony with food resources may result in reduced individual fitness, possibly leading to a reduction in population size.

Many bird species have advanced their migration and breeding dates with increasing spring temperatures (Crick and Sparks 1999; Lehikoinen *et al.* 2004; Dunn 2004; Marra *et al.* 2005; Sparks *et al.* 2005a). Some bird species, such as great tits and pied flycatchers (*Ficedula hypoleuca*) advanced their breeding dates, although not sufficiently to keep up with the advancing peak in food availability (Buse *et al.* 1999; Both and Visser 2001; Visser and Holleman 2001; Visser *et al.* 2004). It is suggested that long-distance migrants (e.g. pied flycatchers) are not able to adapt to climate change, since they cannot predict weather on their breeding sites from that at their wintering sites in Africa (Both and Visser 2001; Coppack and Both 2002; Butler 2003). On the other hand short-distance migrants are better able to predict circumstances in their breeding sites and have advanced their migration date appropriately (Butler 2003).

It thus seems that there are two important factors for birds to adapt to climate change, flexibility and predictability. First of all the timing of the birds needs to be flexible, based on environmental parameters rather than on fixed cues such as photoperiod. Second, the birds must be able to predict circumstances further along their migration route. Here, strong correlations of weather phenomena between consecutive sites will be of utmost importance.

Barnacle Geese, *Branta leucopsis*, depend on seasonal peaks of spring forage availability for successful breeding. They migrate north following consecutive waves of fresh spring growth of their forage plants (Figure 9.1; Chapter 5). At each stopover site they time their arrival to maximise their profit from the temporarily high spring production and the high nutrient content of the forage grasses in order to gain more fat reserves (Prop 2004; Hübner 2006). Individual geese that leave their staging sites in a better condition have a higher reproductive output (Ebbinge and Spaans 1995; Prop and Black 1998). For Barnacle Geese it will thus be extremely important to keep up with advancing spring phenology. However, it is not known whether the geese time their migration based on fixed cues such as photoperiod or on more variable factors such as weather or food conditions at each site. Neither do we know whether weather patterns are linked or predictable from one staging site to the next along the flyway. The population of Barnacle Geese has increased considerably since the 1980's (Ganter *et al.* 1999). Along with the overall growth of the population the geese expanded their breeding range and breeding colonies now occur along most of the northern coast of Russia, in the Baltic Sea and in the Dutch delta (Larsson *et al.* 1988; Filchagov and Leonovich 1992; Syroechkovsky Jr. 1995; Leito 1996; Ganter *et al.* 1999; Chapter 10). Part of the population nowadays does not follow the traditional routes and travel schedules (Eichhorn *et al.* 2006). However, we here focus on the traditional migration route and schedules.

In the present study we will first examine the effects of temperature increase on the growth of forage plants of Barnacle Geese at their different staging and stopover sites. We use this information for predictions about the shift in food availability with increasing temperatures. Secondly, we will investigate how predictable weather and forage availability are along the flyway and, finally, whether geese show flexibility in their ability to adjust to seasonal differences between years so that they time their arrival on the breeding grounds to coincide with the onset of spring growth. We attempt to analyse whether Barnacle Geese will be able to adapt to the imminent climatic changes occurring along their flyway at present. Our study is the first to assess the effects of global warming on migratory herbivores that directly depend on the spring phenology of forage plants.

Methods

Study sites

Barnacle Geese traditionally migrate from their wintering quarters in the Wadden Sea in western Europe (The Netherlands, Germany) to breeding sites in northern Russia (e.g. Novaya Zembyla). On their migration they use several sites in the Baltic Sea (Sweden, Estonia) and in the White Sea (Russia) as stopover for resting and refuelling (Leito 1996; Ganter *et al.* 1999). In all areas they use coastal salt marshes as well as adjacent agricultural pastures for foraging. We will focus mainly on three sites along the migration route (Figure 9.1, Table 9.1). The first site is on the Dutch island of Schiermonnikoog in the Wadden Sea, which is a winter and spring staging site for Barnacle Geese (Box 1). Geese arrive in October and forage on inland pastures and coastal salt marshes until their departure in mid-April. The diet of the geese mainly consists of Red Fescue, *Festuca rubra* (90%). The second site is a stopover site in the western Baltic Sea on the island of Gotland in Sweden (Box 2). The geese stay for a period up to 4 weeks in April and May, before continuing their migration towards the breeding grounds. The geese forage in the salt marshes, mainly in areas with a mixed sward of *Festuca rubra* and *Juncus gerardi*. These species make up respectively 45 and 15 % of the diet on this site (own data). The last site is a breeding site in northern Russia near the village of Tobseida in Kolokolkova Bay. Here, the main vegetation type that is used by the geese consists of a mixture of *Carex subspathacea* and *Puccinellia phryganodes* (Chapter 2), the diet contains these species in equal proportions (own data from Kolokolkova Bay).

Table 9.1: Overview of the study sites and the locations of the weather stations of which we obtained long-term (1950-2004) and short-term (2003/2004) weather data.

Staging Sites	Experimental Area		Weather data – long term		Weather data – short term	
Wadden Sea	Schiermonnikoog,	53°30N	Schiermonnikoog,	53°30N	Schiermonnikoog,	53°30N
	The Netherlands	6°10E	The Netherlands [#]	6°10E	The Netherlands [#]	6°10E
Baltic Sea –	Grötlingboudd,	57°07N	Hoburgen,	56°55N	Hoburgen,	56°55N
Sweden	Gotland	18°27E	Gotland ^{##}	18°09E	Gotland ^{##}	18°09E
White Sea	-		Archangelsk *	64°35N	-	
				40°30E		
Pechora	Tobseida	68°35N	Nar'yan Mar *	67°38N	Khodovarikha **	68°57N
Delta		52°20E		53°03E		53°45E

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^{##} Swedish Meteorological and Hydrological Institute SMHI, Norrköping, Sweden

* European Climate Assessment and Dataset, <http://eca.knmi.nl>

** Russian weather server, <http://meteo.infospace.ru/main.htm>

Experiment

At all three study sites, we conducted the same experiment to test the effect of increased temperature on the growth of forage plants. At all sites we selected an area that was frequently used by foraging geese. To raise air temperature, greenhouses of a modified ‘cloche’ type (Strathdee and Bale 1993; Dormann *et al.* 2004) were used, consisting of an open cylinder (65 cm diameter, 30 cm height) made out of acrylic glass (2 mm), covered with water- and gas-permeable cloth (insect mesh). The insect mesh reduced incoming light with about 9% on cloudy days (inside vs. outside greenhouse: 11667 Lux vs. 12667 Lux) and about 19% on bright days (28667 Lux vs. 24000 Lux). In close vicinity to the greenhouse, we established a similar sized control plot. The control plot was protected from grazing by a chicken wire fence of 50 cm height. A 4-channel data logger (HOBO H8-006-04, Onset Computer Corporation) was installed on each site, measuring air (at 15 cm height) and soil temperatures (at 2 cm depth) inside and outside the greenhouses. The experiment was conducted in 2003 on the Russian breeding site ($N = 5$) and in 2004 on the Wadden Sea staging site ($N = 5$) and on the Baltic stopover site ($N = 5$), distance between the replicates was at all sites more than 10 metres.

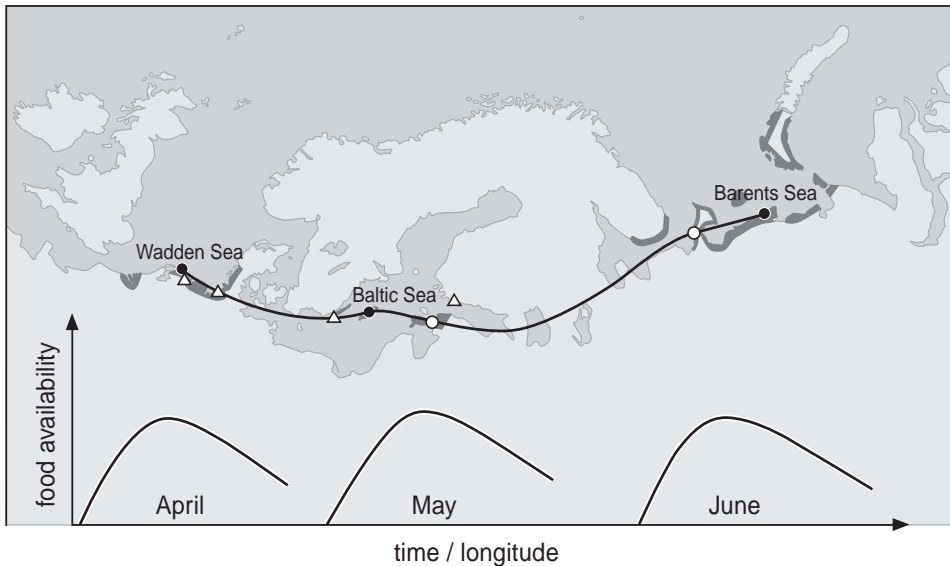


Figure 9.1: Map of the flyway of the Barnacle Goose and a schematic overview of the green-wave hypothesis (Chapter 5). Breeding sites are given with dark grey shading. Closed circles are the experimental sites, open circles indicate additional stopover sites. Arrows show the sites for which we obtained migration data

To measure plant growth, we used a very detailed, non-destructive method, to allow repeated measurements on the same plot. We counted tillers in 10 fixed squares of 5.5 by 5.5 cm in each greenhouse and in a paired control plot every 10-14 days. Tiller counts of the 10 squares within each plot were averaged to avoid pseudo-replication. Additionally, we collected 30 tillers from each greenhouse and control plot to assess individual tiller weights. For collecting tillers we randomly selected a point and collected tillers around that point up to a maximum sample of 30 tillers, in order to achieve a representative sample of tiller sizes. Tillers were dried at 60°C for 48 hours and weighed. The combination of tiller density and tiller weight provides a measure of plant biomass. In the Baltic and Russian area, where two species were abundant in the experimental plots, both species were measured separately.

Long-term climate and migration data

Climate change models predict an increase in globally averaged temperatures of 0.8-2.6 °C for the period of 1990-2050, long-term predictions up to the year 2100 even predict an increase of 1.4–5.8 °C (IPCC 2001). For Arctic regions this increase is predicted to be even stronger, an increase of 2. -14 °C for winter and 4.0-7.5 °C for summer temperatures (IPCC 2001).

Long- and short-term climate data were gathered from several weather stations along the flyway of the Barnacle Goose (Table 9.1). We used daily mean temperatures to calculate growing degree days (GDD), the accumulated product of time and temperature. This is a measure that is frequently used in phenological studies to predict start of flowering or emergence. As starting point we used the 1st of January of each year and we used a threshold temperature of -5°C (Botta *et al.* 2000). Whenever available (see Table 9.1), data from 1970 until present were used.

Long-term data on mass migration of Barnacle Geese along the flyway were gathered from the Hamburger Hallig, Germany (1988-1997; Stock and Hofeditz 2002) and from Eemshaven, The Netherlands (1999-2002, data Kees Koffijberg –SOVON). For all sites and all years, we used the date at which 75% of the Barnacle Geese observed at that site had travelled through the site previously (75% of total migration). Data from Eemshaven and Hamburger Hallig were combined and represent the departure date from the Wadden Sea. We obtained data on peak migration days over southern Finland from Lintukymi, the annual reports of the Kymenlaakso Birding Society (1990-2004). Data on peak hatch and nest initiation were obtained from Gotland, Sweden (1985-2004, pers. comm. Henk van der Jeugd and Kjell Larsson) and Tobseda, Russia (2002-2004, pers. comm. Henk van der Jeugd and Götz Eichhorn).

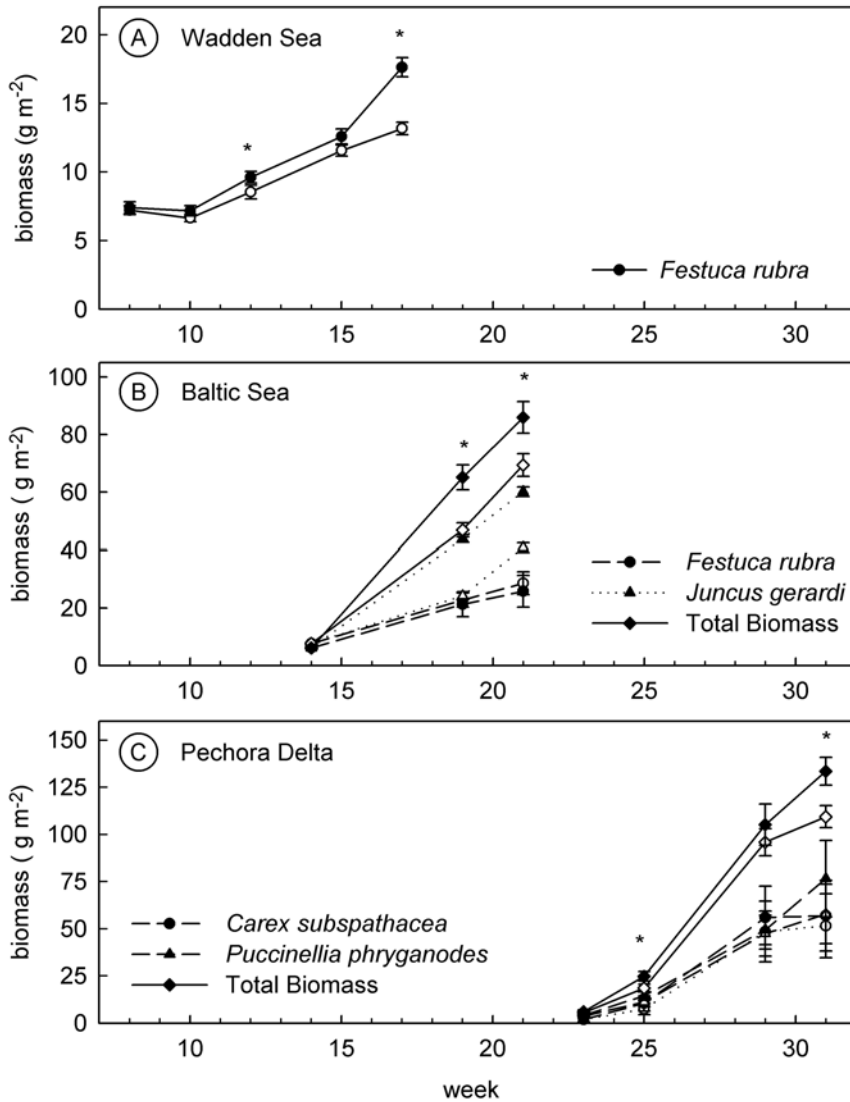


Figure 9.2: Biomass with (closed symbols) and without (open symbols) increased temperatures; (A) for *Festuca rubra* in the Wadden Sea, (B) for *Festuca rubra*, *Juncus gerardi* and total biomass in the Baltic Sea and (C) for *Puccinellia phryganodes*, *Carex subspathacea* and total biomass in the Pechora Delta. * indicate significant differences in total biomass between the control and the increased temperature treatment in that week ($P < 0.05$).

Table 9.2: Average air and soil temperatures ($^{\circ}\text{C} \pm se$) over the experimental period and the temperature increase inside the greenhouses. Average temperature increase is a weighed average, taking into account the number of measuring days at each site. All comparisons between unmanipulated average temperatures and manipulated increased temperatures are highly significant (paired t -test, $N = \#$ days, $P < 0.0001$).

	Experimental Period (day/month, year)	Air Temperature ($^{\circ}\text{C}$)		Soil Temperature ($^{\circ}\text{C}$)	
		Average Control	Increase Greenhouse	Average Control	Increase Greenhouse
Wadden Sea	20/2 – 19/4, 2004	6.79 ± 0.47	0.75	6.51 ± 0.40	0.82
Baltic Sea	7/5 – 20/5, 2004	10.43 ± 0.69	1.20	13.12 ± 0.40	1.25
Pechora Delta	8/6 – 31/7, 2003	8.68 ± 0.71	1.30	7.41 ± 0.55	1.10
Average Increase			1.08		1.06

Statistics

Data on plant growth were tested for normal distribution. When the assumption of normality was not met we applied the following transformations to allow statistical testing: Data from the Wadden Sea staging site and the Russian breeding site were \log_{10} -transformed; data from the Baltic stopover site were squareroot- transformed. Data on plant growth from all sites were analysed using a repeated measurement ANOVA with week as the repeated factor and treatment and replicate within treatment as factors. To analyse the effects of the treatment for each week separately we used a multivariate ANOVA with treatment and replicate within treatment as factors.

Results

Temperature effects on spring biomass

The greenhouses elevated temperature an average of 1°C (Table 9.2). The experimental temperature rise differed slightly between sites, and at each site there was a high variation in temperature from day-to-day. This variance is mainly caused by differing light levels (i.e. day length and direct exposure to sunlight). In general, temperature increase was higher at higher ambient temperatures.

On all sites total biomass of foraging plants was significantly increased by the imposed temperature elevation (Table 9.3, Figure 9.2), except for *Festuca rubra* in the Baltic site (Figure 9.2B). We used a stepwise linear regression to test whether plant growth was dependent on values of growing degree days (GDD) or date. The analyses showed that, along the entire flyway, biomass was better predicted by GDD than by date (Figure 9.3, $P < 0.005$), therefore we used only the relationship between GDD and plant growth for the

following analyses. From our data, we were able to predict biomass at all sites along the flyway for a given date in any year, whenever temperature records are available in order to calculate GDD. We used these relationships to predict biomass for different migration dates and dates of peak hatch and subsequently to calculate the advancement of plant growth under a climate change scenario of 1°C temperature rise, in days per °C (Table 9.5).

Table 9.3: Effects of temperature increase (treatment) on biomass of the study species along the migration route.

Site	Species	Replicate within Treatment			Treatment		
		df	F	P	df	F	P
Wadden Sea							
	<i>Festuca rubra</i>	8,90	5.890	<0.001	1,90	7.843	=0.006
Baltic Sea							
	<i>Festuca rubra</i>	8,90	4.223	<0.001	1,90	2.821	=0.097
	<i>Juncus gerardi</i>	8,90	64.371	<0.001	1,90	40.805	<0.001
	Total Biomass	8,90	36.187	<0.001	1,90	23.528	<0.001
Pechora Delta							
	<i>Puccinellia phryganodes</i>	8,40	25.754	<0.001	1,40	90.748	<0.001
	<i>Carex subspathacea</i>	8,40	22.051	<0.001	1,40	11.718	=0.001
	Total Biomass	8,40	7.488	<0.001	1,40	187.077	<0.001

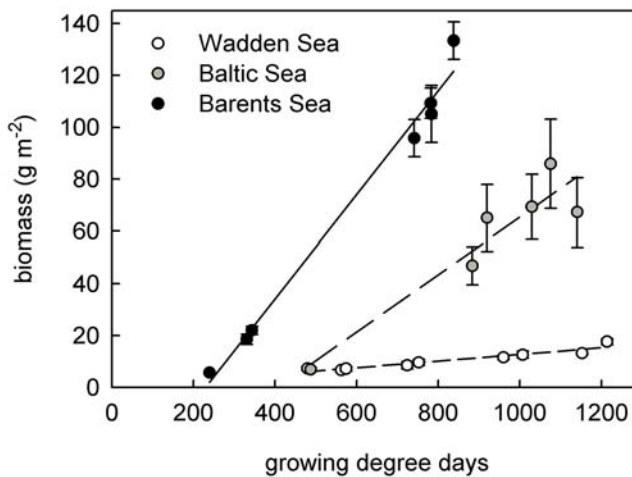


Figure 9.3: The dependence of biomass on growing degree days (GDD) for three areas along the flyway. Regression lines are shown for all areas. Regression line equations (with BM being biomass) are: for the Wadden Sea $BM_{wad}=1.614+0.022GDD$ ($R^2=0.662$, $F_{1,48}=129.371$, $P<0.001$), Baltic Sea $BM_{bal}=-10.867+0.191GDD$ ($R^2=0.588$, $F_{1,33}=73.710$, $P=0.003$) and the Russian breeding site $BM_{rus}=0.225+0.245GDD$ ($R^2=0.860$, $F_{1,63}=202.995$, $P<0.001$).

Table 9.4: Correlation (R^2) between growing degree days (GDD) at the different consecutive locations. Framed blocks indicate the timing of the start of migration from a current site towards a subsequent site. * $P \leq 0.05$, ** $P \leq 0.005$, *** $P \leq 0.001$.

Current Month/ Location		Next month/location					
		March	April		May		June
		Baltic Sea	Baltic Sea	White Sea	White Sea	Pechora	Pechora
March	Wadden Sea	0.69 ***	0.70 ***	0.34 ***	0.15 *	0.09	0.11
April	Baltic Sea			0.51 ***	0.35 ***	0.19 *	0.26 **
May	White Sea					0.60***	0.50 ***
	Pechora						0.78 ***

Spring temperature trends and migratory schedules

GDD is positively correlated between staging sites along the flyway (Table 9.4). The predictability between consecutive sites is 50 to 80%. For the Wadden Sea and Baltic Sea areas, GDD up to April 30th correlates significantly with year ($R^2=0.33$, $P=0.001$ and $R^2=0.14$, $P=0.024$, respectively), demonstrating an increase in spring temperature over the past decades in western/northern Europe. For the Russian areas, no such trend is detectable.

GDD was significantly correlated with the migration dates of the geese. We found that the timing of the migration was best correlated with the GDD from January 1st until the average date of departure. This was end of March for the Wadden Sea ($R^2=0.71$, $P<0.001$, $N=14$) and mid-May for the departure from the Baltic Sea ($R^2=0.45$, $P=0.004$, $N=16$). Peak hatch for the Baltic breeding colonies was best correlated with GDD from January 1st until egg laying (end of April, $R^2=0.82$, $P<0.001$, $N=19$). Departure from the Wadden Sea and the Baltic Sea, as well as breeding date in the Baltic Sea is significantly advanced in years with higher spring temperatures (Figure 9.4). We used a univariate ANOVA with both year and GDD as covariates and included year to control for any trends in migration date that are not temperature-related. For all correlations, year did not have a significant effect on departure dates, when tested together with temperature. We, therefore, show only relationships between temperature and migration. Departure from the Wadden Sea showed a variation of about one month (Figure 9.4A), whereas departure from the Baltic was spread over only a 10-day period (Figure 9.4C). Temperature-related advancement of migration, in days per °C, was calculated from the slopes of Figure 9.4. At departure from the Wadden Sea, advancement of migration is about 10 days per °C, whereas at departure from the Baltic Sea this is only 2 days (Table 9.5). Migration advancement in the Wadden Sea matches the advancement of plant growth, whereas further along the flyway, the timing of departure from the Baltic Sea does not advance as much as plant growth. The geese that follow a different strategy and breed in the Baltic also do not advance their laying dates as much as plant growth is advanced (Table 9.5).

The staging duration in the Baltic Sea area was calculated from departure dates in the Wadden Sea and dates of mass migration over Finland, when birds leave the Baltic Sea area. We found a strong negative relationship ($R^2 = 0.95$, $P < 0.001$) between the moment that the geese leave the Wadden Sea and the duration of their stay in the Baltic Sea (see also Eichhorn *et al.* 2006).

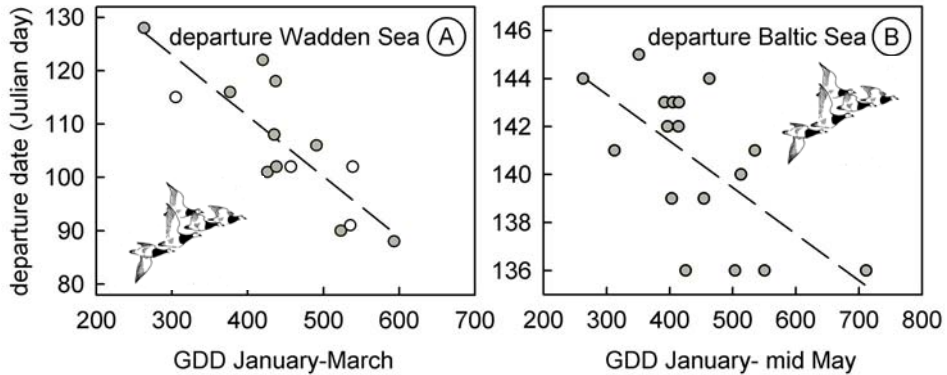


Figure 9.4: Correlation of growing degree days (GDD) with (A) departure from the Wadden Sea – grey dots are data from the Hamburger Hallig (D), open dots from Eemshaven (NL), Departure Day = $208.9 - 0.114 \cdot \text{GDD}_{\text{march}}$ ($R^2=0.71$, $P<0.001$) (B) departure from the Baltic Sea, Departure Day = $155.6 - 0.014 \cdot \text{GDD}_{\text{midmay}}$ ($R^2=0.45$, $P=0.004$).

Table 9.5: Traditional timing of peak spring grazing pressure, migration and peak hatch (average over N years), and the advancement of vegetation growth and goose migration with a 1-degree temperature rise scenario. Timing in brackets give estimated dates, the advancements derived from these dates are, therefore, less reliable (also between brackets).

	Traditional		Advancement (days °C ⁻¹)	
	Timing	N	Vegetation	Geese
Wadden Sea				
departure	April 16 th	14	8	10.2
Baltic Sea				
(arrival)	(April 20 th)	(16)	(11)	-
departure	May 20 th	16	8	1.9
peak hatch	May 29 th	19	8	2.2
Pechora Delta				
arrival	(June 1 st)	(3)	(5)	-
peak hatch	July 11 th	3	4	-

Discussion

Changing tides: advanced spring growth differs along the flyway

In all sites plant growth was enhanced by the increased temperature in the greenhouses. We found that biomass was most closely related to growing degree days (Figure 9.3). Under a scenario of temperature rise by 1 °C (current prediction of IPCC 2001 for the period up to 2050), plant growth will be advanced by eight days in the Wadden Sea and Baltic Sea. At the Russian breeding site, a similar temperature rise will only result in an advancement of four days, due to the strong influence of below-zero temperatures well into the month of May. Under more extreme scenarios (IPCC 2001), plant growth would be even more advanced. In Chapter 5 I showed that Barnacle Geese follow a green wave of spring growth on their spring migration, profiting from peaks in food availability and quality when leaving their spring staging sites, during their stay on the stopover sites and at peak hatch. Our results demonstrate that temperature rise will not have the same effect at different sites along the flyway. With increasing temperatures due to climate change, the green wave of spring growth will, therefore, not advance synchronously along the flyway and food pulses become increasingly difficult to track by migrating herbivores. Similar results were obtained by a study using NDVI data to investigate regional climate change impact in Fennoscandia, Denmark and the Kola Peninsula (Høgda *et al.* 2001). In their paper, Høgda *et al.* (2001) predicted for our Baltic site an even larger advancement of spring than we found, of about 2-4 weeks. In contrast, predictions for the Kola Peninsula (Russia) were no advancement, or even locally a delay in the onset of spring.

Predictability of plant growth and flexibility of migration schedules

Weather patterns in the Wadden and Baltic Sea, as well as in the Russian areas are closely correlated (Table 9.4). However, weather patterns show a lower correlation between the Baltic Sea and the Russian areas (Table 9.4). Predictability of weather and thus of plant growth is high between the Wadden Sea and the Baltic Sea and within the Russian areas, but lower between the Baltic and the White Sea. We expect that goose migration is better matched to spring phenology for these parts of the migration with a high predictability. This is supported by our finding that the geese time their migration from the Wadden to the Baltic Sea accurately with the spring temperatures experienced over the past months and with plant phenology (Table 9.5). In contrast, migration from the Baltic does not seem to be linked to spring phenology. Similarly, Gordo *et al.* (2005) showed for six trans-Saharan migrants that timing of migration was very closely linked to climate in the wintering quarters during the months preceding migration, rather than that in their potential European breeding grounds. However, Ahola *et al.* (2004) showed for the Pied Flycatcher (*Ficedula hypoleuca*) that timing of migration is can be further influenced by temperatures along the migration route.

The large year-to-year variation in departure dates from the Wadden Sea (Figure 9.4A) shows that the geese are very flexible in their timing of this migration step. Apparently, timing of migration from the Wadden Sea to the Baltic Sea is mainly based on weather or vegetation parameters. We thus expect that Barnacle Geese will adjust the timing of migration when temperature increases through climate change. There are no data available on migration within Russia but we expect similar processes there.

The critical step on the migration route thus seems to be the step from the Baltic to the White Sea, where weather patterns between the two areas are uncoupled. Departure from the Baltic Sea shows little variation (Figure 9.4B). In years that geese arrive later in the Baltic Sea due to low spring temperatures, they shorten their stay in the Baltic. The range of departure dates is restricted to a period of only 10 days in all years. Based on these rather fixed departure dates from the Baltic Sea and on the low predictability of the weather and plant growth on the next staging site (Table 9.4), we conclude that migratory timing cannot be ideal in all years. The geese do not advance their migration according to the advancement of plant growth at their departure site in the Baltic Sea. (Table 9.5). Since variation in departure from the Baltic is so small, we suggest that this trait is based on fixed cues, such as photoperiod, rather than on phenological cues at a preceding site along the route. It is interesting to note, that the advancement of migration by about 2 days per °C when departing from the Baltic Sea is within the range of temperature related migration advancements found for many other bird species (Crick and Sparks 1999; Sparks and Menzel 2002; Marra *et al.* 2005).

Keeping up with the green wave under climate change

In conclusion, our data show that part of the Barnacle Goose migration is flexible and that this species of Arctic breeding goose will likely be able to adapt to elevated temperatures as far as the timing of the migration is concerned. On the first step on the migration route, from the Wadden to the Baltic Seas, the geese will still be able to follow the green wave of spring growth, even when the wave itself advances. The timing of the step between the Baltic and White Sea is obviously based on rather fixed cues. We, therefore, expect that under a scenario of a strong temperature increase at the Arctic breeding sites, the geese will not be able to adjust their departure date from the Baltic Sea accordingly. This is especially true if climate change will not result in complementary increases of temperatures at each staging site but a higher rise of temperatures at the Arctic site, as is predicted (IPCC 2001). However, when the geese leave the Baltic Sea, the average GDD on their breeding site is 225 ± 23 GDD, which is still below the threshold for onset of growth of 240 GDD (Botta *et al.* 2000). In general there is a gap of at least two weeks between departure from the Baltic Sea (mid- to late- May) and arrival in the Russian breeding areas (early- to mid-June). The geese are known to spend this time in the White Sea area, or in areas even closer to their breeding sites. It is suggested that from these so-called ‘pre-breeding areas’ the geese can

more accurately predict circumstances at their breeding sites and adjust their arrival to snow melt and plant growth at the colony site (Sedinger and Raveling 1986; Hübner 2006). Unfortunately, we have no time series of either migration or breeding dates of Barnacle Geese in the Russian Arctic, and it is therefore not known how flexible the duration of stay is in these areas. For the Russian breeding sites, we cannot relate advancement in plant growth to advancement of hatching dates. However, in the Canadian Arctic several goose species advanced their nest initiation date in relation to climate change (Macinnes *et al.* 1990; Cooke *et al.* 1995; Skinner *et al.* 1998). Following calculations by Cooke *et al.* (1995) we find that Lesser Snow Geese, *Anser caerulescens caerulescens*, advance their laying dates by about 10 days per degree temperature increase. Barnacle Geese, breeding in the Baltic, also advance their laying dates with increasing spring temperatures (H.P. van der Jeugd and K. Larsson, unpublished data) although this advancement seems insufficient to compensate for the advancement of plant growth (Table 9.5).

Climate change may affect the plant community

In our study, we investigated the effects of elevated temperatures on the growth of food species and the repercussions for forage availability for small herbivores. Our experiments were limited to the most important forage species, but even with the limitations of this experimental design we observed a shift in the relative abundance of the species. At the Baltic site, *Juncus gerardi* became dominant over the main food species, *Festuca rubra*, which profited less from the elevated temperatures. This is an indication of the potential disruption of the competitive balance of species through climate change. Recent studies show that elevated temperatures and the resulting elevated soil temperature will change the abundances of species and, over the long-term, species composition (Van der Wal *et al.* 2003; Dormann *et al.* 2004; Wahren *et al.* 2005; Hollister *et al.* 2005). These studies especially point at an increase in the cover of shrubs, an increased cover of dead material and an increased canopy height. Consequences for small herbivores will be far reaching and remain to be investigated.

Traditional migration versus new strategies

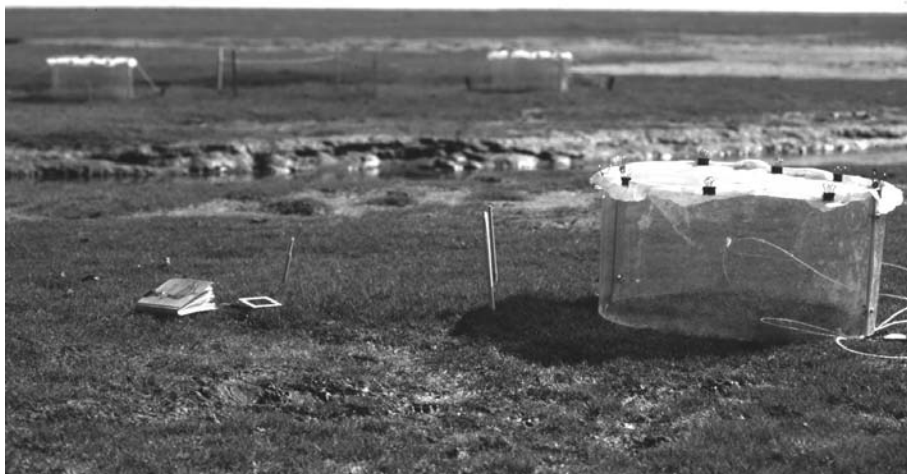
The population of Barnacle Geese showed an exponential increase in the 1980's and along with this increase the breeding range was expanded along the flyway. It is likely that part of the population follows different migration strategies nowadays. Koffijberg and Günther (2004) show that in the last five years the geese stay longer in the Wadden Sea area, a shift which is not in any way related to changing spring temperatures. We looked at additional migration data from the bird ringing station in Ottenby (Sweden, data A. Hedenström) and arrival dates of geese in Estonia (data A. Leito), from 1970 until 2004. For Ottenby only a very small percentage passed the observatory until the 1980's, hereafter the number of

geese that was counted increased in the following years. Besides this, there is a strong positive correlation between date of passage (75% of total migration) and year, showing that the geese pass through later every year. For Estonia, Leito (1996) reported a relation between first arrival date and spring temperatures for the traditional staging area in the Matsalu Nature Reserve. However, other areas did not show this trend, but we found a significant trend with year for Saaremaa, which was colonised later. These analyses support our ideas that part of the population adapted to other strategies after expansion of the population in the 1980's. The changes might be caused by overcrowding at the traditional staging sites, which might spring from a combination of the larger population size as well as a lower availability and suitability of coastal sites brought about by changes in land use and management of nature reserves (Black *et al.* 1991; Prop *et al.* 1998; Stock and Hofeditz 2002; Chapter 10). In contrast, close to these traditional sites new foraging areas on (fertilised) inland pastures have become available which provide an alternative source of high quality food (Owen *et al.* 1987; Leito 1991; Leito 1996; Ganter *et al.* 1999).

In conclusion, we have shown that the phenology of the forage species of Barnacle Geese is significantly advanced under increased temperatures. Increased temperatures as well as changes in land use will further change the timing and amount of forage availability along the flyway. Barnacle Geese can advance their migration in years with an earlier spring, moreover, part of the Barnacle Goose population changed its migration route and schedule in the past decades, probably to adjust to a growing population and changes in land use along the flyway. It is, therefore likely, that the geese will be able to adjust to future changes in forage availability in its staging and breeding areas.

Acknowledgements

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Greenhouses on the salt marsh near Tobseda (top) and on the salt marsh of Grötlingbo-udd (bottom)

Has the recent breeding range expansion of Arctic geese been facilitated by changes in human land use?

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Summary

1. As in many Arctic breeding herbivorous waterfowl species, Barnacle Geese recently showed a strong increase in population size. We have observed a dramatic expansion of their breeding range from the traditional areas in the Russian Arctic to temperate areas in western Europe traditionally used as wintering grounds.
2. We investigated the habitat characteristics of the new nesting and nearby foraging sites in the Baltic and in the Netherlands by means of a questionnaire addressed to nature conservation agencies, farmers and researchers.
3. New nesting sites are mainly situated on small islands, safe from fox predation. Human interference and livestock grazing is usually absent. In contrast, foraging sites used during chick rearing are typically found at the mainland and are grasslands with a short sward, most often grazed by livestock or subjected to a mowing regime.
4. There are no overall changes in land use that explain the breeding range expansion of the Barnacle Geese to the Baltic. New breeding colonies in the Russian Arctic were established following the abandonment of human settlements in these areas. In contrast, the new sites in the Netherlands became available after human land reclamation, dam building and intensification of agriculture.
5. We expect that the growth of the temperate breeding population of Barnacle Geese will level off after recent period of geometric growth as predator-safe nesting sites will become limiting and density-dependent processes will act on the established colonies.

Introduction

Traditionally Barnacle Geese, *Branta leucopsis*, breed in the high Arctic on the islands of Greenland, Spitsbergen, Novaya Zemlya and Vaygach. Since the 1970s, the Russian population of Barnacle Geese has increased dramatically from about 25,000 geese in 1970 to about 400,000 at present (Figure 10.1). Along with the geometric population growth, Barnacle Geese have also expanded their breeding range. In 1971, the first breeding colony was established in the Baltic Sea, formerly used only as a stopover site during migration (Larsson *et al.* 1988). The number of geese breeding in these new colonies increased rapidly (Forslund and Larsson 1991; Leito 1996; Larsson and Van der Jeugd 1998; Leito and Truu 2004) and at present the Baltic sub-population numbers about 21,000 birds. During summer 1988, the first breeding pairs were observed at traditional wintering sites of this species in the Netherlands (Meininger and Van Swelm 1994; Van Dijk *et al.* 2005) and numbers here have increased dramatically since then, reaching almost 6,000 breeding pairs in summer 2005, mainly in the southern delta region (Ouweneel 2001; Van Dijk *et al.* 2005) (Figure 10.1). In 2005, the North Sea population numbered about 25,000 birds in all. Around the same time, in the 1980s, Barnacle Geese expanded their breeding range in Russia all along the coast of the Barents Sea (Filchagov and Leonovich 1992; Syroechkovsky Jr. 1995). The colonies in the Baltic, the Netherlands and Russia initially showed geometric growth (Larsson *et al.* 1988; Mineev and Mineev 2004; Van Dijk *et al.* 2005). The growth of the Baltic population has levelled off during the past five years, whereas the Dutch population is still increasing (Van Dijk *et al.* 2005) (Figure 10.1).

During the same period goose populations around the world have increased tremendously. In North-America, the populations of Greater and Lesser Snow Geese (*Chen caerulescens caerulescens*, Abraham *et al.* 2005) and (*Chen caerulescens atlanticus*, Gauthier *et al.* 2005) went through a period of population explosion from the late 1960's to the mid-1990's. In Japan the population of wintering Greater White-fronted Geese (*Anser albifrons*) increased almost six-fold in a 20-year period (Shimada 2002). In Europe, wintering populations of Pink-footed Geese (*A. brachyrhynchus*, Fox *et al.* 2005), Greenland White-fronted Geese (*A. albifrons flavirostris*, Fox *et al.* 2005), Bean Geese (*A. fabalis*, Van Eerden *et al.* 2005) and Greylag Geese (*A. anser*, Van Eerden *et al.* 2005) have increased since the 1960's. Along with the increase of wintering numbers of Palearctic goose species in Western Europe also the number of exotic species increased and Egyptian (*Alopochen aegyptiacus*, Lensink 1998), Canada (*Branta canadensis*, Van Roomen *et al.* 2004) and Bar-headed Geese (*Anser indicus*, Van Horssen and Lensink 2000) are now common on grasslands in Europe (Lever 1987). These neozoic populations, probably founded by individuals escaped from waterfowl collections, are non-migratory and have bred successfully in the new habitats (Van Dijk *et al.* 2005). Concurrently, Palearctic species

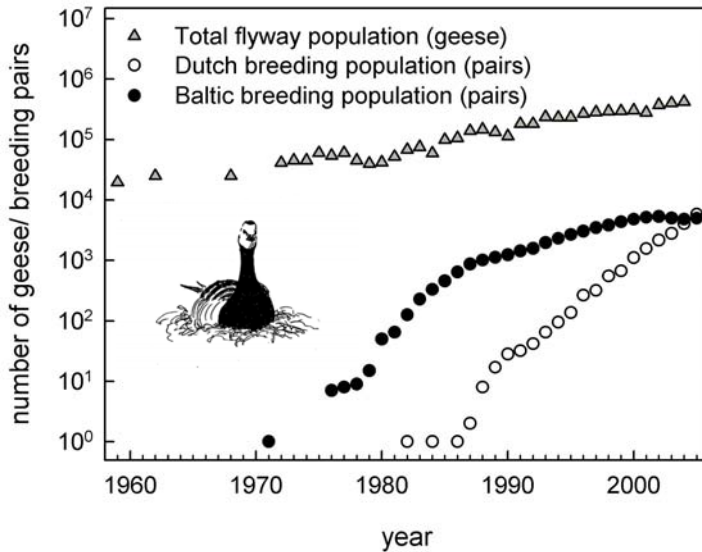


Figure 10.1: Population trend of the East Atlantic Flyway population of Barnacle Geese (triangles) as well as the number of breeding pairs in the more recently established Baltic (open circles, included are birds breeding on the Swedish islands of Öland and Gotland) and Dutch colonies (closed circles).

such as the Greylag and the Barnacle Goose expanded their breeding range towards temperate regions (Forslund and Larsson 1991; Loonen and de Vries 1995; Van Eerden *et al.* 2005).

Changes in hunting regulations and the designation of refuges for wintering and migrating geese are often mentioned as potential causes of the increase in goose numbers (Ebbinge 1991; Menu *et al.* 2002; Ngai and Jefferies 2004). However, most studies attribute the dramatic increase in goose numbers primarily to changes in human land use, such as increased fertilisation of grasslands, cultivation of wheat, corn and rice (Fox *et al.* 2005; Abraham *et al.* 2005; Van Eerden *et al.* 2005) and changes in harvesting techniques (Shimada 2002). In addition, part of the population increase is assigned to alterations in the foraging habits of the geese such as shifts from traditional foraging on (semi-) natural grasslands to agricultural fields (Ganter *et al.* 1999; Fox *et al.* 2005; Gauthier *et al.* 2005). In North America, strong increases in the number of Lesser Snow Geese on the breeding grounds around Hudson Bay led to severe foraging pressure on natural salt marshes and caused habitat degradation and a loss of salt-marsh habitat (Jefferies and Rockwell 2002; Jefferies *et al.* 2006). As a consequence, Lesser Snow Geese have shifted their breeding

areas, and it is expected that they will negatively affect their habitat on these new sites as well (Abraham *et al.* 2005). This quickly growing population uses more and more agricultural fields during wintering and spring staging, causing increasing conflicts with agriculture (Abraham *et al.* 2005). At present the population of Lesser Snow Geese in North America is under an intense hunting regime, but numbers are still rising (Abraham *et al.* 2005). Also in other parts of the world, growing goose populations are causing severe conflicts with agriculture and solutions are being sought (Ankney 1996; Batt 1997; Vickery and Gill 1999; Beck *et al.* 2002; Cope *et al.* 2003; Amano *et al.* 2004; Fox *et al.* 2005; Van der Jeugd and Voslamber 2006).

We conducted a survey of the nesting and adjacent foraging sites of Barnacle Geese in the Netherlands and in the Baltic. In the survey we focused on habitat characteristics and management. Additionally, we provide counts of the number of nesting and foraging birds. First, we will examine habitat parameters required by Barnacle Geese for nesting and gosling rearing at the newly established colonies and compare these with the traditional habitats in the Russian Arctic. Secondly, we will investigate whether land use has changed over the past decades in recently colonised sites, and whether this facilitated the establishment of new colonies. Finally, we will discuss the growth of these new breeding populations in relation to population growth at traditional sites.

Methods

The Netherlands

Data on the number of geese and their breeding areas was supplied by SOVON Dutch Centre for Field Ornithology. SOVON organises nationwide counts of wild birds in the Netherlands. Fieldwork for these surveys is carried out by volunteer ornithologists. To date, 270 different areas have been recorded in which at least one pair of Barnacle Geese bred for at least one year, but this is likely to be an underestimate. In 17 of these areas more than 10 pairs bred for at least five subsequent years (Table 10.1, Figure 10.2). In the larger areas more than one colony was established and several sites were used as foraging sites. We subdivided the data set into sites and analysed data for a total of 20 nesting sites (1-6 sites per area) and 16 foraging sites (0-2 sites per area). Data on site characteristics (location, size of the site, vegetation description, estimate of canopy height) and management (nature protection measures, accessibility for people, livestock grazing, mowing or fertilisation) were collected using questionnaires sent to local birdwatchers, farmers or site-managers working for nature conservation agencies.

Numbers of nesting and foraging geese were related to the size of the nesting and foraging sites by linear regression analyses. Differences in canopy height between nesting and foraging sites were explored with a two-sample *t*-test.

Baltic

For the Baltic area, we relied on detailed surveys of nesting and foraging habitats carried out by K. Larsson and H. van der Jeugd in Sweden and A. Leito in Estonia. Estonia harboured five sites and Sweden 17 sites, each of which had 10 or more breeding pairs for at least five consecutive years (Table 10.1, Figure 10.2). All sites in Sweden used for the analysis were situated along the coast of the island of Gotland. A few colonies at the coast of the Swedish mainland near Stockholm (Forslund and Larsson 1991) and along the coast of the island of Öland were not included in our dataset. For the sites on Gotland, we distinguished mainland sites, situated on Gotland main-island as opposed to the smaller islands along the shore. In Sweden, annual counts of nests were made from 1971 onwards, during the same period numbers of adults and young were counted at the annual wing moult at the end of July on the foraging sites. The most recent counts (2005) of these of nesting and foraging geese were related to the size of the nesting and foraging sites by means of linear regressions. In Estonia nest counts were conducted in the period from 1981-2002 by A. Leito. Differences in canopy height between nesting and foraging sites were explored using a two-sample *t*-test.

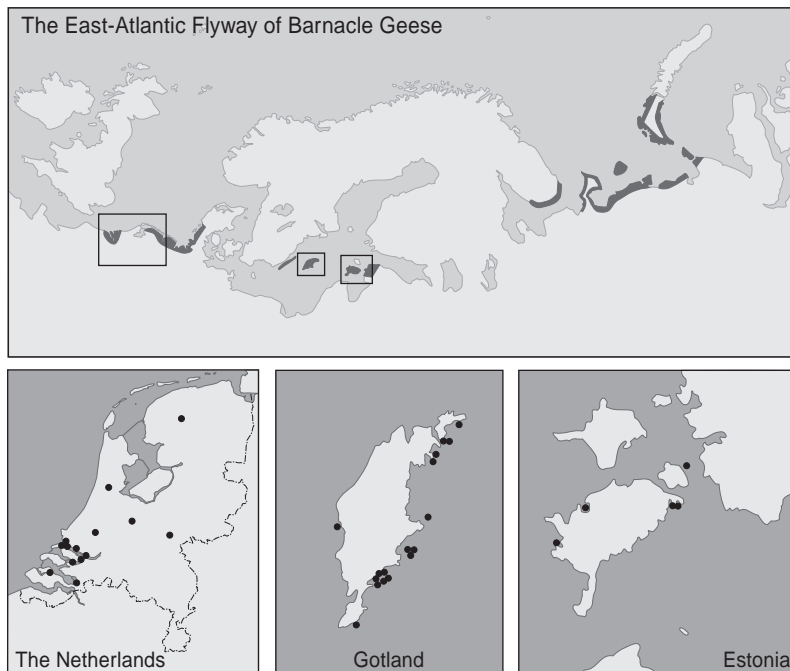


Figure 10.2: The East Atlantic flyway with the breeding grounds of the Barnacle Goose (shaded area) and, in more detail, the newly established breeding areas in the Baltic Sea (Gotland, $N=17$ and Estonia, $N=5$) and in the Netherlands ($N=14$).

Table 10.1: Number of breeding areas and the number of sites used for the analyses in this study

	Total number of breeding areas	Total number with >10 pairs	Number of areas used in analysis	Number of sites used in analyses
<i>Nesting sites</i>				
Estonia	24	5	5	5
Sweden	>44	17	17	17
The Netherlands	270	17	14	20
<i>Foraging sites</i>				
Estonia			5	5
Sweden			17	17
The Netherlands			15	16

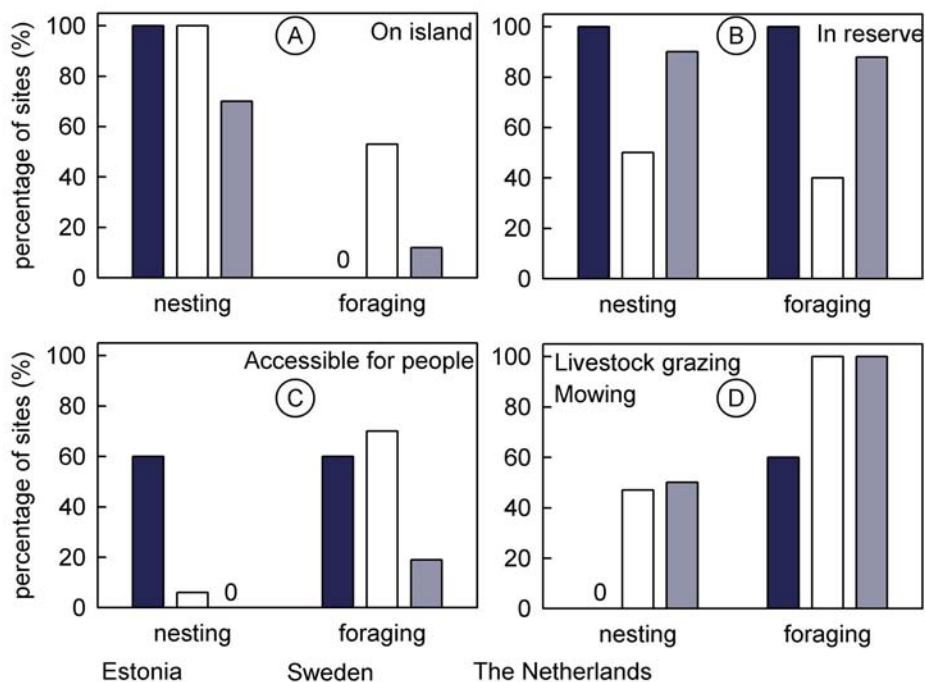


Figure 10.3: Site choice of Barnacle Geese for nesting and foraging in Estonia (black bars, nesting $N=5$, foraging $N=5$), Sweden (white bars, nesting $N=17$, foraging $N=17$) and the Netherlands (grey bars, nesting $N=20$, foraging $N=16$): (A) location, (B) conservation status (C) accessibility to people (D) grazing or mowing

Results

Almost all breeding colonies in the Baltic, as well as in the Netherlands, are situated on islands (Figure 10.3A), within nature reserves (Figure 10.3B) and are not accessible to people during the breeding season (Figure 10.3C). About half of the islands are grazed by livestock or managed by mowing (Figure 10.3D). Foraging sites are more often found on the mainland and in places that are accessible to people (Figure 10.3A,C). A large proportion of these sites is grazed by livestock or mown for haymaking (Figure 10.3D). Nesting habitats can be very diverse, ranging from bare stony beaches to dense scrub or bushes. Foraging habitats, in contrast, almost always comprise grasslands (Figure 10.4). Average canopy height of the nesting sites is higher than that on the foraging sites (two-sample t-test: Sweden $t_{32}=1.93$, $P=0.03$; the Netherlands $t_{34}=3.3$, $P=0.001$; Figure 10.5). All nesting and foraging sites were situated in the close vicinity of water bodies. Table 10.2 summarises the average conditions of nesting and foraging sites.

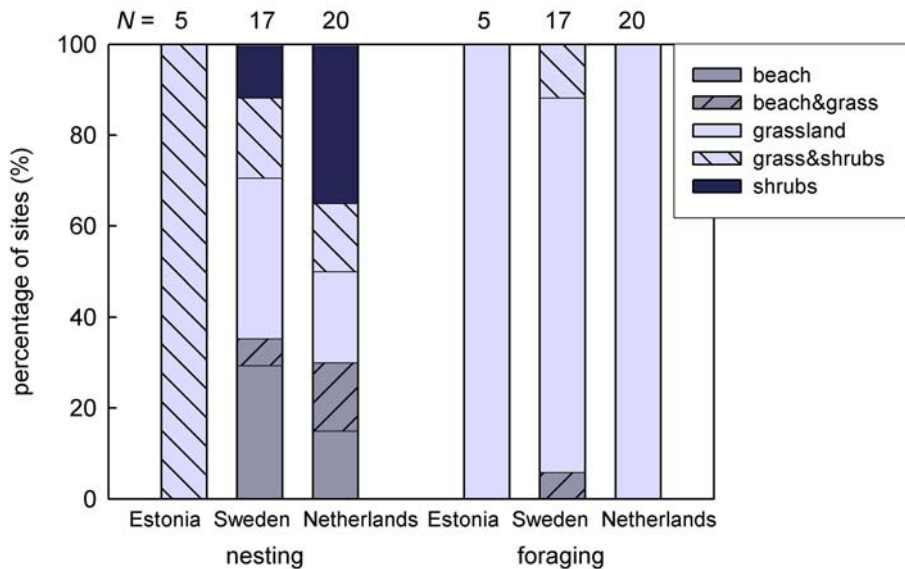


Figure 10.4: Habitat types at nesting and foraging sites in Estonia, Sweden and the Netherlands.

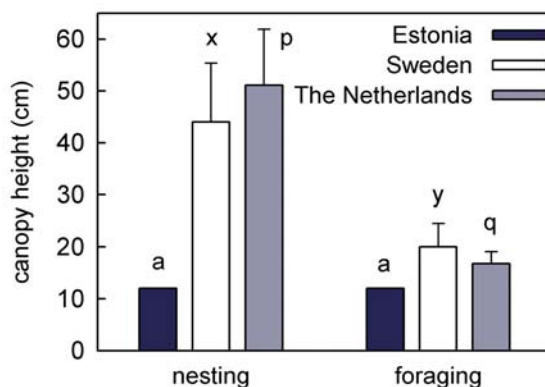


Figure 10.5: Canopy height for nesting and foraging sites in Estonia (black bars), Sweden (white bars) and the Netherlands (grey bars). Different letters indicate significant differences.

For Sweden we found a positive relation between the size of the nesting sites and the number of breeding pairs at the site ($R^2=0.37$, $P=0.01$). Here we also detected a strong positive correlation between the size of the foraging site and the number of adult geese counted at the site by the end of July ($R^2=0.83$, $P<0.01$; Figure 10.6A). The slope of this regression line reveals that the capacity of foraging sites in Sweden is about 20 geese ha^{-1} . For the Netherlands, we did not find a significant relationship between size of the nesting sites and the number of breeding pairs at these sites ($R^2=0.19$, $P=0.06$), nor between the size of the foraging sites and the number of geese on these sites ($R^2<0.001$, $P=0.99$; Figure 10.6B). A better fit might be obtained if more sites and other species of breeding geese were included.

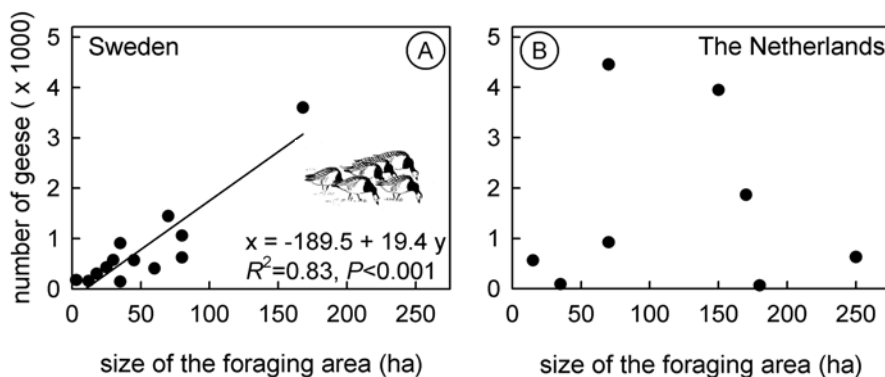


Figure 10.6: Number of foraging geese and goslings in relation to size of the foraging site for (A) Gotland ($R^2=0.83$, $P<0.01$) and (B) the Netherlands (regression n.s.).

Most areas in the Netherlands where geese are nesting (11 out of 14 areas) are islands that came into existence after tidal influence was reduced by the building of dams for flood prevention works. In the Baltic, we do not have any indications of changes in land use that might have facilitated the establishment of goose colonies.

Discussion

Contrasting habitat requirements of nesting and foraging geese

Barnacle Geese can nest in a wide variety of habitats. Traditional breeding areas along the coasts of Novaya Zemlya and Vaygach Island, as well as those on Greenland and Spitsbergen, comprise cliff ledges, rocky outcrops and small islands (Ganter *et al.* 1999). Here the cliffs and the overall isolation of the islands provide safety from ground predators. Traditionally, avian predators mainly predate on goose eggs and chicks in years when few lemmings are around. In such years predation by birds of prey and especially gulls, and in some colonies also by foxes, reduces breeding success to virtually nil (Syroechkovsky *et al.* 1991; Mainguy *et al.* 2002). More recently established nesting sites in the Russian Arctic along the coast of the Barents Sea are more diverse; we observed geese nesting on small islands, salt marshes, dunes, tundra and former hayfields (pers. obs.; Syroechkovsky Jr. 1995; Van der Jeugd *et al.* 2003; Chapter 2). Not only the habitat, but also the nesting substrate, shows a large variation (Litvin and Gurtovaya 2005).

In the Netherlands, Sweden and Estonia we found a wide variety of nesting habitats, from bare stony islands to islands almost completely overgrown with shrubs and trees or tall reed-beds. For nesting sites, clearly the most important requirement is safety from predators, and this is accomplished by nesting sites usually being situated on small islands or on other sites that are inaccessible for ground predators and people. Additionally, a tall canopy on many places prevents detection of the nest from the air by avian predators. Finally, the absence of livestock ensures a tall canopy and decreases the probability of trampling and disturbance of female geese on the nest during the breeding period.

Foraging geese select sites with the highest possible forage quality. Protein requirements of chicks in the early growth phase are at least twice as high as that of adults birds (Murphy 1996). A more nutritious diet positively influences growth rate of goslings, their body size as adults, and, hence, the chance of post-fledging survival and future reproductive success (Cooch *et al.* 1991; Sedinger *et al.* 1995; Loonen *et al.* 1997; Larsson *et al.* 1998; Van der Jeugd and Larsson 1998; Sedinger *et al.* 2004). The breeding islands, though safe havens, are in many cases unsuitable for gosling rearing because of low forage availability. Geese leave the nesting sites as soon as the goslings hatch and move to greener pastures. At that time, they prefer short, nutrient-rich grasslands (Sedinger and Raveling 1986; Forslund and Larsson 1991; Stahl and Loonen 1998). This type of grassland is often

maintained by livestock grazing, fertilising and/or mowing (Summers and Critchley 1990; Vickery *et al.* 1994; Hassall *et al.* 2001; Van der Graaf *et al.* 2002; Bos *et al.* 2005). Safety is still important and explains why all foraging sites of Barnacle Geese are adjacent to water bodies, where the flightless goslings and their moulting parents escape in case of predator attacks or disturbance. Stahl and Loonen (1998) show that in years with foxes present in an Arctic colony on Spitsbergen Barnacle Geese forage only in the proximity of open water. Traditional foraging sites are Arctic salt marshes that reach a peak in nutritional quality around the time of gosling-hatch and the geese have access to high quality forage during the gosling-rearing period (Chapter 5). In natural marshes in temperate regions, the peak in nutritional quality occurs much earlier in spring. Though Barnacle Geese breeding in more temperate regions advanced their laying dates significantly, they have not shifted their laying dates sufficiently to coincide with the peak in the nutritional quality of the vegetation. Instead, the gosling-rearing period is now sub-optimally timed and coincides with a tall canopy and low nutritional quality of the forage (Chapter 5). A similar phenomenon is documented for many other bird species reacting to environmental changes in temperate areas (Visser *et al.* 2004). Geese compensate for the lower forage quality by foraging in livestock-grazed marshes and agricultural fields, where canopy heights are kept low and nutrient content high by large grazers or even by artificial fertiliser application (Summers and Critchley 1990; Vickery *et al.* 1994; Hassall *et al.* 2001; Van der Graaf *et al.* 2002; Bos *et al.* 2005).

From our study we can conclude that nesting and chick-rearing geese have different habitat requirements (Table 10.2). Thus, to successfully breed and raise chicks, Barnacle Geese need a combination of safe nesting sites and high-quality foraging sites within reasonable distance from each other.

Table 10.2: Habitat requirements for nesting and foraging sites of Barnacle Geese, derived from data from the Baltic and Dutch colonies. (n.i. = not important, n.a. = not applicable).

	Nesting	Foraging
Location	Island	close to water
Vegetation	n.i.	grassland
Canopy height	n.i.	low
Management	no livestock	livestock grazing
Accessibility	not accessible	n.i.
Size	1-55 ha	3-80 ha
Distance	n.a.	0-10 km

Changes in land use

In the Baltic area there are no obvious changes in land use that might have triggered the establishment of Barnacle Goose colonies. However, atmospheric nitrogen deposition became obvious in the 1950's in Scandinavia and undoubtedly affected vegetation throughout the Baltic region. The expansion of the breeding range to the Baltic, therefore, seems to be independent of any obvious population or environmental changes. Breeding range expansions to the Dutch delta area and along the Russian coast around 1990 also appear to be independent events. However, at this time goose numbers increased dramatically in the traditional population (Ganter *et al.* 1999) as well as in the Baltic population (Figure 10.1). The establishment of the new colonies in the Dutch delta at this time might have been caused by a lower forage availability during the gosling-rearing period due to increased resource competition, and hence a reduced breeding success in the traditional Russian breeding grounds as well as the Baltic breeding grounds (Larsson and Van der Jeugd 1998). In Barnacle Geese, previous work on Spitsbergen, and especially that in the new populations on Gotland have shown that breeding success rapidly declines with increasing population size, due to density-dependent effects on reproduction (Larsson and Forslund 1994; Loonen *et al.* 1997; Larsson and Van der Jeugd 1998; Drent *et al.* 1998; Loonen *et al.* 1998), concomitantly a higher emigration rate has been documented.

The geese that colonised the Baltic Sea encountered a much lower forage quality during the gosling-rearing period than that at their Arctic foraging sites (Chapter 5). At the same time, overall energetic expenses of the geese on an annual balance are strongly reduced as they skip a large part of their migration route, and the prolonged season allows slower growth of goslings without severe penalties. Indeed, gosling growth in these colonies is slower than that in the Russian and other Arctic colonies, although final body size of the goslings is similar due to the longer foraging season (Eichhorn and Van der Jeugd unpubl; Loonen *et al.* 1997).

In the early 1990's, after the fall of the Soviet regime, many coastal settlements in northern Russia were abandoned. New colonies of Barnacle Geese were established at or near these abandoned settlements soon afterwards (Filchagov and Leonovich 1992; Syroechkovsky Jr. 1995; Van der Jeugd *et al.* 2003). Although the presence of people (goose hunting and egg collecting) probably prevented earlier establishment of colonies, the long tradition of Arctic fox-hunting in these areas may have counteracted the negative human impact. Geese probably profited from a virtually predator-free environment during the early phase of colony establishment when local fox populations still had to recolonise the surroundings of the former settlements.

In the Netherlands, 11 of the 14 main breeding areas are situated in estuaries in the delta area in the south-west, where three major rivers, the Rhine, Meuse and Scheldt, flow into the North Sea. In 1953, a catastrophic flooding event in the Dutch delta gave rise to the construction of several dams to prevent future disasters. The construction of most of these dams was finished between 1960 and 1987. The dams altered not only the salinity of the estuaries from saline to brackish, but also reduced tidal influences and changed water currents. Many small islands and shoals, on which Barnacle Goose colonies are now established, have emerged during this period. At the same time, agricultural exploitation intensified and nitrogen fertiliser was supplied to grasslands; hence, the quality and productivity of these grasslands increased dramatically (Van Eerden *et al.* 2005). In addition, high discharges of N and P from agriculture has led to considerable eutrophication of many of the closed sea arms in the Dutch delta area (Oenema *et al.* 2005). Inundation of foraging sites with these waters has a fertilising effect leading to nitrogen contents of preferred vegetations that are comparable to what is found at the traditional Arctic sites (Pouw *et al.* 2005). Between 1960 and 1980, we can observe the appearance of suitable nesting sites along with high quality foraging sites in the Dutch delta. In 1988, the first successful breeding pair was observed (Van Dijk *et al.* 2005) and this was followed by a geometric increase in numbers. At two of the largest (and oldest) colonies in the Dutch delta the first breeding pairs were observed four years after the completion of dams that reduced tidal influence at the sites. The areas that developed after the reduction of tide soon attracted various numbers of breeding birds, thereby gaining the status of nature reserves soon after. The vegetation, which is tolerant of brackish conditions, is usually grazed in summer by cattle (Bakker *et al.* 1993).

Interestingly, human activities had very contrasting effects on the establishment of new breeding areas for Barnacle Geese, when Russian and north-west European sites are compared. We observed on the one hand that expansion of breeding colonies within Russia is triggered by the abandonment of human settlements, while on the other hand human activities, such as forage quality manipulation and embankment of polders have given rise to new colonies in the Dutch delta.

Flexibility of migratory routines?

There is no unifying factor in the newly established breeding sites that can explain the recent overall expansion of the breeding range of Barnacle Geese. We suspect that the increase in the total population of Barnacle Geese probably has heightened exploration of alternative sites. Recent changes in habitat parameters at previously unsuitable sites can partly be attributed to changes in land use that alter predation pressure and forage availability and facilitated the successful establishment of new colonies along the flyway. Sutherland (1998) reviews historic changes in avian migration routes, and tabulates ‘substantial change’ in 12 populations of geese and swans. Excluding the naturalised

species, the shifts in migratory routines entailed a shortening of the autumn migration allowing the birds to winter closer to the breeding areas (two swan populations and five goose populations, to which the Brant, *Branta bernicla nigricans* can be added; this goose species breeds along the Arctic coasts of Alaska and adjoining Canada and now winters in increasing numbers in south-west Alaska instead of migrating to Mexico as in former times, Ward *et al.* 2005). In these geese and swans with extended parental care, migration routes are shaped by family tradition ('culturally determined') and none of the recorded changes result in sub-optimal solutions, this in sharp distinction to other bird groups with short parental care where about half of the changes in migration routes are considered sub-optimal (involving unnecessary detours). For waterfowl there is circumstantial evidence that these alterations in wintering locality ('short-stopping') are often directly related to changes in agricultural practice, unintentionally providing crop residues (Owen *et al.* 1986; Cooke *et al.* 1995; Gill *et al.* 1997). Previous research on Barnacle Geese from the Spitsbergen breeding population, suggests that the recent northwards expansion of the spring staging area of this population is also caused by changes in spring temperatures and agriculture (Prop *et al.* 1998). We conclude that geese are very flexible in their response to environmental changes by adapting their migratory routines. Aside from the migration between breeding and wintering localities we have been considering here, many waterfowl engage in moult migrations: the non-breeders withdrawing to specific sites to renew their flight feathers (Salomonsen 1968). New traditions in use of moulting sites confirm flexibility in these seasonal movements as well (Greylag Geese, see Loonen *et al.* 1991; Canada Geese, Walker 1970). These opportunistic shifts in moulting sites have implications for breeding range changes. In many documented cases, breeding colonisation by Barnacle Geese followed on a pioneering phase of moulting flocks using the area in late summer in earlier years (Spitsbergen, Drent *et al.* 1998; Gotland, Larsson *et al.* 1988; Russia, Filchagov and Leonovich 1992)

Perspectives

Currently, the colonies on Gotland seem to have reached a maximum size and numbers are now controlled by density-dependent effects (Figure 10.1). For the Netherlands as a whole we still observe a geometric increase in numbers of breeding birds, although growth is slowed down in the oldest and largest colonies. Continuing growth of the Dutch population will depend on the availability of suitable nesting and foraging habitats, as well as on the carrying capacity of the new colony sites. We have demonstrated that Barnacle Geese breed in a variety of habitats as long as their requirements can be met. Absence of foxes is of prime importance. New nesting sites are therefore either in areas without foxes or on sites that are inaccessible to foxes (Van der Jeugd *ms*). Fox populations in the Netherlands have been increasing in recent decades and there are now only a few remaining areas with a low density of foxes. Restrictions on foxhunting might halt or even overturn the increase of

breeding Barnacle Geese and other goose species in the Netherlands into a decrease. However, under the current nature management policy in the Netherlands there is some leeway to lift such restrictions locally.

Counts of adult geese and goslings in the newly established breeding colonies in Sweden show that there is a strong relation between the size of the colony and the size of the foraging site. The slope of this line gives the maximum number of geese per unit area; for Sweden this number, 20 birds ha⁻¹, is twice as high as the number found near breeding colonies in Spitsbergen (Drent *et al.* 1998). In the Netherlands we do not detect this relationship, probably because the breeding areas have not yet reached their maximum capacity. It is likely that in the Dutch breeding colonies, as numbers increase, density-dependent processes will act, similar to those in the Baltic colonies. In the Baltic population the number of fledged young per breeding pair decreased dramatically as colonies grew (Larsson and Van der Jeugd 1998). It is therefore likely that we are not facing a continuing increase in populations in the Netherlands, but that a ceiling will be reached when there are no new suitable habitats to colonise and when the existing colonies have ceased to grow. Some of the older colonies in the Netherlands already stopped growing. Until now the establishment of breeding populations of Barnacle Geese in the Netherlands has not resulted in conflicts with agriculture. This is primarily due to the fact that so far, birds have kept to semi-natural pastures, usually within nature reserves. At few sites there is concern for interference by the birds with long-term goals for nature management, e.g. maintaining healthy populations of meadow birds. However, with populations still increasing it is likely that more conflicts, especially with agricultural activities, will arise in the near future. We hope, therefore, that the results and insights presented in this paper may be of some use for finding sustainable, long-term solutions to resolve such conflicts.

Acknowledgements

Large numbers of volunteers collected data on geese over the years and filled in the questionnaires in the Netherlands, without their input the analyses would have been impossible to conduct. Vereniging Natuurmonumenten (NL), Staatsbosbeheer (NL) and Länsstyrelsen Gotland (SE) supported our study by supplying data. SOVON (NL), University of Oldenburg (DE), University of Groningen (NL) and Gotland University (SE) provided logistic and financial support.

Synthesis



Female Barnacle Goose on the nest with her partner standing guard (Tobseda, July 2003)

Foraging choices of Barnacle Geese, from temperate to arctic

Herbivores and their food resources

Plants are potentially poor food for herbivores, because of their chemical composition (Hartley and Jones 1997): plant material is often low in nutrient content and high in structural components (Demment and Van Soest 1985). Herbivores have evolved different strategies to deal with the low quality diet that plants provide (Demment and Van Soest 1985; Illius and Gordon 1992). In general, large herbivores can deal with low quality forage better than small herbivores since their energy requirements relative to their body weight are lower. Metabolic rate scales with body weight as $MR \sim W^{0.75}$ and length of digestive tract scales linearly with body weight. Furthermore, large non-ruminant herbivores compensate a low quality diet by high intake and a long retention of forage in the gut. In contrast, ruminants can handle a lower forage intake on the premise of a more efficient digestion, as they profit from gut microbial fermentation. Microbes also degrade structural, otherwise indigestible components of the cell. Small herbivores, such as geese, do not have these adaptive traits: their digestive tract is short and food passes through rapidly, enabling them to digest only a small percentage of the food during its passage (Prop and Vulink 1992). Since geese are also both physically and time constrained in the amount of food they can take up (Sedinger and Raveling 1988; Prop and Vulink 1992), they cannot compensate for low quality food by consuming larger amounts. In order to extract sufficient nutrients from the forage, therefore, geese have to be very selective and choose only highly nutritious forage.

The extracted nutrients are used for maintenance and locomotion, but in spring the geese also need to build up energy reserves for their migration and subsequent breeding. They acquire these reserves as a result of a period of intensive foraging in spring. In this period they store energy as proteins and fat. Nitrogen is one of the main constituents of proteins. In most studies described in this thesis, we use nitrogen content as an indicator of plant quality, nitrogen content can be translated to (crude) protein content by multiplying with a factor of 6.25 (Robbins 1993). Carbon is present in plant tissue largely as a structural component. When grasses mature, the relative amount of structural components increases, whereas the amount of proteins declines. Young grass has a low C/N ratio and is therefore a high-quality food resource. During the season, however, as the forage matures, the C/N ratio increases and digestibility of the plant material decreases. An increase in plant biomass usually co-occurs with a decline in shoot nitrogen content (Lepage *et al.* 1998; Bos *et al.* 2004; Chapter 5).

Plant forage availability and its quality at foraging sites play a crucial role for geese as the amount of body reserves accumulated by individuals prior to migration directly affects breeding success (Ankney and Macinnes 1978; Ebbs and Spaans 1995; Prop and Black 1998; Madsen 2001). At the breeding sites, food availability and its quality during the

gosling rearing period influence final adult body size of the goslings as they affect gosling growth rates (Cooch *et al.* 1991; Sedinger *et al.* 1995; Loonen *et al.* 1997; Larsson *et al.* 1998), while fledgling weight influences post-fledgling survival (Loonen *et al.* 1997; Van der Jeugd and Larsson 1998) and hence the likelihood of breeding for the individuals that survive the post-fledgling period (Sedinger *et al.* 2004).

Foraging choices of Barnacle Geese

All foraging sites described in this thesis are coastal meadows, with short swards, dominated by grasses or sedges (Chapter 2, Box 1, Box 2, Chapter 10). Over 90% of the diet of Barnacle Geese in these areas consists of grasses (Van Dinteren 1988; Wolfs and Pardijs 2004; unpublished results). Nitrogen content of grasses, in general, is low; at our study sites, the values for unfertilised grasses ranged between 1.5 and 4.5 % of the dry weight. Moreover, nitrogen content of grasses peaks at the beginning of the growing season but declines rapidly as the season progresses (Van Soest 1994; Hassall *et al.* 2001; Bos *et al.* 2004). It is therefore important that within foraging sites, the geese time their staging period to coincide with the peak in sward quality and, within sites, select the most profitable areas for resource acquisition.

Attractiveness of a foraging site can be related to a combination of plant nutrient content and plant biomass, a measure of total nitrogen availability for the geese (Chapters 3 and 5). In very young swards at the beginning of the growing season, total nitrogen in the vegetation is low: plant quality in young swards is very high, but biomass is too low to provide sufficient high quality forage for the birds. As biomass increases, nitrogen content per unit dry weight of the grasses decreases, so that the total nitrogen available in the vegetation first increases to a peak level and then decreases. In my thesis, I have shown that the total nitrogen available in the vegetation is an important criterion in forage choice and habitat selection by migrating geese. Not only do Barnacle Geese actively select areas with highest nitrogen per unit weight of biomass at a staging site (Chapter 3), they also appear to follow waves of peak nitrogen levels in the biomass all the way from their temperate staging sites, to their Baltic stopover sites to the Arctic breeding sites (Chapter 5). The geese utilise the staging site in the Wadden Sea and stopover sites in the Baltic at the time of peak levels of total nitrogen availability in the vegetation. At the Russian breeding site, geese arrive prior to the flush of spring growth of forage plants and profit from the peak in nitrogen content in plant shoots during the gosling-rearing period.

Intake rate, the amount of food a bird can consume in a given time, interacts with peak nitrogen levels in the biomass in the selection of preferred foraging sites. A site might have plants with a high nitrogen content, but if intake rates are low, nutrient intake can be insufficient for migration and reproduction. I have shown that intake rates when feeding on low swards of *Festuca rubra* are mainly dependent on canopy height (Chapter 4). With increasing canopy height, geese can achieve a larger bite size and therefore a higher intake

rate (Prop *et al.* 1998; Lang and Black 2001; Durant *et al.* 2003). However, when tall swards are present, intake rate decreases because the geese encounter handling problems with long leaves (Van der Wal *et al.* 1998; Hassall *et al.* 2001; Durant *et al.* 2003), increased costs of locomotion and increased vigilance due to changes in the perception of predation risk (Van de Koppel *et al.* 1996).

The critical factor determining site choice will thus be a combination of the nitrogen content of the forage and intake rate, i.e. nitrogen intake rate (Durant *et al.* 2003). This might explain why most studies show that geese prefer much lower canopy heights than those on which they could maximise intake rates. Experimental results indicate that Barnacle Geese can obtain a maximum intake rate at sward height of about 8 cm (Lang and Black 2001; Chapter 4). However, a study by Durant *et al.* (2003) reveals that Barnacle Geese prefer foraging on swards of 2-3 cm, rather than on 5-6 cm or 10-12 cm. Concurrently, field studies indicate a preference of wild geese for swards lower than 8 cm (Summers and Critchley 1990; Hassall *et al.* 2001; own data). Since forage quality decreases with increasing biomass and canopy height (Summers and Critchley 1990; Hassall *et al.* 2001; Durant *et al.* 2004; Bos *et al.* 2005a) maximum nitrogen intake rates will be reached at a lower level of biomass or canopy height than maximum intake rates of biomass (Figure 11.1).

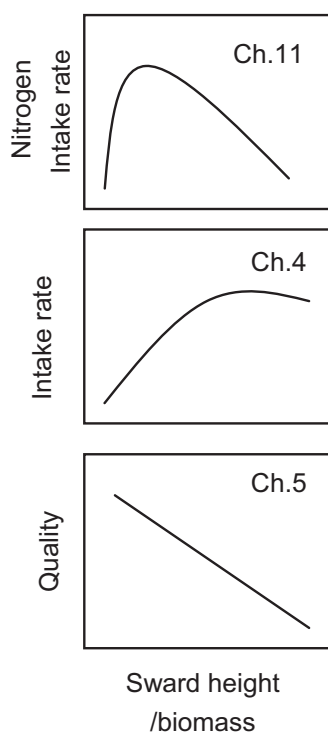


Figure 11.1: Schematic overview of the effects of maturing sward with increasing biomass and height on sward quality (in percentage Nitrogen), the intake rate geese can achieve (in mg s^{-1}) and the nitrogen intake rate (in $\text{mg Nitrogen s}^{-1}$)

Facilitation and competition between herbivores

Food resources along the flyway are scattered in space as well as in time. The timing of maximum utilisation is different for each area, depending in the first place on local abiotic and climatic factors that determine the onset and rate of plant growth (Chapters 5 and 9). Furthermore, the availability and the nutritional quality of the forage plants are influenced by the geese themselves and by other herbivores. The grazing optimisation hypothesis, postulated in the 1970's by Dyer (1975) and McNaughton (1979), describes the reaction of plants to increasing herbivory. It predicts that grazing at intermediate intensities stimulates plant production and enhances the net primary production of grazed plants above that of ungrazed plants. McNaughton (1979) developed the theoretical framework of grazing optimisation in view of the large-scale movements of herbivores in the Serengeti. McNaughton (1976) describes how dense concentrations of migratory Wildebeest (*Connochaets taurinus*) deplete plant biomass in the Serengeti Plains, while at the same time grazing stimulated net primary production and Thomson's Gazelles (*Gazella thomsonii*), which arrived in the area a month later and profited from the low dense biomass created by the preceding Wildebeest grazing. Several other studies also demonstrated a positive response of plant production to grazing (Cargill and Jefferies 1984; Pandey and Singh 1992; Frank and McNaughton 1993; Nolet 2004), but evidence is limited to certain ecosystems and remains controversial (Belsky 1986; Belsky *et al.* 1993). Many more studies in various ecosystems have reported an increase in nutrient concentration of previously grazed tissue (Ydenberg and Prins 1981; Gauthier *et al.* 1995; Ruess *et al.* 1997; Fox *et al.* 1998; Green and Detling 2000). Finally, some studies also report on changes in shoot densities or live/dead ratios as side-effects of grazing (Coughenour 1991; Van de Koppel *et al.* 1996; Loonen and Solheim 1998; Zacheis *et al.* 2001). Sites which are grazed repeatedly by herbivores are characterised by a low, dense and highly nutritious sward; these sites are often referred to as grazing lawns (McNaughton 1984; Drent and Van der Wal 1999). We use the term herbivore facilitation when the foraging opportunities of one species are enhanced indirectly by the feeding activities of another. In contrast, depletion of resources and direct competition negatively affect resource acquisition by a particular herbivore species, and potentially influences foraging choices and induces strategies of resource partitioning by different herbivores (Belovsky 1984; Gordon and Illius 1989; Edwards *et al.* 1996; Murray and Illius 2000).

In ecosystems that are periodically visited by many different migratory herbivores, such as the Serengeti and our own study system, grazing facilitation as well as competition are likely to occur. In the following paragraphs I will describe the interactions between other herbivores present on foraging sites along the flyway of the Barnacle Goose, namely livestock and hares, and forage resources as well as the effects of geese on their own forage supply (Figure 11.2).

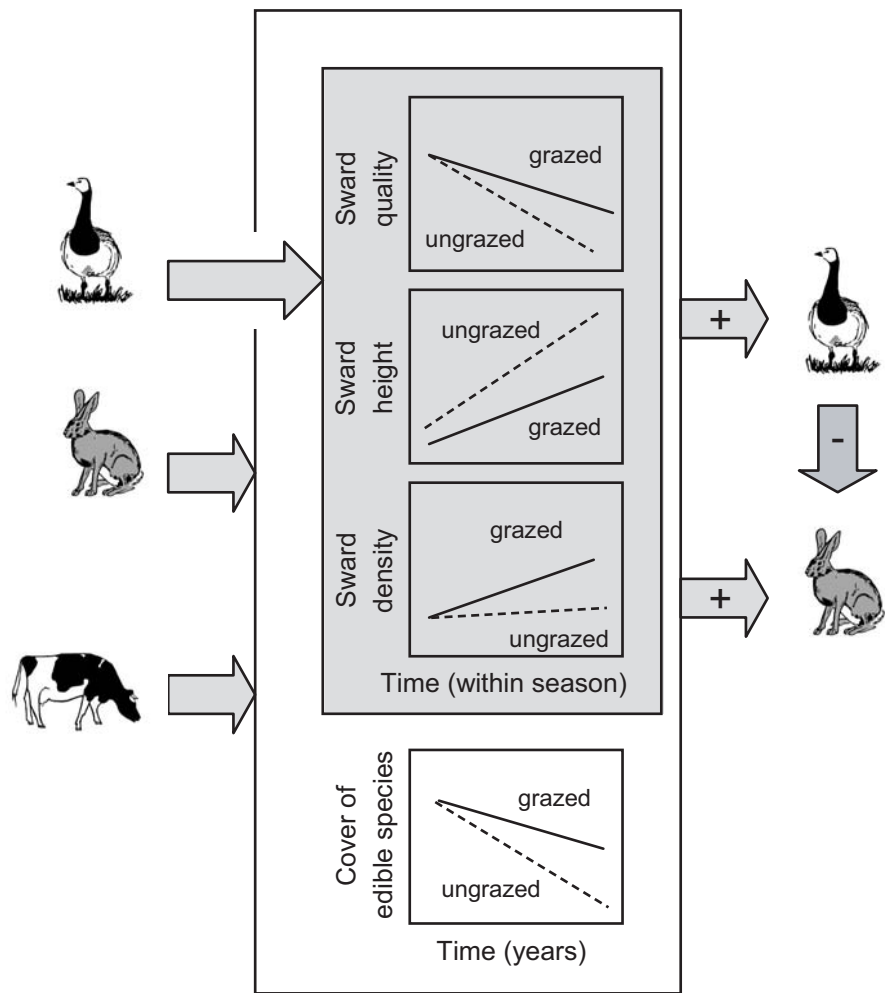


Figure 11.2: Overview of the short- and long-term effects of grazing on sward properties during spring and the consequences for subsequent use by wild herbivores. Dashed lines represent the ungrazed swards, solid lines grazed swards.

Livestock

Most coastal meadows and salt marshes in temperate areas are traditionally grazed by livestock. Grazing by livestock promotes a short dense sward, in which the shoots have a high nitrogen content (Van de Koppel *et al.* 1996; Hassall *et al.* 2001; Van der Graaf *et al.* 2002; Bos *et al.* 2005b). This thesis (Box 2; Chapter 10), as well as other studies, show that geese prefer these swards (Summers and Critchley 1990; Vickery *et al.* 1994; Prop *et al.* 1998; Hassall *et al.* 2001; Van der Graaf *et al.* 2002; Bos *et al.* 2005b). Moreover, grazing favours a high cover of grasses and prevents the encroachment of reeds, shrubs and tall plants such as *Elytrigia atherica* into the coastal meadows (Andresen *et al.* 1990; Olff *et al.* 1997; Jutila 1999; Bakker *et al.* 2003; Kuijper and Bakker 2004). In my study, I found a preference of geese for short grazed swards, in particular during the gosling-rearing period (Chapter 10). In those highly productive marshes in temperate areas, such as our study sites in the Wadden and Baltic Sea, grazing is of prime importance for the maintenance of good foraging sites for geese (Box 2).

Hares

The European Brown Hare (*Lepus europaeus*) is a wild herbivore that co-occurs with geese in temperate salt marshes. Similar to the geese, hares prefer to graze in areas with a low canopy height (Kuijper and Bakker 2003). However, studies on the temperate salt marsh of Schiermonnikoog have shown that hares themselves can retard vegetation succession for at least 20 years by preventing woody or fibrous plants becoming dominant, such as the woody forb, *Atriplex portulacoides*, in the low marsh and the tall grass *Elytrigia atherica* in the higher marsh (Van der Wal *et al.* 2000; Kuijper and Bakker 2003; Kuijper and Bakker 2004; Box 1). However, hares cannot stop succession in the long term. By preventing the dominance of tall species, hares enhance feeding conditions for geese (Van der Wal *et al.* 2000). Geese do not have similar effects on the vegetation: when only geese were excluded experimentally there were no significant changes in species composition of the vegetation (Kuijper and Bakker 2004). Geese profit from the presence of hares on salt-marsh sites. Besides this facilitative interaction, I show in this thesis that there is also indirect competition between geese and hares, forcing hares to forage on less preferred sites (Chapter 6).

Geese

Though geese cannot retard succession or influence vegetation composition, similar to livestock and hares, they can potentially impact forage quantity and quality. Geese can facilitate future grazing of a patch in two ways: by the mechanical removal of plant material as a result of grazing and by the fertilisation effect of their droppings on the vegetation. In Chapter 6, I show evidence for within-species facilitation: utilisation of foraging sites by geese is positively correlated with previous grazing by either hares or geese. At my study site in the Wadden Sea, I found positive effects of Barnacle Goose grazing on the vegetation. In grazed sites the nitrogen content of shoots of *Festuca rubra* was significantly higher than that in ungrazed sites (Chapter 6). Moreover, grazing had significant effects on sward characteristics; the proportion of dead material in the vegetation was reduced and production of additional axillary tillers increased as compared to that in ungrazed swards (Chapter 7). When extrapolating these experimental findings to foraging opportunities for staging geese, I calculated that under the current grazing pressure of the geese, potential harvest and carrying capacity of the marsh is maximised.

Besides the effects of tissue removal by grazing, many studies report a fertilising effect of herbivore faeces on grazed vegetation. The best-known example is the salt-marsh of La Pérouse Bay, where goose-grazed sites have significant higher production and nutritional quality than ungrazed sites. I did not find effects of fertilisation by goose droppings either on plant biomass or quality on marshes along the Barnacle Goose flyway (Chapter 8). A comparison of studies on the effects of goose grazing on the growth and quality of forage plants reveals that a fertilising effect of droppings is only found under very specific conditions, a high natural grazing pressure and very low nitrogen availability in the soil. We can conclude that, along the flyway of Barnacle Geese, geese can improve their forage quality and biomass by the mechanical removal of tissue through grazing which enhances tillering and maintains a young sward, however, fertilisation by droppings does not play a role in the short-term.

A changing world: human impact along the flyway

Goose populations: growth and range expansion

In recent years we observe a tremendous increase in the size of goose populations all over the world. In North-America, the populations of Greater and Lesser Snow Geese (*Chen caerulescens atlanticus* and *Chen c. caerulescens*) increased dramatically from the late 1960's to the mid-1990's (Gauthier *et al.* 2005; Abraham *et al.* 2005). In Europe, wintering populations of Pink-footed Geese (*A. brachyrhynchus*), Greenland White-fronted Geese (*A. albifrons flavirostris*), Bean Geese (*A. fabalis*), Greylag Geese (*A. anser*) and Barnacle Geese increased since the 1960s (Fox *et al.* 2005; Van Eerden *et al.* 2005). Along with the

increase of wintering numbers of Palearctic goose species in Western Europe, the number of exotic species also increased and Egyptian (*Alopochen aegyptiacus*), Canadian (*Branta canadensis*) and Bar-headed Geese (*Anser indicus*) are now common sights on grasslands in Europe (Lensink 1998; Van Horssen and Lensink 2000; Van Roomen *et al.* 2004). These neozoic populations are non-migratory and breed successfully in the new habitats (van Dijk *et al.* 2005). Simultaneously, palearctic species like the Greylag and the Barnacle Goose expanded their breeding range towards temperate regions (Forslund and Larsson 1991; Loonen and de Vries 1995; Van Eerden *et al.* 2005; Chapter 10).

The increase in goose numbers is usually attributed to changes in human land use, such as increased fertilisation of grasslands, cultivation of wheat, corn and rice (Abraham *et al.* 2005; Van Eerden *et al.* 2005) and changes in harvesting techniques (Shimada 2002). The expanding goose populations increasingly started to shift their foraging habits, especially in the wintering range, from foraging on natural grasslands to foraging on crops (Ganter *et al.* 1999; Fox *et al.* 2005; Gauthier *et al.* 2005). The expanding goose population and the increased use of agricultural fields leads to strong conflicts with agriculture (Prop *et al.* 1998; Vickery and Gill 1999; Cope *et al.* 2003; Amano *et al.* 2004; Fox *et al.* 2005; Abraham *et al.* 2005).

As a consequence of increasing numbers, many populations experience a density-dependent decline in reproductive output. In North America, the populations of Black Brant, *Branta bernicla nigricans*, as well as Lesser Snow Geese show a strong density-dependent decline in gosling growth, body mass and survival as population size increases at the local level (Williams *et al.* 1993; Sedinger *et al.* 1998; Person *et al.* 2003), in the Russian Arctic a density-dependent effect on reproduction was found for Red-breasted Geese, *Branta ruficollis* (Prop and Quinn 2003). For the Barnacle Geese, previous research has shown that the Spitsbergen breeding population as well as the new breeding populations on Gotland experience decreasing breeding success with increasing population size, due to density-dependent effects (Larsson and Forslund 1994; Loonen *et al.* 1997; Larsson and Van der Jeugd 1998; Drent *et al.* 1998; Loonen *et al.* 1998). Despite these declines in breeding success that have been reported locally, there is no suggestion of stabilisation of numbers at the population level, except on some specialised maritime species such as Dark-bellied Brent Geese.

Traditional versus new breeding sites

The green-wave hypothesis predicts that avian herbivores travel along a climatic gradient during their spring migration from temperate staging sites to Arctic breeding sites, taking advantage of the successively delayed spring flush of plants at each staging site, hence “surfing on a wave of forage availability” as they move along the migration corridor (Drent *et al.* 1978; Owen 1980). In my study, I show that Barnacle Geese time their migration to coincide with peaks of nutrient availability in the vegetation along the flyway (Chapter 5).

In the Wadden and Baltic Sea they profit from the peak in nutrients just before migration. In the Russian breeding sites the geese arrive soon after snow melt and well ahead of the peak in nutrient content of the biomass, and start nesting upon arrival. When the goslings hatch, nutrient levels in the vegetation just reached their peak and the goslings and their moulting parents profit from this highly nutritious forage (Sedinger and Raveling 1986; Bos *et al.* 2004; Chapter 5). The high peaks of nutrients in plant biomass at hatching in the Arctic breeding sites is combined with a low canopy height of the sward that ensures a high intake rate (Chapter 4). The long daylight period enables the geese to forage for almost 24 hours each day. These are ideal conditions for the growing goslings that have high nutrient requirements as well as for their parents that need to compensate for reserves lost during the incubation period and for the energetically costly period of wing moult.

Furthermore, on the islands where barnacle geese traditionally breed, Vaygach and Novaya Zembyla, human disturbance is now absent. Along the Russian mainland coast many small settlements were established during the former Soviet regime. It is suggested that these coastal sites could have been part of the traditional breeding range of the geese prior to human settlement (Syroechkovsky Jr. 1995). However, records of early Arctic explorers indicate that the area was already populated in the 17th century by people living from fishing and hunting (Van Linschoten 1601, re-issue of the logbooks by Van der Moer 1979). For the people living in these small coastal villages, eggs and geese formed an important supplement to their diet of dried fish which was the main winter food. It is likely that human disturbance eradicated former breeding colonies in the surroundings of the settlements and prevented the establishment of new ones. Van Linschoten, however, did observe large numbers of (Brent) geese and other waterfowl in mid- July, indicating that the area was used for foraging at least during wing-moult. With the disappearance of human activities from these coastal sites after the fall of the Soviet regime, the salt marshes were re-colonised as breeding sites for waterfowl and geese expanded their breeding range within the Russian sub arctic.

The first colonies in the Baltic were established in the time that most of the Russian settlements were still inhabited and the breeding range of barnacle geese was restricted to the islands of Novaya Zembyla and Vaygach. Though breeding sites were probably not limited on the traditional breeding grounds of these islands (Filchagov and Leonovich 1992) it is likely that, with a rapidly expanding goose population, foraging resources started to form a constraint. As a consequence density-dependent processes could have started to act during the gosling-rearing period resulting in a reduction of the reproductive output of these colonies. There are no vegetation data from these areas, but we assume vegetation on the foraging sites is largely comparable to that on our Russian study site (note – the nesting sites are very different). In recent years on Gotland we have seen that the geese themselves strongly influence their food supply. Because of the high grazing pressure early in spring,

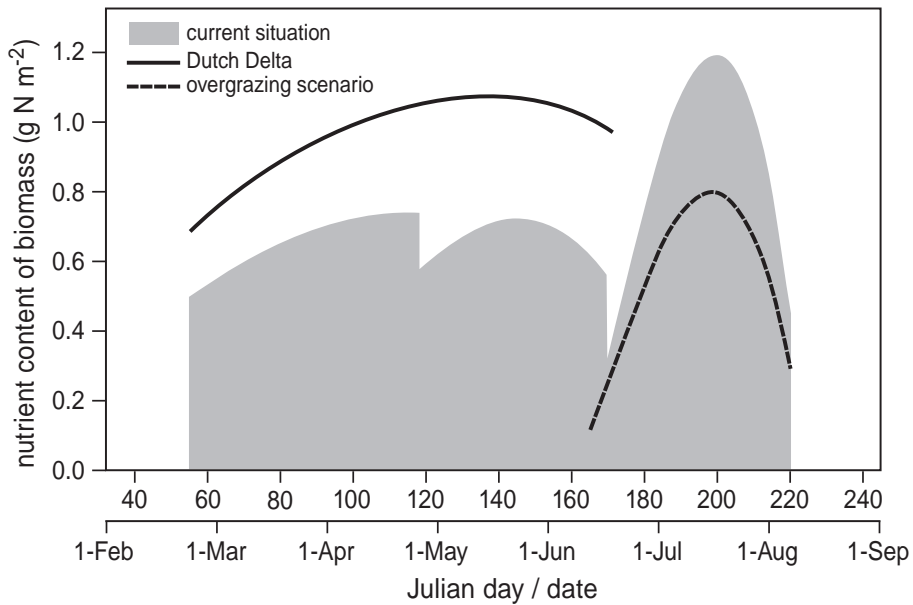


Figure 11.3: The green wave of nitrogen content of biomass per unit area (g N m^{-2}) at the Dutch Wadden Sea, the Baltic Sea and northern Russia (Chapter 5, shaded areas) with an alternative scenario for the Russian sites under heavy grazing pressure by geese (dashed line) and the current situation in the Dutch Delta (solid line).

biomass levels are depressed throughout the staging period (Chapter 5). When the traditional Arctic breeding colonies of the Barnacle Goose grew, food supply during the gosling-rearing period may have become limited. We might assume that the development of biomass and its nutrient content at the traditional Russian breeding sites were similar to values at our study site in the Pechora Delta, and that the grazing pressure was as high as that on Gotland early in the season, where the geese consumed approximately $0.5 \text{ g DWT m}^{-2} \text{ d}^{-1}$. Under these assumptions we can construct a scenario of the seasonal development of nitrogen content of the vegetation at the traditional breeding sites with this specific grazing pressure (Figure 11.3). In this scenario the peak in nutrient-rich biomass on the traditional breeding sites is severely reduced. In fact, the level of nutrient-rich biomass is becoming comparable to that of the ungrazed situation on Gotland (Figure 11.3). Under this scenario, Gotland, during the period the colony was established, may have proven to be a more profitable foraging site with a similar nutrient content in the biomass as that at the Russian breeding sites, but with less competition for these resources.

Larsson *et al.* (1988) concluded that the establishment of the colonies in the Baltic was genuine and that the founder birds originated from the Russian population. This founder population probably consisted of non-breeding birds that had lagged behind on Gotland in the previous years during the moulting period (Larsson *et al.* 1988). These pioneers may have recognised that foraging opportunities on Gotland were comparable to those on the traditional breeding (Figure 11.3) grounds and attempted to breed in Gotland. This strategy proved successful and the colony grew rapidly as a result of a high reproductive output (Forslund and Larsson 1991; Larsson and Van der Jeugd 1998). However, also further immigration from the Russian population took place (Larsson *et al.* 1988). During a recent period, when population growth in the Baltic levelled off due to density-dependent effects (Larsson and Forslund 1994), geese remained behind in the wintering areas in the Netherlands during summer and finally started breeding in the Dutch Delta (Meininger and Van Swelm 1994). In the Netherlands, eutrophication of surface water and high levels of fertilisation of pastures (Van Eerden *et al.* 2005) resulted locally in grass swards with an extremely high nutrient content during summer (Pouw *et al.* 2005). Due to this high quality food supply and the absence of ground predators on the breeding sites, breeding success is high and the population is rapidly expanding.

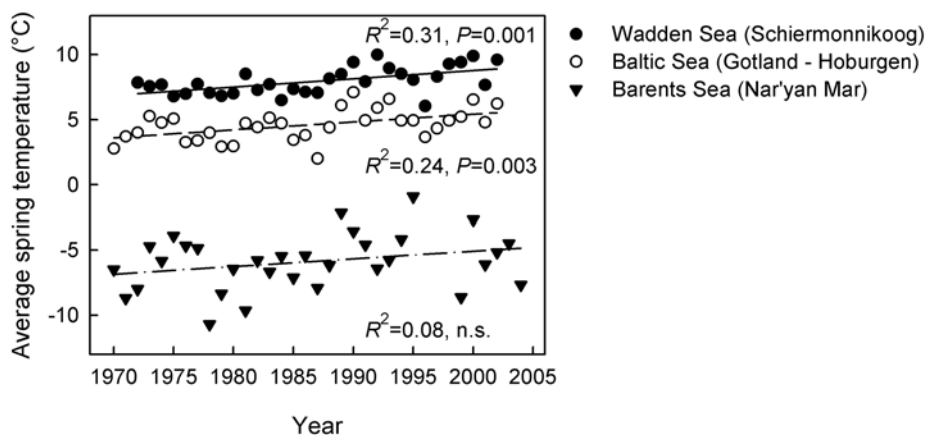


Figure 11.4: Average spring temperature from 1970 until present in the three study areas, with the results of a linear regression. Mean increase in all three regions amounts to an approximately 2°C increase in the past 30 years.

Climate change

The recent expansion of the breeding range of Barnacle Geese does not raise concerns for the persistence of the species in the future. It appears that the geese are increasing in numbers and expanding into new breeding areas. However, human impact along the flyway becomes also evident through a change in spring temperatures, likely caused by global warming. Climate change models predict an increase in globally averaged temperatures of 0.8-2.6 °C for the period of 1990-2050, long-term predictions up to the year 2100 even predict an increase of 1.4 – 5.8 °C (IPCC 2001). For Arctic regions this increase is predicted to be even stronger, an increase of 2.5-14 °C for winter and 4.0-7.5 °C for summer temperatures (IPCC, 2001). In the Wadden and Baltic Seas, we can observe an average increase in spring temperatures (March-May) of about 2 °C in the last 30 years (Figure 11.4). Since plant growth is strongly linked to temperatures in the growing season, increasing spring temperatures will advance peaks in forage availability and quality and thus the most suitable timing of spring migration for Barnacle Geese. I have shown that with a conservative climate change-scenario which predicts a 1°C- increase in temperatures along the flyway, Barnacle Geese will be able to adjust to shifts in plant phenology and the earlier occurrence of spring by adjusting their migration dates (Chapter 6). Moreover, the White Sea offers a buffer area where they can stay for variable periods depending on the advancement of spring at their breeding site. I predicted that the total nitrogen content of the biomass in the White Sea area, based on climatic data from Archangelsk combined with vegetation data from our Russian study site, since forage species are similar in these areas (pers. obs.). The peak in the nitrogen content of the biomass per unit area in the White Sea area falls exactly in between the peaks in the Baltic Sea and on the Barents Sea breeding site and therefore establishes the White Sea coast as an ideal pre-breeding site.

Figure 11.5 A and B depict consequences of climate change for the green wave, the peaks of nutrient availability in biomass per unit area that Barnacle Geese follow on their migration for a conservative 1°C- increase scenario and a less conservative 5°C-increase scenario. For the conservative scenario, we observe only slight changes; however, with a scenario of a 5°C we observe a dramatic advancement of plant growth. It also becomes clear that forage plants in the three regions differ in their response to rising temperatures. An average increase of 5°C has less significant consequences for plant phenology on the Arctic sites than it has at the more temperate sites. If geese adjust their travel schedules to major shifts of plant phenology at these temperate sites, advancing their migration by more than one month, they would arrive too early in their breeding sites and find them covered in snow. However, the White Sea still acts as a buffer zone; peak nitrogen levels in biomass per unit area still fall in between the peaks at the Baltic Sea and the Barents Sea breeding sites.

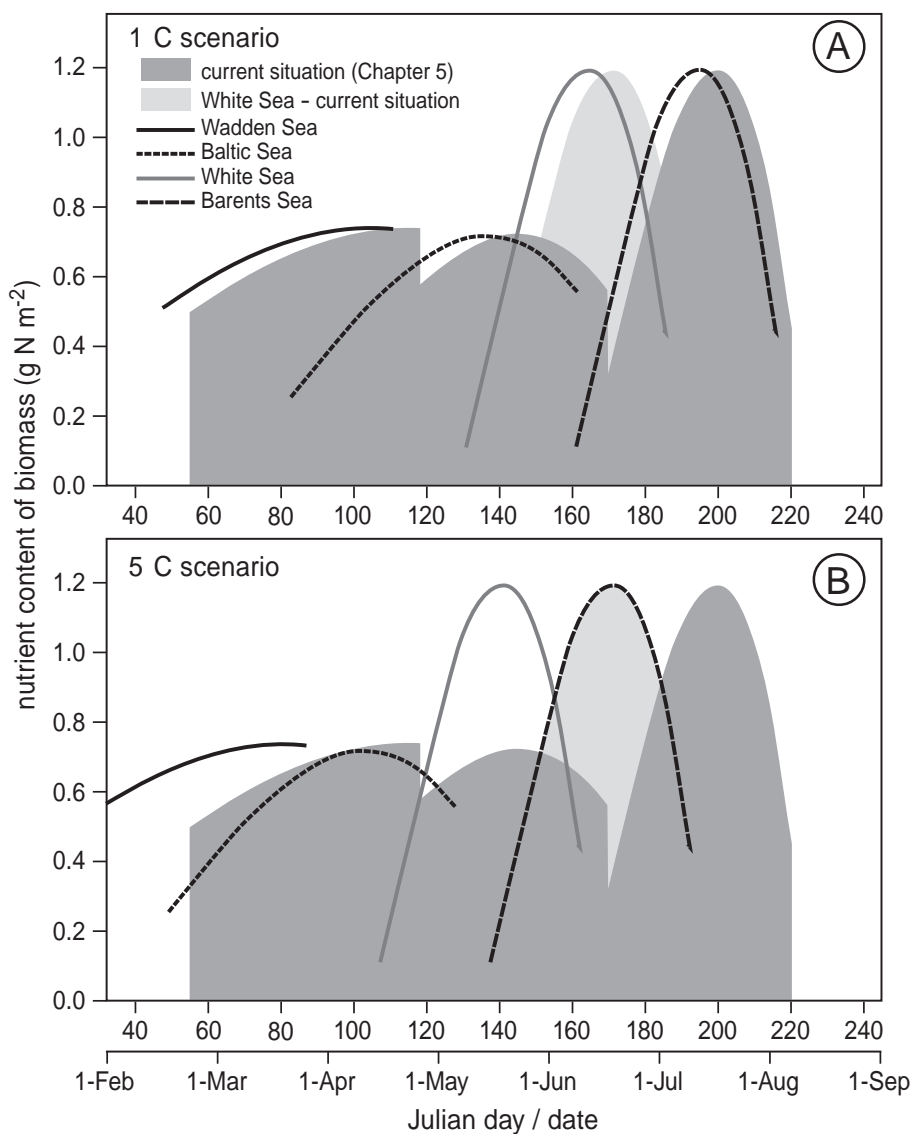


Figure 11.5: The green wave of nitrogen content of biomass per unit area (g N m^{-2}) at a Wadden Sea staging site, a Baltic Sea stopover site and a Russian breeding site (Barents Sea), as described in Chapter 5 (dark shaded area), as well as in a White Sea pre-breeding site (light shaded area) at present and under a conservative climate change scenario of 1°C increase (A) and a progressive scenario of 5°C increase (B).

In my study on the effects of temperature increase on the forage resources of the geese along the green wave, I disregarded long-term vegetation changes. With increasing temperatures plant species that were previously only found in more southern areas can expand their northern distributional range and invade existing northern plant communities (Metzing 2005). Increased competition may lead to changes in plant communities and possible disappearance of the communities favoured by geese. For example, with climate change a species such as *Elytrigia atherica*, which currently has its northern boundary in Northern Germany, may extend its range, and form a threat for salt marshes in the Baltic, where current levels of grazing intensity by livestock are insufficient to prevent the species from becoming dominant. Similarly, on some sites along the Baltic Sea coasts the low stocking rate can not avert the encroachment of *Phragmites australis* (Juttila 1999; Juttila 2001; Dupré and Diekmann 2001). These kinds of changes are, however, beyond the scope of a PhD period and invite long-term monitoring in a coordinated international programme.

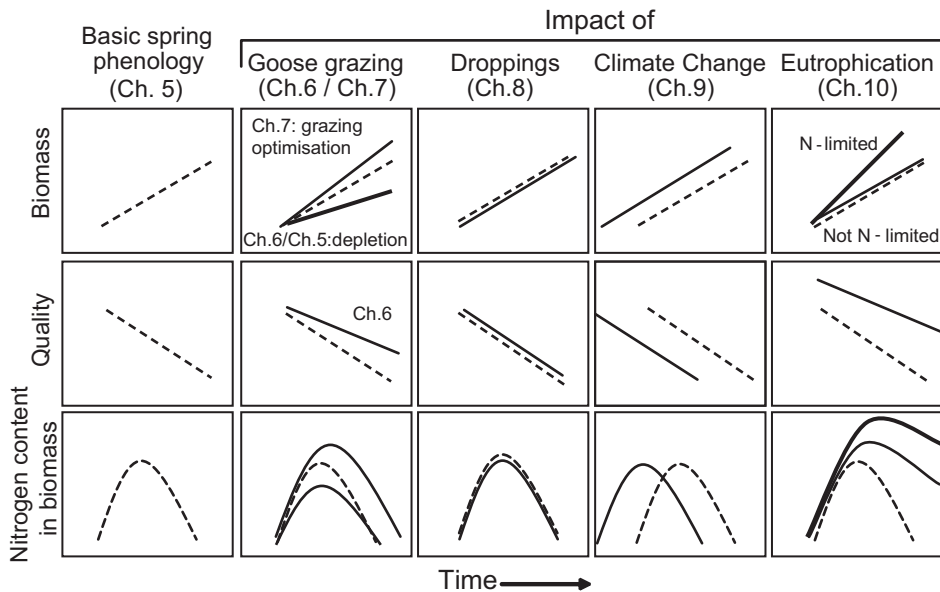


Figure 11.6: The phenology of plant growth in spring and additional effects of goose grazing, fertilisation by goose droppings, climate change and eutrophication on the "green wave" of nitrogen content in biomass per unit area. Dashed lines indicate the basic spring phenology, solid lines the additional effects. Where appropriate, an alternative scenario is indicated with a bold line.

Flexible migrants in a changing world

Flexible migrants

My results suggest that even with large increases in temperatures in the next decades the “green wave” of food availability from temperate staging sites, to stopover sites in the Baltic and White Sea to breeding sites in the Russian Arctic, will remain intact. However, based on my investigations, I cannot predict whether Barnacle Geese will prove flexible enough to keep up with this advancement in phenology. The geese will have to advance their migration by more than one month in order to keep up with the green wave. We can, nonetheless, speculate about the flexibility of the migratory schedule of the geese by looking at their response to changes in the past. For example, when Barnacle Geese expanded their breeding range to the Baltic Sea they encountered a completely different set of environmental variables. Optimal timing of peak hatch was earlier (Chapter 5) and the geese adapted rapidly by moving the timing of peak hatch more than one month from mid-July in the Arctic areas (Van der Jeugd *et al.* 2003) to the end of May in the Baltic breeding sites (unpubl. data H. van der Jeugd). At present, in the Baltic colonies young hatch just a week after Russian geese have left on their migration to the breeding grounds (Chapter 5). Timing of wing moult also advanced significantly though not as much as the breeding dates (Van der Jeugd *et al.* 2003). Similarly, dates of peak hatch have advanced even more in the recently established Dutch colonies (end of April; Pouw *et al.* 2005). In the past decade overall timing of departure from the Wadden Sea and Baltic Sea has changed (Stock and Hofeditz 2002; Leito and Truu 2004; Günther and Koffijberg 2005; Eichhorn *et al.* 2006). These new strategies may either be a result of an adaptation to increasing temperatures (Chapter 9) or can be seen as a completely new strategy in order to avoid overcrowding on the traditional spring staging sites (Günther and Koffijberg 2005; Eichhorn *et al.* 2006). Whatever the underlying causes maybe, it shows that migration and breeding date, as well as the choice of staging areas of Barnacle Geese are flexible.

And a changing world: future predictions

With changes in climate as well as in land use, phenology of the forage plant species of Barnacle Geese will alter dramatically and differently in each area along the flyway (Figure 11.7). First of all, in all areas global warming will advance plant phenology and peaks in forage availability. For the spring staging areas in western Europe two trends exist; traditional salt-marsh habitats will show a reduction in quality of the foraging sites as well as a reduction in the number of suitable sites, due to cessation of livestock grazing. Secondly, the livestock-grazed pastures in the Dutch Delta region and at sites adjacent to the Wadden Sea that are at present used by part of the population during wintering and during spring-staging, will provide forage of high quality. This can be attributed to a high nitrogen input from eutrophicated surface water (pers. comm. HvdJeugd), artificial fertiliser

and aerial nitrogen deposition (Van Eerden *et al.* 2005). Although salt marshes are still favoured as foraging sites by Barnacle Geese, we will most likely witness an increased use of agricultural pastures as a refuge for the surplus number of geese during the spring-staging period (Bos and Stahl 2003). Furthermore, the agricultural pastures remain at a level of high tissue quality throughout the spring season, when natural marshes show a rapid decline of plant quality due to tissue maturation. The geese here will thus be able to stay longer and depart later. This delay in spring migration has already been observed during the past decade (Stock and Hofeditz 2002; Günther and Koffijberg 2005; Eichhorn *et al.* 2006). It is likely that the effects of the prolonged availability of high quality forage within one spring season (enabling the geese to stay longer), and the effects of an advancement of spring through climate change (forcing the geese to advance migration, Chapter 9), will partly counteract each other.

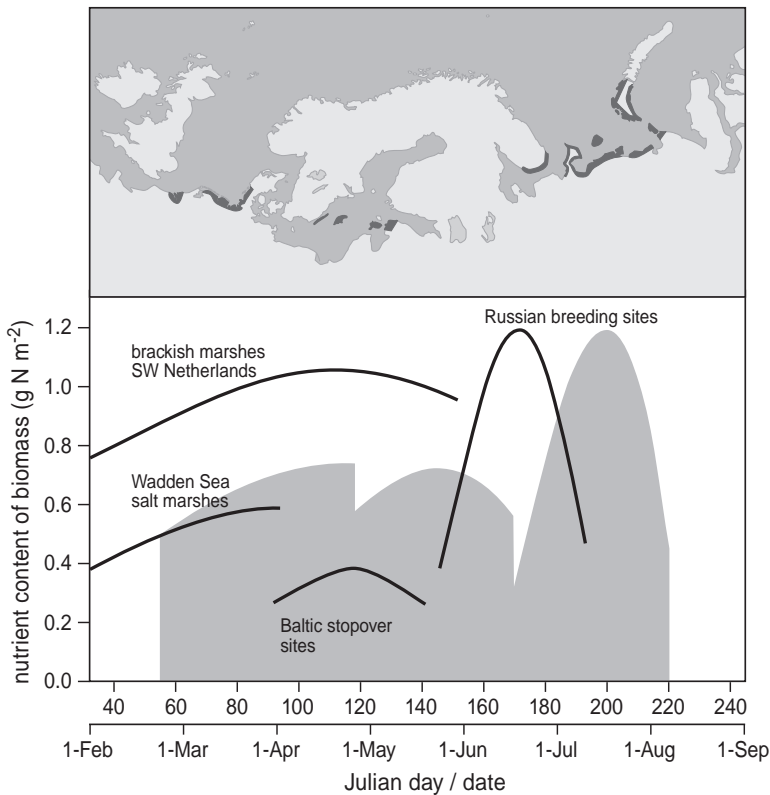


Figure 11.7: The green wave of nitrogen content of biomass per unit area (g N m^{-2}) at a Wadden Sea staging site, a Baltic Sea stopover site and a Russian breeding site (Barents Sea), as described in Chapter 5 (dark shaded area) with projected scenarios for the different areas with changes in climate and in land use (solid lines).

On the traditional stop over sites on Gotland food availability is low due to a high grazing pressure of geese. However, in other coastal areas in the Baltic Sea, geese are present in low numbers and will not deplete forage within one season or retard successional change of the vegetation in the long term. Due to the cessation of livestock grazing at many Baltic coastal sites, it is likely that the availability of suitable foraging sites as well as the cover of edible species will further decline in the near future. Partly as a result of the low forage availability and overcrowding on the Baltic stopover sites, part of the population already changed its migration pattern and now skips the stopover period in the Baltic Sea (Eichhorn *et al.* 2006). These birds depart later from the spring-staging areas in the Wadden Sea and probably stay for an extended period of time along the White Sea coast near Archangelsk.

Extensive parts of the coastline of northern Russia where human disturbance is absent will probably host an increase in numbers of breeding pairs of barnacle geese in the coming decades. The island of Kolguyev was colonised by Barnacle Geese in the early 1990's (Syroechkovsky Jr. 1995) and currently harbours the largest colony of Barnacle Geese in the world, geese breed here along 20 kilometres of coastal wetlands (pers. comm. K.Litvin). At our study site at the Kolokolkova Bay, the Barnacle Goose colony was founded soon after the village of Tobseda was deserted by its human inhabitants in 1996/1997 and horse grazing on the marshes ceased (pers. comm. Wasily, Tobseda). The population grew rapidly from 56 nesting pairs in 1999 to 3454 nests in 2003 (Mineev and Mineev 2004).

It is difficult to make predictions concerning future population trends of this flexible species; the increased availability of breeding sites in the Russian Arctic as well as on the more temperate sites might well be counteracted by a loss of good-quality stopover sites in the Baltic Sea. The apparently high quality of fertilised agricultural pastures that are used increasingly as foraging sites might be deceiving. Prop and Black (Prop and Black 1998) observed that geese foraging on agricultural fields in Norway had a lower retention efficiency of nitrogen. These geese acquired more fat relative to protein and subsequently had a lower breeding success than birds foraging on non-fertilised habitats. The authors suggest that birds from fertilised agricultural sites have acquired fewer protein reserves and either lack adequate muscle development to carry sufficient reserves on migration, or lack the necessary proteins for egg production after arrival on the breeding grounds (Prop and Black 1998).

Advancing phenology through climate change, forces birds to advance their laying dates in order to keep up with the time of maximum food availability for rearing of young. Many bird species in temperate areas have been unable to advance their laying dates sufficiently over the past decades to avoid a fitness cost (Visser *et al.* 2004). However, Barnacle Geese have proven rather flexible in timing of reproduction. From Figure 11.5 we can derive that under a scenario of a 5°C increase in temperatures, Barnacle Geese nesting

in the Russian Arctic must advance their laying date by about one month in order to profit from peak nitrogen levels in biomass during the gosling-rearing period; a shift similar to that already achieved in the Baltic

Further research is needed into the reproductive consequences of foraging decisions during spring staging in order to make predictions on the effects of changes in land use and climate on the dynamics of the Barnacle Goose population.

Conclusion

At present, food resources along the East Atlantic Flyway of Barnacle Geese are subject to rapid changes. People are influencing coastal areas along the flyway, but their impact differs at each site. In northern Russia and eastern Europe coastal areas are abandoned and livestock grazing has ceased. On the other hand, in western Europe areas are continuously grazed and heavily fertilised, while areas designated as nature reserves are either grazed at low stocking rates or left ungrazed. Finally, climate change will become an even more prominent factor influencing coastal habitats in temperate and arctic regions in the very near future. In a world that is continuously changing, Barnacle Geese face a completely new set of foraging parameters along the entire flyway on which they have to base decisions of migration and breeding. However, Barnacle Geese have proven rather flexible in the past and probably will be able to adjust to the imminent changes in the future.



Foraging Barnacle Goose families on Gotland (June 2004)



Rudi Drent measuring temperature at the salt marsh near Shoina, Kanin peninsula, Russia (May 2002).

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Reindeer sledge from visiting Nenets in the village of Tobsseda, June 2003

Summary

Background

In historical times, the biology of Arctic breeding geese was shrouded in mystery. In the first months of the year they used to be present in large numbers in Europe, but they disappeared at the end of spring, only to return in autumn. People had never seen geese breeding and people in the Middle Ages, therefore, believed that Barnacle Geese grew from the shells of Goose Barnacles, hence their name. Only in the 16th century, Dutch explorers discovered the breeding sites of this species. At present, we can find breeding Barnacle Geese even in their former wintering areas, but the story above shows that it has not always been like this. The recent expansion of the breeding range of the Barnacle Goose raises questions, not only about the reasons for this expansion, but also on the traditional restriction of geese to Arctic regions which required a long energy-demanding journey in order to breed. In the first part of my thesis I will investigate the choice of geese for staging and foraging sites along the traditional migration route. In the second part I will investigate changes in forage availability in these areas, caused by the geese themselves, by other herbivores and by human activity, as well as the consequences of these changes for the geese.

Foraging choices of Barnacle Geese, from temperate to Arctic

Study sites

During my study I had the opportunity to work along the entire flyway of the Barnacle Geese. My main study sites were a temperate staging site in the Dutch Wadden Sea: the island of Schiermonnikoog (*Box 1*), a stop-over site in the Baltic Sea: the Swedish island of Gotland (*Box 2*) and a breeding site in the Russian Arctic, near the village of Tobse, Russia (*Chapter 2*). The food sources of the geese change from *Festuca rubra* on salt marshes of the Wadden Sea and Baltic to *Puccinellia phryganodes* and *Carex subspathacea* at the Russian stopover and breeding sites. However, in temperate regions the geese also have started to feed in agricultural fields, where they forage mainly on *Lolium perenne* (Wadden Sea) and *Phleum pratense* (Baltic Sea).

On all sites we determined usage of the sites by means of transects. On these transects we measured several vegetation parameters and counted droppings on a fixed area to determine usage by the geese. In all areas geese preferentially foraged in areas with a short, dense canopy and a high cover of grasses (*Box 1*, *Box 2*, *Chapter 2*).

Foraging choices

Barnacle Geese traditionally breed in the Arctic and winter in more southern, temperate areas. During spring migration, the birds have to balance their energy expenditure and food intake, in order to build up sufficient energy reserves to be able to migrate to their breeding areas and breed successfully. The birds usually migrate in several distinct steps, and refuel and rest at each stopover site. Plant forage availability and quality on these sites play a crucial role for these small herbivores, as the amount of body reserves accumulated by individuals prior to migration directly affects breeding success. At the breeding sites, food availability and quality influence gosling growth rates, which determine final adult body size and post-fledging survival. Food availability and quality along the flyway, thus, shape fitness and life history parameters. However, the herbivores are faced with a dilemma on their migration; as an increase in plant biomass frequently corresponds with a decline in food quality.

In order to unravel the relative contribution of forage quality and forage biomass to foraging choices in Barnacle Geese, we experimentally manipulated biomass and quality of main forage plants through fertilisation and grazing exclusion at three sites along the migration flyway and offered these treatments to wild geese in a multifactorial, replicated design (*Chapter 3*). Fertilisation increased the nitrogen content of the forage and grazing exclusion increased biomass levels. Goose visitation was measured based on dropping counts. At all sites, goose visitation was highest on plots with a combined increase of biomass and quality. Generally, geese preferred plots with the highest nitrogen availability per surface area. The numerical response of the geese to forage changes was supported by behavioural observations at one site. Plots with a combined increase of biomass and quality were defended vigorously against flock mates. The geese maximised nutrient intake through distinct choices for forage of the highest quality and optimal biomass levels.

In the literature, much attention has been given to the selection of high quality forage by geese and other small herbivores. However, besides food quality, the rate in which the geese can process their food, their intake rate, is another very important factor determining foraging patch selection for small herbivores. We have tested the effects of sward density and height on the functional foraging response of Barnacle Geese (*Chapter 4*). The functional response curve for herbivores describes how intake rate is affected by food availability. We conducted feeding trials in order to determine intake rate and bite size on experimentally manipulated swards. Results indicate that intake rate is mainly dependent on sward height, and that there is a strong correlation between bite size and intake rate. In general, wild herbivores are found to prefer patches with a lower canopy height than that on which they could maximise intake rate. Most likely, patch choice is a combination of selection for a high intake rate and for high forage quality (*Chapter 11*), which usually occurs at even lower canopy heights.

Geese on a green wave

Along the flyway, the availability of high quality forage peaks reaches a maximum at different points in time, depending on timing of the onset of spring. The “*green-wave hypothesis*” predicts that during spring migration to northern breeding sites, geese travel along a climatic gradient, taking advantage of the flush of spring growth of forage plants at each stopover site along the gradient. In *Chapter 5*, we explore a basic assumption of the green wave hypothesis which states that there are successive waves of forage availability along the East Atlantic Flyway from temperate to Arctic sites, as spring advances. We collected data on forage biomass and quality at the three salt-marsh sites along the traditional migration route. At all sites forage biomass increased in spring, while the nutritional quality peaked early in the season and declined with increasing biomass. For all sites, nitrogen in biomass per unit area, the combined measure of forage biomass and nutritional quality, showed a peak in early spring.

We used observations on goose migration to examine whether the geese utilise these peaks in nutrient biomass, as the green wave hypothesis predicts. We found that the geese use the Wadden Sea staging site and the Baltic stopover site at the moments of peak availability of nitrogen in biomass per unit area. At the Russian breeding site, however, geese arrived prior to the flush of spring growth of forage plants, but profited from the peak in nitrogen when the goslings hatched and adult birds started moulting. The spring increase of nitrogen in biomass at the successive sites along the flyway is, therefore, a key factor driving the timing of the annual northern migration of avian herbivores

Flexible migrants in a changing world

Facilitation and competition between herbivores

Overlap in habitat use between herbivores can result in both competitive and facilitative interactions. Competition usually occurs through resource depletion, in which one species of herbivore depletes forage reserves for another (or the same) species. Facilitation occurs when foraging conditions for one herbivore species are improved through the foraging activities of another or the same herbivore species, at an earlier point in time. A well-known example describes how dense concentrations of migratory Wildebeest (*Connochaetes taurinus*) deplete plant biomass in the Serengeti Plains, while at the same time their grazing stimulates net primary production. Thomson’s Gazelles (*Gazella thomsonii*), which arrive in the area a month later, are thus able to profit from the low canopy and dense highly nutritious biomass that was created by the preceding Wildebeest grazing.

We investigated competitive and facilitative interactions between wild Barnacle and Brent Geese and European Brown Hares on our study site in the Dutch Wadden Sea (*Chapter 6*). In a multifactorial experimental design we manipulated biomass and quality of

grass swards and determined foraging preferences of the wild herbivores. We found that both goose species selected plots with plants which had a higher nitrogen content, Barnacle Geese avoided plots with high plant biomass. Furthermore, we found that grazing increased the quality of the vegetation within a season. Hares, on the other hand, preferred the combination of high biomass with high plant quality, when geese are absent. However, in the natural situation with geese present, hares selected high biomass swards. Indirect competition through forage depletion by large numbers of geese in spring, thus played a significant role determining the foraging choices of hares. In contrast, Barnacle Geese profited from grazing facilitation by other small herbivores which delayed the maturation of forage tissues and, thus, ensured high quality forage.

In another experiment we tested whether geese could increase their own harvest by repeated grazing (*Chapter 7*). We manipulated grazing intensity on *Festuca rubra* swards through trials with captive Barnacle Geese in early spring and measured the growth response of individually marked tillers. Aboveground biomass production of the individual tillers was not different among different grazing intensities. The biomass lost in grazed tillers was compensated by a lower senescence. Goose grazing significantly affected sward characteristics; the proportion of dead biomass in the vegetation was reduced and production of additional axillary tillers increased. When we extrapolated these experimental findings to foraging opportunities for staging geese, we calculated that goose grazing at naturally occurring levels increases potential harvest. The experiment demonstrated an increase in carrying capacity of the staging site for migratory geese through grazing. When comparing the experiment with grazing levels of wild Barnacle Geese, it turns out that current goose densities maximise potential harvest.

Besides impacting forage availability through grazing activities, herbivores can also affect forage availability and quality as a consequence of fertilisation by faeces. In systems with low plant productivity, such as our study sites, these enhancing effects can be significant for the herbivores themselves. Using field experiments, we investigated the effects of goose droppings on biomass production of the main forage species of the geese and its nutritional quality, at the three study sites along the migration route (*Chapter 8*). We expected that fertilisation from droppings would have a significant effect on the forage species because of presumed low nutrient availability in the soil and the high inputs of droppings from high numbers of migrating geese. However, at all sites, addition of droppings did not have any effect on the biomass, production or nutritional quality of the main forage species. At the Dutch and Baltic sites this lack of effect can be explained by the fact that the growth of *Festuca rubra* is not nutrient-limited and that nitrogen input of droppings is negligible in comparison to inorganic nitrogen released through mineralisation. The Arctic species, *Puccinellia phryganodes* and *Carex subspatheacea*, are frequently nutrient-limited in their growth and have been shown to react to addition of droppings at a Canadian salt marsh site. However, at our Russian study sites we did not find this reaction.

An overview of studies on the effect of goose droppings on vegetation reveals that the combination of a high grazing intensity and a very low natural availability of nutrients is a prerequisite for this reaction. We conclude from our experimental evidence that fertilisation by droppings does not affect forage plant biomass, production, nutritional quality or tillering at the main staging sites of Barnacle Geese along the East Atlantic Flyway.

Forage availability and quality for Barnacle Geese along the flyway thus seems to be mainly influenced by the grazing activities of the geese themselves and of other herbivores, increasing both the nutritional quality of the vegetation and the potential harvest.

Human impacts along the flyway

Besides the naturally occurring interactions between herbivores and their food resources, human activities also impact forage availability and quality along the flyway, as a result of climatic change and changes in land use. Climate change models predict an increase in average temperatures globally by 1.4-5.8°C by the end of the century. Climate change influences the life histories of many species in temperate and Arctic regions and is inevitably becoming more severe. Rising temperatures will advance the onset of spring growth and, therefore, the consecutive waves of fresh spring growth that the geese follow from temperate wintering to Arctic breeding sites. On small experimental plots, we experimentally induced a small increase in temperature (+1°C), using portable green houses, at the three study sites along the flyway (*Chapter 9*). We measured the growth responses of the forage plants and found that plant growth was significantly advanced by small increases of spring temperatures and was closely related to cumulative spring temperatures.

Additionally, we analysed weather data along the East Atlantic flyway from the past 30 years and compared weather patterns of the traditional staging sites, in order to assess the predictability of spring temperatures and food availability en route. These analyses showed that weather patterns between sites are correlated, allowing the geese to predict circumstances at the next destination. An analysis of migration patterns of the geese demonstrated that timing of migration is advanced in warmer years; however this advancement does not match the advancement of plant growth at all staging sites. It is suggested that the geese use areas close to their breeding areas as pre-breeding staging areas. From these areas, according to recent tracking results located in the White Sea region, they can more accurately predict weather circumstances at their breeding sites in order to optimally time their arrival. Using the data from this experiment I calculated a scenario with an increased temperature of 5°C. With this higher change in temperature, the gap between the peaks in the availability of high quality forage at the Baltic stopover and the Russian breeding site increases. However, the White Sea still acts as a buffer area in this scenario, with a forage peak in between those of the Baltic stopover and Russian breeding site.

Along the flyway, human land use has an impact on forage availability for geese and thereby on population size. Recently, Barnacle Geese showed a strong increase in population size as well as a dramatic expansion of their breeding range from the traditional areas in the Russian Arctic to temperate areas in western Europe traditionally used as staging and wintering grounds. We investigated the habitat characteristics of the new nesting and foraging sites in the Baltic and in the Netherlands by means of a questionnaire addressed to nature conservation agencies, farmers and researchers (*Chapter 10*). We found that new nesting sites are mainly situated on small islands, safe from fox predation. Human interference and livestock grazing is usually absent. In contrast, foraging sites used during chick rearing are typically found at the mainland and are short grasslands, most often grazed by livestock or mown. We could not determine any overall changes in land use that explain the breeding range expansion of the Barnacle Geese to the Baltic. In the Russian Arctic, new breeding colonies were established following the abandonment of human settlements in these areas. In contrast, the new sites in the Netherlands became available after human land reclamation, dam building and intensification of agriculture. Increasing population size at the traditional breeding sites and the associated decline in forage availability for individual geese probably resulted in the expansion of the breeding range that we observe nowadays (*Chapter 10, 11*). We expect that the growth of the temperate breeding population of Barnacle Geese will level off after recent periods of geometric growth as predator-safe nesting sites will become limiting and density-dependent processes will act on the established colonies.

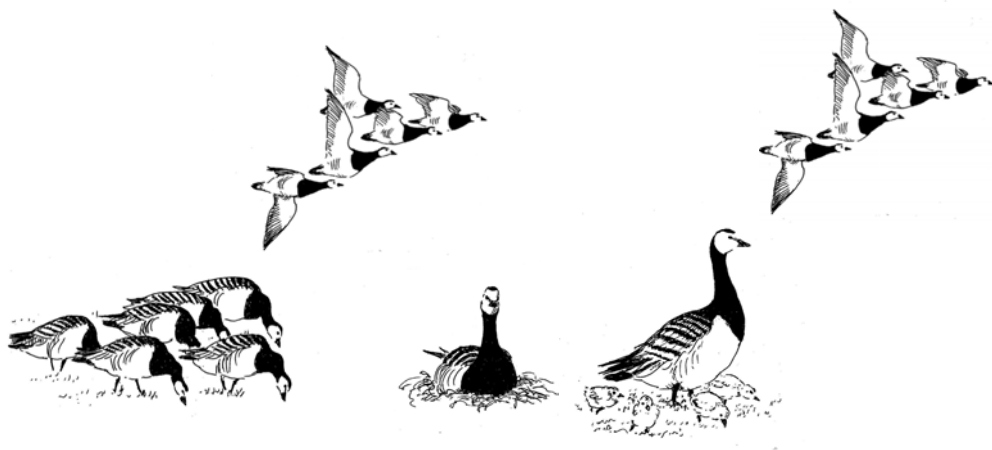
Future perspectives and conclusions

Barnacle Geese have proven to be very flexible in their timing of migration and breeding and in their choice of foraging sites, as is demonstrated by their breeding range expansion to former wintering areas and the advancement in breeding date in these new areas. Changes in climate and in land use will, however, dramatically change the timing of availability of high quality forage. In a continuously changing world, Barnacle Geese face a completely new set of foraging parameters along their entire flyway on which they have to base decisions of migration and breeding. We expect, however, that the geese are flexible enough to adapt to these changes, although the changes might halt current population increase.

Samenvatting

Inleiding

De biologie van ganzen was voor mensen in de Middeleeuwen een enorm mysterie. Ganzen waren in de winter en in het voorjaar in grote aantallen aanwezig, maar verdwenen plotseling in het voorjaar om vervolgens in het najaar weer op te duiken. Men zag nooit broedende ganzen; daarom dacht men in de Middeleeuwen dat rot- en brandganzen uit schelpen van mossels groeiden. Pas in de 16^e eeuw, toen Hollandse zeevaarders Spitsbergen ontdekten en probeerden via het Noorden een weg naar Zuidoost Azië te vinden, werden de broedplekken van deze ganzensoorten ontdekt. Tegenwoordig hoeven we ons niet meer af te vragen of en waar brandganzen broeden, want we kunnen ze in de zomer overal in Nederland broedend aantreffen. Toch maakt het bovenstaande verhaal duidelijk dat dit niet altijd zo was. Oorspronkelijk broedden ganzen uitsluitend in het Hoge Noorden en verbleven ze alleen in Nederland in de winter en in het voorjaar. De uitbreiding van het broedareaal van de brandgans roept niet alleen vragen op over de oorzaak van deze uitbreiding maar ook waarom de ganzen oorspronkelijk uitsluitend in het Hoge Noorden broedden en dus een lange, energieverblindende, migratie moesten ondernemen. De recente groei van de brandgans populatie en de uitbreiding van hun broedareaal vormen de motivatie voor mijn onderzoek. In het eerste deel van mijn proefschrift ga ik dieper in op de traditionele migratie en de gebieds- en voedsel keuzes die de ganzen maken. In het tweede deel kijk ik naar veranderingen in de gebieden langs de trekroute.



Jaarlijkse cyclus van de Brandganzen: opvetten in het voorjaar in het Waddengebied en de Oostzee, migratie naar de broedgebieden in Rusland, broedperiode in Rusland, opgroeiperiode voor de jongen in Rusland, herfstmigratie terug naar het Waddengebied

Voedselkeuzes van brandganzen langs de trekroute

Brandganzen zijn echte vegetariërs (herbivoren): hun dieet bestaat voor ongeveer 90% uit gras. Plantaardig materiaal bevat minder voedingstoffen dan vlees, bovendien kunnen dieren niet alle voedingstoffen zelf uit het plantaardige materiaal halen. In het darmstelsel van de meeste dieren bevinden zich daarom bacteriën die dit wel kunnen. Ganzen en andere kleine herbivoren hebben een kort darmstelsel en het voedsel is hier snel doorheen, er is dus weinig tijd om voedingstoffen uit het voedsel te halen wat resulteert in een heel lage verteringsefficiëntie. Ganzen zijn daarom bijna continu aan het eten, bovendien selecteren ze voedsel met een hoog eiwitgehalte.

Het binnenkrijgen van genoeg voedingstoffen is erg belangrijk voor ganzen, omdat ze veel reserves moeten opslaan in hun lichaam. Deze reserves worden gebruikt tijdens de migratie en tijdens de broedperiode. In de broedperiode kunnen de ganzen namelijk nauwelijks foerageren omdat de plantengroei in hun broedgebieden pas later op gang komt. Ganzen die in het voorjaar met meer lichaamsreserves vertrekken hebben een hogere kans op succesvol broeden. Ook tijdens de opgroeiperiode is het voor ganzen en hun jongen van belang om veel te eten: jonge ganzen met een beter dieet, groeien sneller, worden grotere volwassen ganzen en hebben een grotere kans om later zelf succesvol te broeden.

Selectie van foerageergebieden

De selectie van foerageergebieden en binnen die gebieden van foerageerplekken is dus erg belangrijk, het eerste deel van mijn proefschrift gaat dieper op deze keuzes in. Tijdens mijn studie heb ik de kans gehad om langs de gehele trekroute van de brandgans te werken, vooral in drie gebieden: het eiland Schiermonnikoog waar de ganzen in het voorjaar opvetten in de polders en op de kwelder (**Box 2**), het Zweedse eiland Gotland in de Oostzee, waar de ganzen een korte tussenstop maken tijdens hun migratie (**Box 1**) en de kwelder bij het dorpje Tobseä aan de westkant van de Pechora Delta in Rusland (**Hoofdstuk 2**). In al deze gebieden heb ik gekeken naar de gebiedskeuze van ganzen. Dit heb ik gedaan aan de hand van keuteltellingen en metingen aan de vegetatie op verschillende momenten in de drie gebieden. Het tellen van keutels is een goede manier om te bepalen hoeveel ganzen van een bepaald gebied gebruik hebben gemaakt: omdat de ganzen zeer regelmatig (ongeveer elke 5 minuten) een keutel laten vallen, kun je dus uit het aantal keutels op een bepaald oppervlak berekenen hoelang er op een bepaalde plek gevoerageerd is. Het blijkt dat ganzen het liefst foerageren op natuurlijke graslanden. Binnen deze graslanden kiezen ze voor stukken waar de vegetatie relatief laag is en een dichte mat vormt. Bovendien hebben ze een sterke voorkeur voor bepaalde soorten, in Nederland en Zweden voor het Rood Zwenkgras (*Festuca rubra*) gecombineerd met Zeeweegebree (*Plantago maritima*) en Schorrezoutgras (*Triglochin maritima*), in Rusland voor een variant op ons kweldergras *Puccinellia phryganodes* en een zegge-soort, *Carex subspatheacea*.

Selectie binnen foerageergebieden

Met een experiment heb ik de voedselkeuzes van ganzen binnen de graslanden langs de trekroute nog nauwkeuriger bekeken (**Hoofdstuk 3**). Ik heb stukken vegetatie gemanipuleerd door ze ofwel te bemesten om het eiwitgehalte van het gras te verhogen, ofwel door het tijdelijk uitsluiten van begrazing om de voedselhoeveelheid (biomassa genoemd) te verhogen. Een aantal weken na het bemesten en uitsluiten van begrazing heb ik de hekjes verwijderd en aan de hand van keuteltellingen gekeken, waar de ganzen het meeste foerageerden. Het bleek, dat de ganzen vooral kozen voor de combinatie van een verhoogde biomassa en een verhoogd eiwitgehalte, goede tweede keus waren de stukken met alleen een verhoogd eiwitgehalte.

We weten nu dus dat de ganzen gebieden selecteren waar de voedselkwaliteit hoog is, gecombineerd met een voldoende hoge biomassa. In de rest van deze samenvatting zal ik de gecombineerde maat van biomassa en eiwitgehalte van de voedselplanten aanduiden als de *kwaliteit van de vegetatie*. Behalve de kwaliteit van de vegetatie, nemen we aan dat de snelheid waarmee de ganzen kunnen eten ook van belang is voor de gebiedskeuze (**Hoofdstuk 4**). Over het algemeen wordt aangenomen dat ganzen bij een hogere biomassa een lagere opnamesnelheid zullen hebben omdat het gras te lang wordt om goed te kunnen eten, het zogenaamde spaghettiprobleem. Om dit te onderzoeken hebben we plaggen van Rood Zwenkgras opgekweekt in de kassen. Deze plaggen werden op een bepaalde hoogte afgeknipt en vervolgens voorgezet aan tamme brandganzen. Tijdens een korte periode werd vervolgens gemeten hoeveel tijd de gans aan het eten was en hoeveel happen hij had genomen. Uit deze gegevens en het gewicht van de plag voor en na het experiment konden we bepalen wat de opnamesnelheid van de ganzen was.

Het bleek dat binnen de door ons voorgezette vegetatiehoogtes de ganzen een hogere opnamesnelheid en een grotere hapgrootte bereikten met hogere vegetatie. Helaas was het niet mogelijk om nog hogere plaggen op te kweken, onze verwachting was dat met nog hogere vegetatie de opnamesnelheid weer af zou nemen. Uit onze eigen gegevens en uit andere studies blijkt dat ganzen in de natuur gebieden selecteren die veel lagere vegetatie hebben dan waarmee ze een maximale opnamesnelheid zouden kunnen bereiken, we vermoeden dat dit komt doordat vegetatie van een dergelijke hoogte meestal minder eiwitten bevat. De ganzen selecteren dus voor een optimale *combinatie* van hoogte en kwaliteit van de vegetatie, waarmee ze de grootste opnamesnelheid van eiwitten kunnen verkrijgen.

Ganzen en de groene golf

We hebben gezien dat ganzen bij het selecteren van foerageergebieden vooral letten op de vegetatiehoogte en op de kwaliteit van de vegetatie, maar wat betekent dit nu voor de migratie van de ganzen? Wanneer het gras in het voorjaar begint te groeien, bevat het veel eiwitten; naarmate het gras doorgroeit en hoger wordt neemt het eiwitgehalte af en word het dus minder aantrekkelijk. In Noordelijke gebieden begint het voorjaar en de plantengroei pas later. Op het moment dat in Nederland het eiwit gehalte van het gras dus al afneemt, is het in Zweden nog maar pas begonnen met groeien! Een van de ideeën die centraal staan in mijn proefschrift is de zogenaamde “groene golf hypothese”. Deze hypothese veronderstelt dat de ganzen tijdens hun migratie een groene golf van voorjaarsgroei van hun voedselplanten volgen. In **Hoofdstuk 5** heb ik onderzocht of er inderdaad een dergelijke groene golf bestaat. Hiervoor heb ik in drie gebieden biomassa en eiwitgehalte van de voedselplanten gevolgd door het seizoen heen. Mijn metingen laten zien dat in de opeenvolgende gebieden die de ganzen aandoen tijdens hun migratie de plantengroei telkens later begint en de kwaliteit van de vegetatie telkens later piekt. De pieken in de kwaliteit van de vegetatie voor de Wadden Zee en de Oostzee vallen rond het moment van vertrek, in Rusland valt de piek precies op het moment dat de jongen net uit het ei zijn gekropen. In alle gevallen valt de piek in de kwaliteit van de vegetatie dus samen met momenten dat de ganzen een grote behoefte hebben aan veel eiwitrijk voedsel.

Flexibele migranten in een veranderende wereld

De natuur is continu onderhevig aan veranderingen. Veranderingen worden zowel veroorzaakt door de ganzen zelf, door andere herbivoren, door het klimaat en door mensen. In het tweede deel van mijn proefschrift heb ik door middel van experimenteel onderzoek gekeken naar veranderingen in foerageergebieden van de ganzen.

Invloed van herbivoren

Herbivoren kunnen de hoeveelheid en de kwaliteit van elkanders voedsel zowel positief als negatief beïnvloeden. Negatief doordat het voedsel door de ene herbivoor opgegeten wordt en dus niet meer beschikbaar is voor de andere, dit wordt depletie genoemd. Aan de andere kant kunnen herbivoren elkanders (of hun eigen) voedsel ook positief beïnvloeden. Dit kan op twee manieren, ten eerste door het grazen, dus door het verwijderen van plantaardig materiaal. Hierdoor wordt in sommige gevallen de groei van het gras gestimuleerd waardoor er na een bepaalde tijd weer nieuw gras beschikbaar is. Dit nieuw aangegroeide gras bevat meer eiwitten dan het weggegraasde gras op dit moment zou bevatten. Ten tweede kunnen herbivoren de vegetatie bemesten door hun keutels of urine waardoor de vegetatie ook sneller kan gaan groeien en een hoger eiwitgehalte kan hebben.

Op de kwelder van Schiermonnikoog komen naast brandganzen ook rotganzen en hazen voor. Hazen verblijven het gehele jaar door op de kwelder terwijl ganzen hier alleen in het voorjaar zijn. Zowel hazen als ganzen eten bij voorkeur het Rood Zwenkgras, we vermoedden daarom dat ganzen en hazen invloed hebben op elkaanders voedselkeuzes. Hiervoor hebben we een experiment opgezet, identiek aan het experiment van hoofdstuk 3 waarbij de biomassa en het eiwitgehalte van het gras werden gemanipuleerd door middel van bemesting en het uitsluiten van begrazing. In dit experiment werd een deel van de proefvlakken na een aantal weken geopend voor zowel hazen als ganzen terwijl een ander deel zo werd beschermd dat hazen er wel konden grazen maar ganzen er niet in konden (**hoofdstuk 6**). Uit dit experiment bleek weer dat ganzen een sterke voorkeur hebben voor plekken met een hoog eiwitgehalte. Hazen lieten in de aanwezigheid van ganzen een voorkeur zien voor plekken met een hoge biomassa, in de afwezigheid van ganzen kozen ook zij voor de plekken met een hoog eiwitgehalte gecombineerd met een hoge biomassa. Het lijkt er dus op dat hazen door de aanwezigheid van ganzen niet op hun meest favoriete plekken kunnen foerageren, we noemen dit een geval van indirecte competitie, aangezien er geen directe confrontatie tussen de twee herbivoren plaatsvindt.

Ganzen beïnvloeden dus de voedselkeuze van hazen, maar ze kunnen ook hun eigen voedselkeuzes beïnvloeden. In hoofdstuk 6 laten we zien dat ganzen het liefst foerageren op plekken die al eerder in het seizoen door ganzen of hazen begraasd zijn. In een experiment heb ik tamme brandganzen op natuurlijke kweldervegetatie laten grazen voor verschillende tijdsperiodes en vervolgens zes weken lang de groei van gemerkte grassprietjes gevolgd (**hoofdstuk 7**). Hieruit blijkt dat begraasde sprietjes meer nieuwe sprietten aanmaken en dat na een aantal weken er dus meer te halen valt voor de ganzen op een stuk dat al eerder begraasd is dan op een onbegraasd stuk. Het bleek dat de ganzen van nature de vegetatie in een dusdanige mate begrazen, dat ze een optimale opbrengst kunnen bewerkstelligen.

Ganzen kunnen de vegetatie waarvan ze eten ook beïnvloeden door middel van bemesting door hun eigen keutels. Dat dit proces kan spelen is aangetoond in een kwelder in Canada. Ik heb geprobeerd om dit effect te vinden in mijn studiegebieden door middel van het nauwkeurig volgen van de groei van vegetatie direct naast ganzenkeutels (**hoofdstuk 8**). In geen van de gebieden vond ik een effect van keutels op de groei of op het eiwitgehalte van het gras. Blijkbaar vindt dit proces alleen plaats als de condities precies goed zijn: een heel lage natuurlijke nutriëntenvoorraad in de grond, een heel hoge begrazingsdruk en een versnelde kringloop van nutriënten door de aanwezigheid van bepaalde micro-organismen.

Invloed van klimaat

Het tijdstip waarop de vegetatie een piek in de kwaliteit bereikt hangt af van de temperaturen in het voorjaar. Verschillende klimaatsmodellen voorspellen dat de komende eeuw de gemiddelde temperatuur tussen de één en zes graden zal stijgen. In **hoofdstuk 9** kijk ik naar de gevolgen van klimaatsveranderingen op de leefgebieden van de brandgans. Door middel van kleine kasjes heb ik de temperatuur van kleine proefvlakken met één graad verhoogd. Met deze hogere temperatuur komt de plantengroei eerder op gang en wordt dus de piek in de kwaliteit van de vegetatie ook eerder bereikt. Met een verhoging van één graad in de gemiddelde dagtemperatuur verschuift deze piek in de Wadden Zee en Oostzee al met acht dagen, in Rusland verschuift de piek met ongeveer vier dagen. Uit analyses van weergegevens van de afgelopen 30 jaar blijkt dat een koud of warm voorjaar in het ene gebied vaak samen te vallen met een koud of warm voorjaar in het volgende gebied. De ganzen kunnen dus het weer op de volgende plek “voorspellen” aan de hand van het weer op de plek waar ze zijn. Uit trekgegevens verzameld op verschillende punten langs de trekroute van de ganzen blijkt dat brandgansen in de afgelopen 30 jaar wel eerder zijn vertrokken uit de Wadden Zee en Oostzee in warme dan in koude jaren, toch is de verandering in migratiedatum van de brandgansen vaak niet genoeg om de verandering in plantengroei bij te houden. Als klimaatsverandering nog sterker zou doorzetten zou dit kunnen betekenen dat de ganzen te laat in de broedgebieden aankomen en dus suboptimale voedselomstandigheden tegenkomen.

Invloed van mensen

Recentelijk heeft de brandgans zijn broedgebieden uitgebreid langs de gehele noordkust van Rusland (eind jaren 80), de Oostzee (eind jaren 70) en zelfs helemaal naar het delta gebied (eind jaren 80). In **hoofdstuk 10** bekijken we wat de kenmerken zijn van deze nieuwe broedgebieden en de aangrenzende gebieden waar de ganzen met hun jongen naartoe gaan om te eten. De broedplekken van de ganzen zijn zeer variabel, ganzen kunnen blijkbaar in allerlei soorten vegetatie broeden. Wel is het belangrijk dat de broedplekken ontoegankelijk zijn voor roofdieren, zoals vossen; vandaar dat de meeste broedplekken op kleine eilandjes zijn gelegen. Zodra de jongen zijn uitgekomen, gaan de ganzen met hun jongen naar de vaste wal om te foerageren. Deze foerageergebieden, waar de families blijven totdat de jongen kunnen vliegen, zijn vooral graslanden met korte vegetatie die begraaasd worden door vee (Oostzee en delta gebied). De foerageergebieden zijn wel altijd in de buurt van water waar de families naartoe kunnen vluchten als er gevaar dreigt.

De nieuwe broedgebieden verschillen in vele opzichten van de traditionele broedgebieden in Noord Rusland waar de ganzen vooral op rotskusten broeden en met hun jongen op door de mensen onbereikbare kwelders eten. Waarschijnlijk hing de uitbreiding van het broedareaal van de brandgansen samen met de toename van het aantal ganzen.

In Noord Rusland werden nieuwe kolonies gesticht in gebieden waar dorpen door mensen verlaten waren na de val van het Sovjetregime. Waarschijnlijk maakten jacht en het verzamelen van eieren het vóór die tijd onmogelijk om op deze plekken te broeden. De nieuwe broedplekken in Nederland zijn vooral gelegen op eilanden die pas in de jaren 80 ontstaan zijn, na voltooiing van de Deltawerken. De uitbreiding van de broedgebieden in Nederland valt bovendien samen met een verhoogde stikstofgift aan graslanden in Nederland, waardoor de vegetatie een uitzonderlijk hoog eiwitgehalte heeft. We verwachten dat de groei van de populatie in Nederland zal afnemen wanneer de nu gekoloniseerde gebieden vol raken en er een tekort zal ontstaan aan veilige gebieden om te broeden.

Conclusies

Op het moment zijn gebieden langs de trekroute van de brandgans onderhevig aan grote veranderingen. Mensen hebben een grote invloed op de graslanden langs de kust waar ganzen foerageren. Deze invloeden zijn heel verschillend in de drie gebieden langs de trekroute: in Noord Rusland en in de Oostzee worden gebieden verlaten door mensen en wordt begrazing door vee gestopt, in West Europa worden veel graslanden juist hevig bemest en zwaar begraasd, aan de andere kant worden ook veel gebieden aangewezen als natuurreservaat waar begrazing wordt gestopt of verminderd. Ten slotte, zal klimaatsverandering in de komende jaren een nog grotere rol gaan spelen. In een continu veranderende wereld worden de ganzen telkens geconfronteerd met een geheel andere situatie waarop ze de keuzes van foerageer- en broedgebieden en de timing van de trek moeten baseren. In het verleden is echter gebleken dat brandganzen heel flexibel zijn in het kiezen van nieuwe foerageer- en broed gebieden en het veranderen van het tijdstip van de trek. De verwachting is dan ook dat de ganzen zich zullen weten aan te passen aan de nieuwe omstandigheden. De brandgans zal dus zeker niet uit onze kustgebieden verdwijnen, maar de veranderingen in de toekomst zouden wel ten koste kunnen gaan van de omvang van de populatie.



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Curriculum Vitae

Alexandra Johanna van der Graaf (Sandra)

I was born on October 25th 1977 in Seria (Brunei). My parents moved frequently during my childhood and I grew up and attended primary school in Stavanger (Norway) and in Vlaardingen. I started secondary school at the 'Groen van Prinsterer Lyceum' in Vlaardingen, but switched after two years to the 'CS Vincent van Gogh' in Assen. Here I graduated in 1995.



In the same year I started my studies in biology at the University of Groningen, specialising in Ecology and in particular plant-herbivore interactions. During my studies I did three MSc. projects. I started with a project on site choice of Brent Geese in relation to livestock grazing on the island of Ameland. During my second project I studied the effects of climate warming on the food availability of Reindeer on Spitsbergen (via the ITE-Banchory). In my third project I investigated the effects of weather on the energetics and site choice of Barnacle Geese on the island of Schiermonnikoog. Next to this I did several literature studies and some extra field work, all involving plant-herbivore interactions. My first project with some additional field work resulted in two publications (Van der Graaf *et al.* 2002; Bos *et al.* 2005b). During my studies I worked as a teaching assistant in the computer courses for undergraduate biology students. In the final phase of my study I followed a TBA (Tropical Biology Association) course in Kenya, where I met Moses. I graduated from my studies in December 2000, 'Cum Laude'. After my studies I worked as a field assistant in a project on the carrying capacity of Yellowstone NP (USA) for Bison and in a project on energy expenditure of incubating Great Tits in the Netherlands. In September 2001, I started my PhD. study at the University of Groningen. My study required field work in the Netherlands, Sweden and Russia. Besides working on my thesis, I supervised several BSc. and MSc. students, assisted in several undergraduate courses and led an undergraduate animal ecology practicum for several years. Within the framework of my PhD study, I attended several workshops and conferences and on many occasions presented part of my research in the form of oral presentations or posters. All of the chapters in my thesis are currently submitted or have already been published (Van der Graaf *et al.* 2004; 2005; 2006; 2005 online). During two periods, I have lived for a couple of months in Kenya.

At present, I am unemployed. I am looking for a postdoc position or work as an ecologist, preferable in the field of plant-herbivore interactions.