

Effects of biomass and quality of forage on grazing by breeding and spring staging barnacle geese (*Branta leucopsis*)

Field observations and experiment on Gotland



Ciska Veen
Rijksuniversiteit Groningen
Department of Animal Ecology
May 2003-February 2004
Supervision: Julia Stahl & Sandra van der Graaf

Contents

Contents	2
Abstract	3
Samenvatting	3
Introduction	4
Methods.....	6
Study area	6
Transects	7
Experiment	7
Data analyses	8
Results.....	10
Transects	10
Experiment	12
Discussion.....	15
Transects	15
Experiment	17
Acknowledgements	20
Appendices	21
Appendix 1: Forage availability along the flyway	21
Appendix 2: Forage quality along the flyway	21
Appendix 3: Production measurements	22
Appendix 4: Indications for goose preference	23
References.....	24

Abstract

Barnacle geese (*Branta leucopsis*) are strongly dependent on the quality and availability of forage plants to compensate for limiting digestive capabilities. In spring geese are migrating from temperate wintering grounds to high Arctic breeding grounds following a 'green wave' of spring growth. On three different stepping stones along the East Atlantic Flyway (Schiermonnikoog, Gotland, Pechora Delta) we carried out an experiment where we manipulated biomass and quality of forage to investigate the relative importance of these factors for grazing pressure and to study whether the relative importance changed along the flyway and over the season. This report describes the results for Gotland, a spring staging site for the Arctic and a breeding site for the Baltic population. On Gotland we also studied food availability, food quality and grazing pressure in four intensively goose grazed areas to get a general idea of changes of these parameters over the season. Grazing pressure was strongly increased on experimental plots that were both biomass and quality enhanced. In the natural situation habitats with high quality and low biomass were more intensively grazed than areas with low quality and high biomass, which indicates that quality is an important factor determining goose presence. These results correspond with results from earlier research showing that in a natural situation there was a negative relationship between sward height and grazing pressure, due to the negative correlation between sward height and nitrogen content. When this relation was eliminated by application of fertiliser a higher preference for longer swards was shown (Hassall *et al.* 2001; Riddington *et al.* 1997).

Samenvatting

Brandganzen (*Branta leucopsis*) zijn afhankelijk van een goede kwaliteit en beschikbaarheid van voedselplanten om te compenseren voor hun limiterende verteringscapaciteit. In de lente trekken de ganzen van hun overwinteringsgebieden naar Arctische broedgebieden, waarbij ze de lokale piek in voedselkwaliteit volgen. In drie verschillende gebieden langs de "East Atlantic Flyway" (Schiermonnikoog, Gotland, Pechora Delta) hebben we een experiment uitgevoerd, waarbij we de biomassa en kwaliteit van voedselplanten hebben gemanipuleerd om de relatieve invloed van deze parameters op de begrazingsdruk te bestuderen en om te kijken of de invloed van deze factoren op de aanwezigheid van ganzen verschilt in verschillende gebieden langs de trekroute en gedurende het seizoen. In dit verslag worden de resultaten beschreven van het onderzoek op Gotland, een pleisterplaats voor de Arctische en een broedgebied voor de Baltische populatie. Daarnaast hebben we op Gotland de voedselbeschikbaarheid, voedselkwaliteit en de begrazingsdruk gemeten in vier intensief begraasde gebieden om een idee te krijgen van het verloop van deze parameters door het seizoen. De begrazingsdruk was sterk verhoogd op experimentele plots die zowel in biomassa als in kwaliteit waren verbeterd. Onder natuurlijke omstandigheden werden habitats met een hoge kwaliteit en een lage biomassa intensiever begraasd dan die met een lage kwaliteit en een hoge biomassa, waaruit blijkt dat voedselkwaliteit belangrijk is voor de aanwezigheid van ganzen. Deze resultaten komen overeen met eerder onderzoek, dat liet zien dat er in een natuurlijke situatie een negatieve relatie bestaat tussen de vegetatiehoogte en de begrazingsdruk, als gevolg van het negatieve verband tussen vegetatiehoogte en stikstofgehalte van de vegetatie. Als dit verband verdwijnt, bijvoorbeeld door bemesting, wordt hogere vegetatie geprefereerd (Hassall *et al.* 2001; Riddington *et al.* 1997).

Introduction

Geese have a short digestive system with a rapid passage of food and a low digestive efficiency (Prop & Vulink 1992). To compensate for their limiting digestive capabilities they are strongly dependent on high quality food (Drent & Prins 1987; Karasov 1990). The forage quality during spring staging is important for geese, because they have to gain weight for migration and breeding. The amount of body reserves accumulated by adults prior to migration affects breeding success (Ebbinge & Spaans 1995). Moreover, food quality affects gosling growth rate and final adult body size (Cooch *et al.* 1991; Larsson & Forslund 1991). Body weight of fledglings in turn influences post-fledgling survival (van der Jeugd & Larsson 1998).

The need for high quality food influences diet composition (Prop & Deerenberg 1991) and habitat choice (Prins & Ydenberg 1985). Geese show a preference for young growing shoots whenever available (Drent & Prins 1987), because quality decreases in maturing grasses, whereas the proportion of structural components increases (Crawley 1983; Ulyatt 1981).

Barnacle geese (*Branta leucopsis*) are long distance migratory birds. The Russian population migrates from their temperate wintering grounds in the Wadden Sea area to breeding grounds in the high Arctic in Russia; following the East Atlantic Flyway. They are found breeding from the Kola and Kanin peninsulas in the west to Vaygach and Novaya Zemlya in the east (Ganter *et al.* 1999). The much smaller Baltic breeding population is found mainly on Swedish and Estonian islands and was established in the 1970s (Forslund & Larsson 1991; Ganter *et al.* 1999; Larsson *et al.* 1988; Larsson & Forslund 1994). Both populations, about 267,000 individuals in 1997 (Ganter *et al.* 1999), mix on their wintering grounds (Ebbinge & van Biezen 1987), where they forage on salt marshes and adjacent agricultural pastures along the coasts of the Netherlands, Germany and Denmark. Although the geese use the same wintering areas, range and habitat choice differ at a subtler scale (van der Jeugd *et al.* 2001).

The timing of spring migration of geese is strongly dependent on seasonal changes in the quality and availability of food plants along the flyway. In the south-western part of the East Atlantic Flyway the movement of barnacle geese from one stop-over site to the next corresponds with the onset of forage growth, when forage plants have the highest quality, i.e. nitrogen content (Klimkowska 2003). The hypothesis is that geese follow this 'green wave' of spring growth of their main food plants to their breeding sites (Owen 1980). Several successive stop-over sites (stepping stones) are used by barnacle geese to fill-up fuel reserves (e.g. Wadden Sea, Baltic Sea and White Sea). In brent geese (*Branta b. bernicla*) it was shown that refuelling is necessary to accomplish both migration and successful breeding (Ebbinge & Spaans 1995). Within the East Atlantic Flyway birds belonging to the Russian barnacle goose population use the Baltic areas (Gotland, Öland and Estonia) as stop-over sites, at the same time the Baltic breeding geese settle down into colonies and start egg-laying (Larsson & Forslund 1994). The Arctic breeders follow the nutritional peak of their forage plants, while the Baltic breeders stay at a former stop-over site and have to cope with a seasonal decline in forage quality (Larsson & Forslund 1991), but profit from an extended breeding season.

Several studies focused on the development of the recently established Baltic breeding population (Larsson *et al.* 1988; Larsson & Forslund 1994; Larsson & van der Jeugd 1998), but little is known about food quality and availability throughout the season and the relation of these factors with habitat selection by Arctic and Baltic

breeding geese on Gotland. In this study we focus on barnacle goose presence in different habitats and food patches on Gotland. We address the following questions: (1) how do food quality and availability change over the season in different habitats, (2) which habitats have the highest grazing pressure and (3) how is grazing pressure related to quality and quantity of forage plants? To investigate whether grazing pressure was related to forage quality and quantity an experiment was carried out where these vegetation parameters were manipulated. The same experiment was carried out on Schiermonnikoog (Wadden Sea, wintering and spring staging site) and in the Pechora Delta (Russian breeding site) in 2003.

The hypothesis is that food quality determines habitat and patch choice by barnacle geese (Bos *et al.* 2002b) and, hence, grazing pressure. Immediately after arrival on Gotland, at the end of April, high biomass may attract geese, as the growing season just started and standing crop is still low. Because quality of the forage plants decreases during the season selection for high quality forage might become more important later on in the season. At the same time biomass will be less limiting due to grass growth. Therefore biomass and quality enhanced plots are expected to receive the highest grazing pressure at the start of the season, whereas later in the season grazing pressure should become higher on quality enriched plots.

Methods

Study area

The study was carried out on Gotland, a Swedish island in the Baltic Sea (Fig 1). Gotland is an important spring staging site for migrating barnacle geese belonging to the Russian population (Ganter *et al.* 1999). The geese are mainly concentrated along the east coast of the island (Larsson & Forslund 1994) on narrow strips of salt marsh, dominated by *Festuca rubra*, which is the main food plant of the geese on Gotland (Ganter *et al.* 1999), and *Agrostis stolonifera* (van der Veen 1994). In the North of Gotland geese are also using agricultural fertilised fields (van der Jeugd, pers. comm.). Arctic breeding geese arrive at the beginning of April and depart again around the 20th May (van der Jeugd, pers. comm.).

The Baltic population arrives at the same time as the Arctic geese. Most Baltic breeding geese settle down into colonies situated on small islands along the east coast of Gotland (Ganter *et al.* 1999) and start egg-laying by the end of April (Larsson & Forslund 1994). A couple of days after hatching families leave the breeding islands for suitable feeding areas on the mainland of Gotland (van der Jeugd, pers. comm.). These areas are also used by Arctic geese during spring staging. Adults and goslings feed to a large extent on *Festuca rubra*, but also on *Puccinellia maritima*, *Agrostis stolonifera* and *Juncus gerardii* (Larsson & Forslund 1991; van der Veen 1994). From the beginning of June till the end of September coastal areas are extensively grazed by cattle or sheep.

The study was carried out at 4 different intensively goose grazed salt-marsh areas along the east coast of Gotland (Fig 1): Närsholmen (NH; 57°14'N 18°41'E), Hummelbosholm (HU; 57°12'N; 18°33'E), Ronehamn (RH; 57°09'N; 18°29'E) and Grötlingboud (GB; 57°07'N; 18°27'E). All sites were used by both Arctic and Baltic barnacle geese.

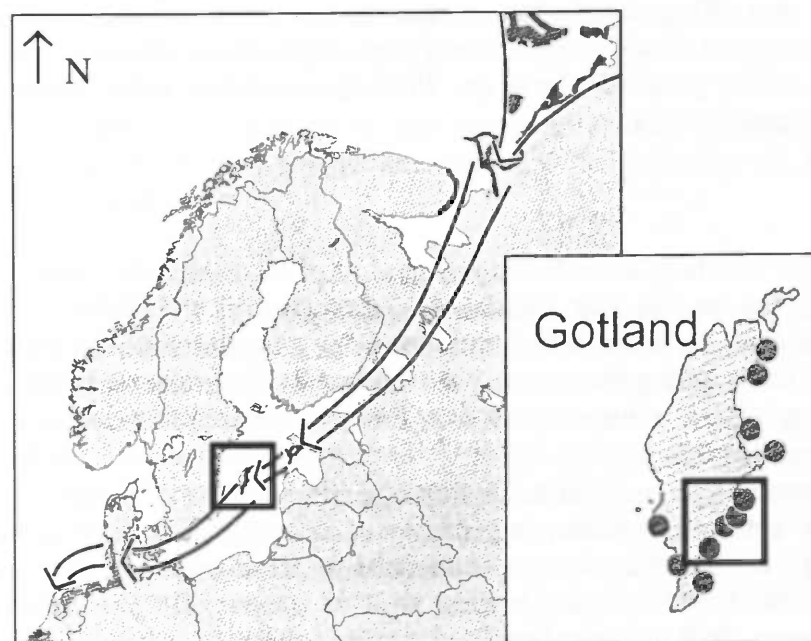


Fig 1. Left: East Atlantic flyway for barnacle geese (Ganter *et al.* 1999). Right: Gotland. All dots represent staging sites of migrating Russian barnacle geese. The four dots in the square are the four areas used in this study, from North to South: Närsholmen (NH), Hummelbosholm (HU), Ronehamn (RH) & Grötlingboud (GB).

Transects

Food quality, food availability and grazing pressure were studied in Närsholmen (NH), Hummelboshom (HU) and Grötlingboud (GB). In Ronehamn (RH) grazing pressure was studied only. Two different habitat types were studied per area: lower parts (referred to as salt marsh) and higher parts (referred to as grassland). Salt marshes were mainly dominated by *Festuca rubra* and *Agrostis stolonifera* (van der Veen 1994), grasslands were mainly dominated by *Festuca ovina* and dicotyles (point-quadrat measurements 2003). Per habitat type three transects, comprising 5 plots placed at 10 metre distance, were created. Each circular plot of 4 m² was marked with a stick in the centre. The areas NH, HU and GB included both habitat types, RH included only the salt marsh habitat type.

Droppings in the plots were counted every week. Geese produce droppings at regular and frequent intervals of about 4 – 5 minutes (Ydenberg & Prins 1981), and the number of droppings thus provide a good measure of grazing pressure.

Vegetation measurements were carried out every second week and included measurements of available biomass, quality of *Festuca rubra* and the cover percentages of different plant species. Total available biomass (g dry m⁻²) per transect was calculated by multiplying the number of tillers per m² by the dry weight (g) of one tiller. Living tillers of *Festuca rubra* were counted in squares of 5.5 cm by 5.5 cm. Counts were repeated 6 times per plot, squares were placed randomly. One sample of 50 living *Festuca rubra* tillers was collected per transect. Tiller samples were dried at 60°C and weighed.

To assess forage quality, one sample of green leaf tips of *Festuca rubra* was collected every second week per transect by pulling the tips carefully between thumb and forefinger, imitating the grazing of geese (Ydenberg & Prins 1981). Samples were dried at 60°C and analysed in the lab to determine nitrogen content, using CNHS-automated element analysis (Interscience EA 1110).

Plant-species composition was measured using the point-quadrat method (Grant 1981). Per plot 20 point-quadrat measurements were taken. Twelve different plantcategories were distinguished: *Festuca* sp., *Agrostis* sp., *Poa* sp., *Cynosurus* sp., other grass, *Juncus gerardii*, *Carex* sp., *Plantago maritima*, other dicotyles, mosses, dead material and bare soil.

Experiment

An experiment in which availability and quality of *Festuca rubra* were manipulated was carried out on the salt marsh of Grötlingboud (57°06'N; 18°26'E). The experiment was set up in a full-factorial block design with 6 replicate blocks and was repeated two times during the season (set 1 and set 2). Six replicate blocks, containing 4 plots of 4m by 4m, were selected in a *Festuca rubra* dominated vegetation type (*Festuca* cover: 24.0% ± 2.2% for set 1, n=6; 35.9% ± 2.2% for set 2, n=6). Four different treatments to manipulate quality and biomass, were assigned randomly to plots within a block. Fertiliser application was used to achieve a high quality treatment (Q), herbivore exclosures were used to achieve a high biomass treatment (B), both fertiliser and exclosures were used to achieve a high biomass and high quality treatment (BQ), one plot remained unmanipulated as a control (C).

Plots were fertilised and exclosed 3-4 weeks before the start of the experiment. Fertilisation was done with commercial fertiliser (N-P-K 12-10-18; 12% N), resulting in a net addition of 10 gram nitrogen per m². Geese were excluded using chicken wire

(50 cm high). The experiment was carried out in two series to investigate seasonal changes in grazing pressure on different treatments. Series 1 was established at the 3rd of April and opened for the geese at the 5th of May, when both the Arctic and Baltic population were present on Gotland. Series 2 was established at the 5th of May and opened at the 26th of May, when most of the Arctic geese had left. Baltic families started to arrive from the breeding islands at the mainland of Gotland a couple of days after removal of the exclosures (pers. obs.).

The day before the exclosures were removed the available biomass, the quality of *Festuca rubra* and the cover percentages of different plant species were measured in each plot. Vegetation measurements were carried out in the same way as described for the transects and samples were treated similarly. Tillers were counted 20 times per plot and one sample of 50 tillers was collected. One quality sample of green leaf tips of *Festuca rubra* was collected per plot. Point-quadrat measurements were carried out 100 times per plot. After removing the exclosures droppings were counted on the experimental plots at least every week, for 3 to 4 weeks.

The same experimental set-up was used on Schiermonnikoog (Lubbe 2003) and in the Pechora Delta (Havinga 2003).

Data analyses

All statistical analyses were carried out using SPSS 11.0 for Windows. Data were tested for normality and for homogeneity of variances, with a Kolmogorov-Smirnov test and a Levene's test, respectively. Data were log-transformed ($y' = \log(y + 1)$) for vegetation parameters, a square root transformation ($y' = \sqrt{y + 0.5}$) was used for count data and percentages were arcsine-transformed ($y' = \arcsin \sqrt{y}$) to improve normality and homogeneity of variances (Zar 1999). Dropping counts were converted to number of droppings per day per m². Biomass data were converted to gram dry weight per m². Point-quadrat measurements of dead material are divided by measurements of *Festuca sp.* to calculate a cover ratio referred to as dead/*Festuca*-ratio.

Hares are not taken into account in the analyses, as hare droppings were not encountered on plots. It is therefore assumed that the influence of hares on the vegetation is negligible.

Transects

Biomass, quality, number of droppings and dead/*Festuca*-ratio were analysed using univariate general linear models. Area (GB, HU, NH) and habitat (salt marsh and grassland) were entered as fixed factors. Day number was entered as a co-variate. Significant interactions between fixed factors were included in the model.

To determine the relationship between number of droppings and quality and biomass of food a univariate general linear model was used. Data were split into three different periods: (I) Arctic and Baltic geese present (till day 144), (II) Arctic geese left for Russian breeding grounds, Baltic non-breeders present (day 145 till day 157), (III) Baltic families present (from day 157 and further) (Fig 2). Subdivision into periods was necessary to reduce the effect of large scale changes in total number of geese present on Gotland due to e.g. migration. Subdivision into periods was based on dropping counts in 2003 and on long-term data on hatching date (Larsson & van der Jeugd, unpubl. data).

Biomass and quality of *Festuca rubra* were measured at the start and at the end of a period. Per period an average of these values was calculated and it was assumed that these averages represented the biomass and the quality during the whole period. Number of droppings per day per m² was related to the average values of biomass and quality. In the model, quality (nested within period) and biomass (nested within period) were entered as co-variates, period and habitat were entered as fixed factor.

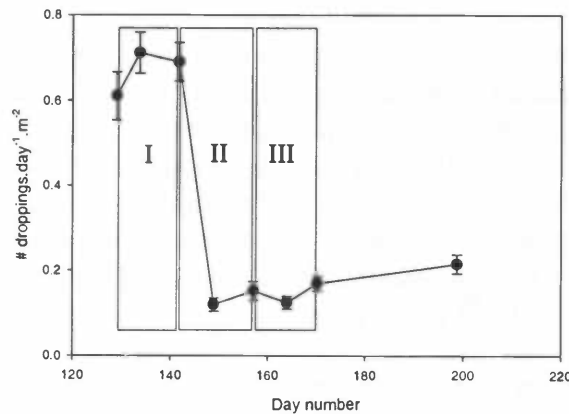


Fig 2. Number of goose droppings (mean \pm SE) in salt-marsh areas per day per m² plotted over time. Three periods (I, II & III) used in the analyses of the relation between number of goose droppings and the vegetation parameters are displayed in the graph.

Experiment

Biomass, quality, dead/*Festuca*-ratio and total number of droppings per plot (i.e. grazing pressure) at the first count were analysed using univariate general linear models. Grazing exclusion, fertilisation and set were entered as fixed factors. Replicate block (nested within set) was entered as a random factor. Interactions between fixed factors were included in the model when they had a significant influence on one or more of the dependent variables.

The relationship between vegetation parameters (quality and biomass) and number of droppings was tested using a univariate general linear model with set and treatment as fixed factors and biomass, quality and dead/*Festuca*-ratio as co-variates. Replicate block (nested within set) was entered as a random factor. When significant, interactions were included in the model.

Seasonal changes in grazing pressure were analysed using 'treatment' (C, B, Q & BQ) and replicate block as fixed factors and day number as co-variate. Set 1 and set 2 were analysed separately.

Results

Transects

Vegetation parameters

In 4 areas along the east coast, we investigated seasonal changes in biomass and quality of forage and the grazing pressure. There was a seasonal increase in biomass of *Festuca sp.* ($F_{1,65}=7.10$, $p=0.010$; Fig 3A). Quality of *Festuca sp.* ($F_{1,65}=28.89$, $p<0.001$) and dead/*Festuca*-ratio ($F_{1,65}=75.87$, $p<0.001$) decreased over the season (Fig 3B,C). On salt marshes the biomass of *Festuca sp.* was significantly lower ($F_{1,65}=18.58$, $p<0.001$) than in adjacent grasslands, while the quality was significantly higher ($F_{1,65}=107.07$, $p<0.001$). Between salt marshes and grasslands dead/*Festuca*-ratio did not differ ($F_{1,65}=2.19$, $p=0.144$). Significant differences were found between areas (NH, HU, GB) for biomass ($F_{2,65}=6.42$, $p=0.003$) and dead/*Festuca*-ratio ($F_{2,65}=3.74$, $p=0.029$), while there was a trend towards differences in quality ($F_{2,65}=2.69$, $p=0.075$).

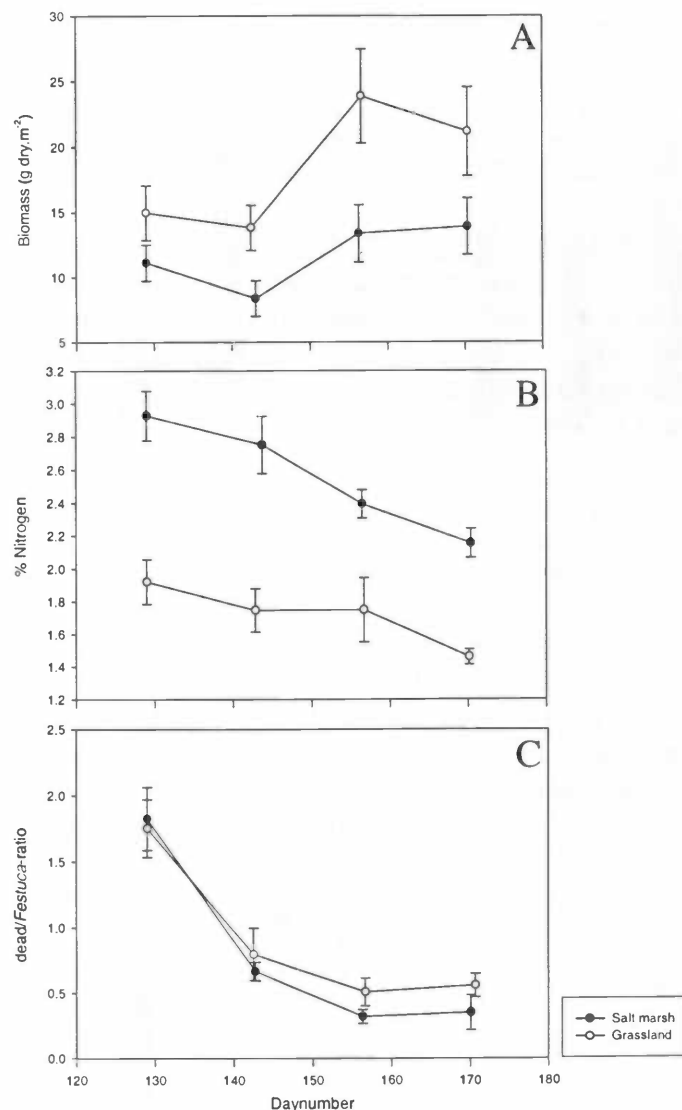


Fig 3. (A) Biomass (mean \pm SE) of *Festuca sp.* (g dry per m²) over time. (B) Quality (mean \pm SE) of *Festuca sp.* (% Nitrogen) over time. (C) Ratio dead/*Festuca sp.* (mean \pm SE) over time.

Grazing pressure

Grazing pressure decreased over the season ($F_{1,774}=208.83$, $p<0.001$). Number of goose droppings on salt marshes was significantly higher than on adjacent grasslands ($F_{1,774}=168.60$, $p<0.001$, Fig 4). No significant differences were found between areas ($F_{3,774}=2.55$, $p=0.055$).

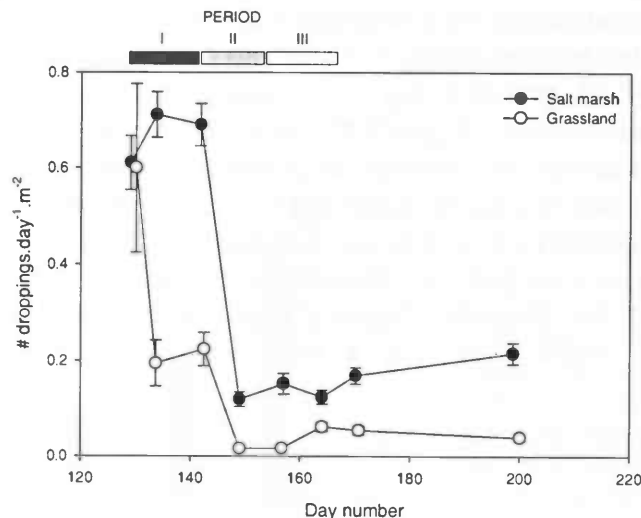


Fig 4. Mean number of goose droppings (\pm SE) per day per m² over time. Periods are indicated by the bars above the graph: Black = period I (Arctic & Baltic geese present); Grey = period II (Arctic geese gone, Baltic non-breeders present); White = period III (Baltic families at the mainland).

Grazing pressure related to biomass and quality of forage

Most of the variance in grazing pressure was explained by the factor habitat ($F_{1,44}=12.63$, $p=0.001$) and not by the vegetation parameters biomass ($F_{3,44}=0.40$, $p=0.751$) and quality ($F_{3,44}=2.37$, $p=0.083$). With respect to quality and quantity of forage, grazing pressure did not differ between periods ($F_{2,44}=0.71$, $p=0.474$), which indicates that there is no seasonal change.

Experiment

The effect of the treatment on the vegetation

After removal of the exclosures biomass and quality of *Festuca rubra* were measured (Fig 6A,B). Plots excluded from grazing (B, BQ) had a higher biomass compared to plots that were continuously grazed (C, Q; $F_{1,32}=33.78$, $p<0.001$). Fertilisation had a positive effect on quality, i.e. nitrogen content was higher in fertilised plots (Q, BQ) than in unfertilised plots (C, B; $F_{1,32}=44.14$, $p<0.001$). Grazing exclusion also had a significant negative effect on quality ($F_{1,32}=12.20$, $p=0.001$).

There were no significant differences between replicate blocks for biomass ($F_{10,32}=1.29$, $p=0.275$) and quality ($F_{10,32}=0.861$, $p=0.577$). Quality was significantly lower in set 2 ($F_{1,32}=11.65$, $p=0.002$), while biomass did not differ between sets ($F_{1,32}=3.74$, $p=0.062$). Significant interactions were found between exclusion and fertilisation for biomass ($F_{1,32}=6.20$, $p=0.018$) and for the dead/*Festuca*-ratio ($F_{1,32}=8.49$, $p=0.006$).

Biomass and quality of *Festuca rubra* were not significantly related ($F_{1,47}=1.558$, $p=0.218$, $r^2=0.033$).

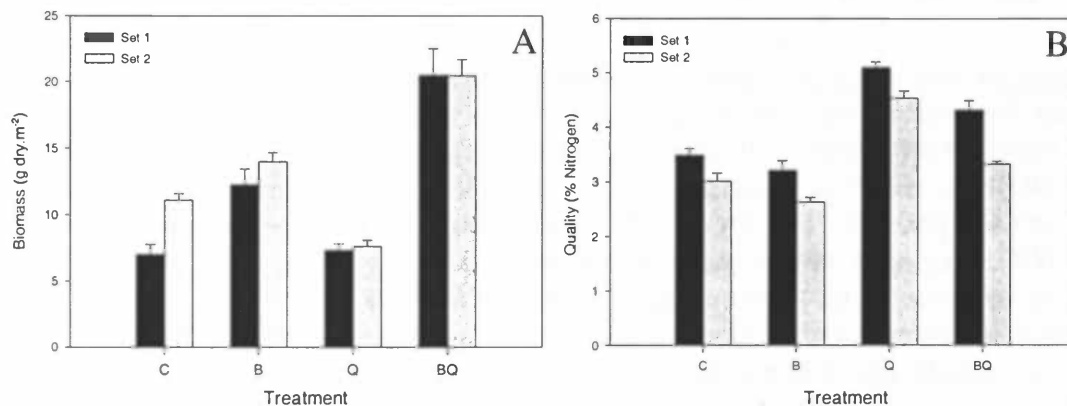


Fig 6. (A) Mean biomass (\pm SE) of *Festuca rubra* (g.m⁻²) per treatment. (B) Mean nitrogen content (\pm SE) of *Festuca rubra* (% nitrogen) per treatment. C = control treatment, B = high biomass treatment, Q = high quality treatment, BQ = high biomass and high quality treatment.

Excluding of grazing ($F_{1,32}=13.26$, $p=0.001$) and fertilisation ($F_{1,32}=35.71$, $p<0.001$) had a significant negative influence on the dead/*Festuca*-ratio (Fig 7). The proportion of dead material was lowest on BQ-plots. Dead/*Festuca*-ratio was significantly lower in set 2, later in the season ($F_{1,32}=187.59$, $p<0.001$), which indicates that the cover of dead material decreased compared to the cover of *Festuca rubra*. The ratio differed between replicate blocks ($F_{10,32}=2.61$, $p=0.019$).

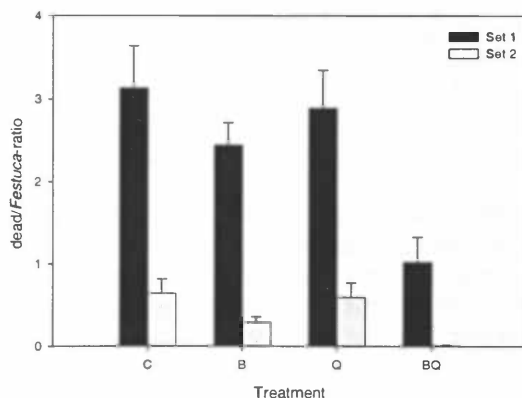


Fig 7. Dead/*Festuca*-ratio (\pm SE) per treatment treatments. C = control, B = high biomass, Q = high quality, BQ = high biomass and high quality.

Grazing pressure

Grazing exclusion ($F_{1,32}=96.59$, $p<0.001$) and fertilisation ($F_{1,32}=155.02$, $p<0.001$) had a significant positive effect on grazing pressure (Fig 8). Most geese were found on high biomass & high quality plots (BQ), while control plots (C) were least visited. There were no significant differences between replicate blocks ($F_{10,32}=2.14$, $p=0.051$) and between sets ($F_{1,32}=2.26$, $p=0.143$). Significant interactions were found between exclusion and fertilisation ($F_{1,32}=9.62$, $p=0.004$) and between set and exclusion ($F_{1,32}=9.33$, $p=0.005$).

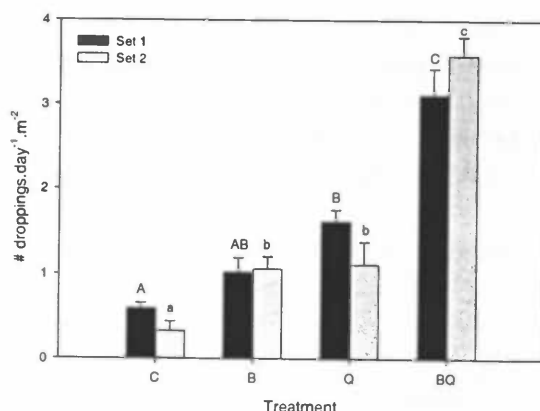


Fig 8. Number of goose droppings per day per m^2 (Mean +SE) for the first count after opening the experiment. C = control treatment, B = high biomass treatment, Q = high quality treatment, BQ = high biomass and high quality treatment. Different letters represent significantly different groups.

Grazing pressure related to biomass and quality of *Festuca rubra*

When the relationship between grazing pressure and biomass and grazing pressure and quality were analysed, treatment still had a highly significant effect ($F_{3,28}=33.20$, $p<0.001$). In addition biomass had a positive influence on grazing pressure ($F_{1,28}=9.44$, $p=0.005$, Fig 9A), while quality did not have an effect ($F_{1,28}=0.28$, $p=0.601$). Replicate blocks were significantly different ($F_{10,28}=3.00$, $p=0.011$), no differences were found between sets ($F_{1,12.6}=0.99$, $p=0.338$).

Results are comparable if biomass and quality are regarded as one factor, i.e. the nitrogen supply (gram N per m^2 = available biomass * nitrogen content). Treatment again had a strong effect on goose grazing pressure ($F_{3,29}=37.47$, $p<0.001$). In addition total nitrogen supply in gram per m^2 had a positive effect on goose presence ($F_{1,29}=10.20$, $p=0.003$, Fig 9B). Replicate blocks were significantly different ($F_{10,34}=2.92$, $p=0.012$), no differences were found between sets ($F_{1,10.0}=0.56$, $p=0.474$). Dead/*Festuca*-ratio had in both analyses no influence on the presence of geese.

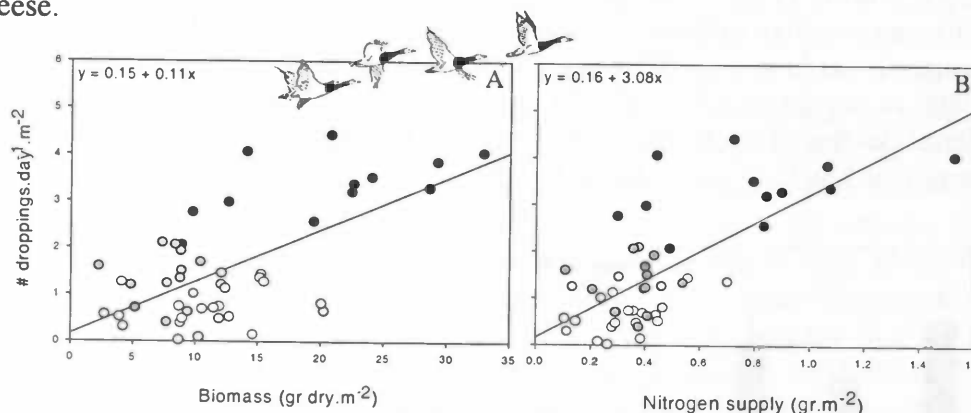


Fig 9. (A) Number of goose droppings plotted against the biomass of *Festuca rubra* (gr dry weight per m^2). (B) Number of goose droppings plotted against the nitrogen supply (gr Nitrogen per m^2). Gram Different coloured dots represent different treatments: white = C, light grey = B, dark grey = Q, black = BQ. It was too complicated to show the complete model in the graphs. Therefore they give only an indication of the relation between vegetation parameters and the goose preference.

Grazing pressure over time

Differences in grazing pressure between experimental plots slowly diminished during approximately four weeks (Fig 10A,B), due to a decrease in number of droppings on manipulated plots (B, Q & BQ) compared to control plots (C). Number of goose droppings found on a plot was significantly decreasing over time for both set 1 ($F_{1,62}=72.19$, $p<0.001$) and set 2 ($F_{1,110}=94.00$, $p<0.001$). Grazing pressure was different between treatments for set 1 ($F_{3,62}=52.87$, $p<0.001$) and set 2 ($F_{3,110}=27.26$, $p<0.001$). Replicate blocks of set 2 differed significantly ($F_{5,110}=3.98$, $p=0.002$).

At the first counts (about three days after opening the plots for the geese) a high grazing pressure was found on BQ-plots and C-plots were least preferred, shown in Fig 8. After a couple of days grazing pressure was higher on quality-enhanced plots (Q & BQ) than on plots with a normal quality (C & B). At the last counts (approximately three weeks later), no clear difference in goose presence could be distinguished, grazing pressure on all plots was equal to the grazing pressure on the control plot.

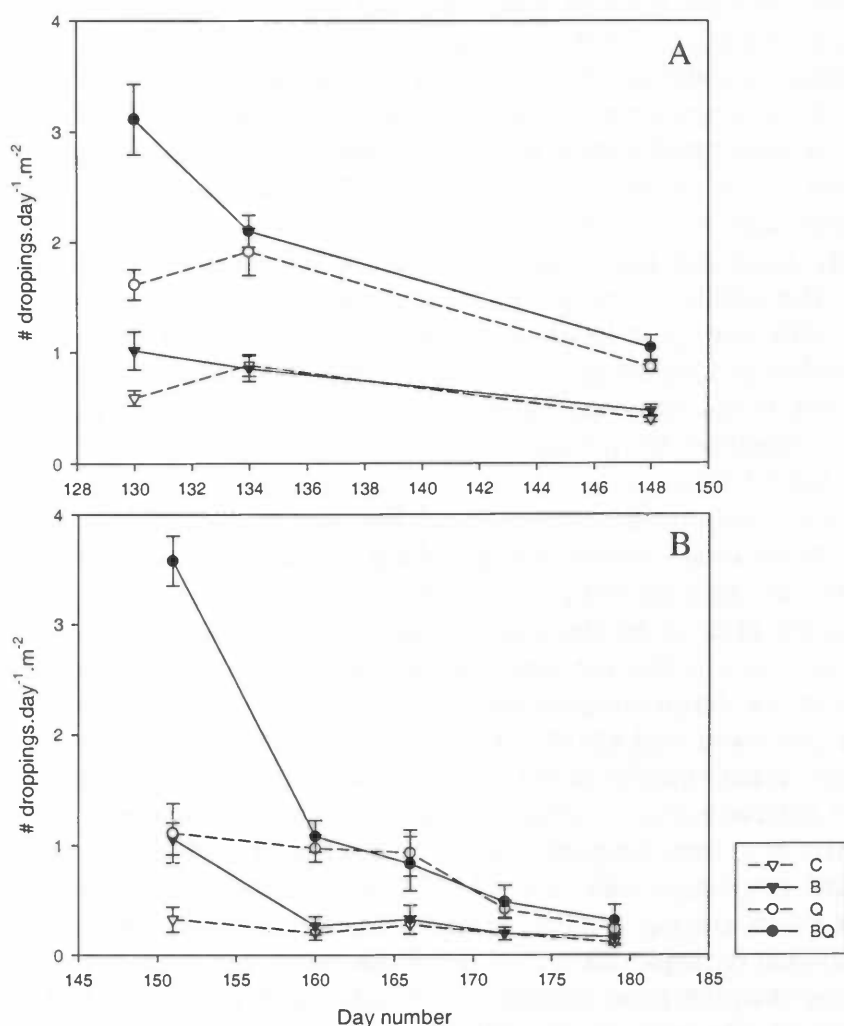


Fig 10. Number of goose droppings (Mean \pm SE) over time for set 1 (A) and set 2 (B). Different lines represent different treatments.

Discussion

Transects

The two different habitats (grassland and salt marsh) investigated along the East coast of Gotland differed in quality and available biomass of *Festuca* sp. Most geese were present at the salt marshes, where grazing pressure could be more than three to six times higher than on adjacent grasslands from mid-May until the end of June, respectively. In 1992 and 1993 a strong increase in grazing pressure was found on the salt marsh of Gotland at the start of June (van der Veen 1994), probably due to arrival of Baltic families at the mainland. In 2003 only a slight increase in grazing intensity was observed when families were using the mainland salt marshes, and dropping numbers were over three times lower than at the peak staging of Arctic geese. This may be due to a decreasing trend in number of goslings produced the last years (van der Jeugd, pers. comm.).

The quality of forage on the salt marsh was about 1.5 times higher than on the grasslands while the biomass was more than 1.5 times lower. The intensive grazing pressure on the salt marsh may be explained by the trade-off between forage quality and forage availability. Short swards are preferred, because of the negative relationship between sward height and forage quality (Riddington *et al.* 1997). An increase in plant standing crop may be paralleled by a decrease in plant quality due to maturation effects (Summers & Critchley 1990) and by an increase in the proportion of standing dead material (Bakker *et al.* 1984; Bazely & Jefferies 1986). However, in this study I did not find a difference in the dead/*Festuca*-ratio between the two habitats. The quality of forage on the salt marsh declined from 2.9% nitrogen in early May to 2.2% nitrogen in late June. These values correspond with values measured in earlier studies on Gotland (Larsson *et al.* 1998; van der Veen 1994), although they are in the lower part of the range. The spring of 2003 was dry, which probably caused low Nitrogen contents of the forage as rainfall is positively correlated with forage quality (van der Veen 1994).

Some geese were grazing at agricultural fertilised grasslands (dominated by *Phleum* sp.) near to the coast. Agricultural grassland situated more inland were not used very intensively on the southern part of Gotland, which is striking because the nitrogen content of the grass on fertilised fields was much higher than on salt marshes (6.4% N compared to 2.9 % N, first week of May 2003). However, it is possible that the biomass on the fertilised grasslands was limiting early in the season, because the spring of 2003 was cold and dry. The distance to the sea, the pine forest between salt marsh and agricultural fields and the disturbance by farmers may prevent geese from using the agricultural fields situated inland. However, the number of geese observed on these fields is increasing over the last years (Kjell Larsson, pers. comm.).

At the first dropping counts (around 10th May), corresponding with the peak staging of Arctic geese, grazing pressure on grasslands was almost as high as on salt marshes. It is likely that the high numbers of geese present at this time forced part of the birds to forage in less preferred habitats, i.e. grasslands. It is possible that the geese were distributed ideally over the two habitats, in accordance to their respective carrying capacities, or, alternatively, that the most competitive birds occupied the most profitable habitat, i.e. the salt marsh. For example, brent geese (*Branta bernicla bernicla*) defended high quality patches more actively than low quality patches (Bos *et al.* 2002b). It has also been shown that dominant geese or families benefit more from high quality food patches than subordinates (Prop *et al.* 1984).

A next step in the goose grazing investigation on Gotland would be to collect information about the minimal requirements with respect to forage quality and availability for barnacle geese on Gotland, and to investigate whether the salt marsh can provide these requirements. Research on barnacle geese breeding on Spitsbergen has shown that the requirements are dependent on several factors: (1) the nutritional and energetic requirements of an individual given its activities (e.g. migrating, breeding, moulting), (2) the passage time of food through the gut and (3) intake rate of food (e.g. dependent on the time spent foraging, the height of the sward) (Jouke Prop, pers. comm). With the help of assumptions on minimal energy requirements for a barnacle goose (around 1000 kJ per day) and the maximum possible food intake rate (0.25 gr dry weight per min), the necessary energy yield of the food can be calculated (Jouke Prop, pers. comm.). It needs to be investigated whether the geese on Gotland reach maximum food intake rate (e.g. through observations of bite frequency and bite size; or dropping interval and dropping weight).

On Gotland, food availability appeared to be low compared to other staging sites, e.g. Schiermonnikoog (Bos 2002; Lubbe 2003; van der Graaf 2004) and the Pechora Delta (Havinga 2003; van der Graaf 2004), and did hardly increase throughout the study period (Appendix 1, Fig 14). The biomass measure we used (available biomass in g dry weight per m² at a specific moment in time) did not provide information on the production of new forage, which may be an important factor in determining the actual food availability. We tried to measure the production of new forage during the 2003 field season, but we did not obtain a reliable measure (Appendix 3).

An important question in the research project is how Baltic breeding geese are able to cope with the low quality of forage (Appendix 2, Fig 15), and with the seasonal decline in forage quality. Successful breeding in temperate regions (Baltic region, Dutch Delta region) proved that the current nutritional situation at these latitudes is adequate (Larsson *et al.* 1988). We have no information whether food quality on Gotland changed over the last decades. Protein content of the food may have increased due to the an increase in nitrogen input in grazing areas. Fertilisers have never been used in the areas where the geese spend most of their time feeding (Larsson *et al.* 1988). However, large regions of Europe have received high inputs of inorganic nitrogen for the past 20-30 years (Wright *et al.* 2001) e.g. through human related activities which caused eutrophication. In addition larger herbivores as cattle and sheep but also Arctic staging geese may increase the attractiveness of grazing areas to Baltic geese. This process of one herbivore creating or maintaining swards attractively for other herbivores is known as facilitation. In general grazing causes a rapid turnover of plant material as plants produce fresh new leaves or tillers of a higher quality compared to the old leaves and it reduces the standing dead and litter biomass (e.g. Bos 2002; Fox *et al.* 1998). Under ungrazed conditions salt marsh vegetation changes due to natural succession and tall plant species, unpalatable to geese, become dominant (Bos *et al.* 2002a; Olff *et al.* 1997). There is no evidence for a recent increase in grazing pressure by livestock in the goose grazing areas on Gotland (Larsson *et al.* 1988), however the total population of barnacle geese (and therefore the number of spring staging geese) did increase rapidly over the last decades. To investigate which factors cause successful settlement of new barnacle goose breeding populations, it may be interesting to compare sites with and without established colonies.

There is evidence that goslings on temperate breeding grounds grow slower than on goslings on Arctic breeding grounds (Loonen *et al.* 1997). Based on the nitrogen

content of the food geese encounter a comparable situation on arctic breeding grounds on Spitsbergen (Prop & Vulink 1992) and on temperate breeding grounds on Gotland (van der Veen 1994, this study) during the moulting period, i.e. the period in which the goslings are growing. However, nitrogen content is not the single determinant of forage quality. For a herbivore, nutrient assimilation is an important factor, which depends on several factors, e.g. on the nutrient *and* fibre content of a plant (Manseau & Gauthier 1993). Moreover, restriction on total foraging time by daylight period influences the nutrient intake rate.

Experiment

The manipulation of the plots resulted in clear differences in quality and availability of *Festuca rubra*. The nitrogen content was higher in fertilised plots than in unfertilised plots and the available biomass was higher in ungrazed plots than in grazed plots. Nitrogen content was also influenced by exclosures and was significantly lower in ungrazed plots, which is probably caused by decreased plant quality when plant standing crop is higher (Summers & Critchley 1990). As a result of the manipulation the "natural" negative correlation between biomass and quality of *Festuca rubra* was disentangled and therefore the relative influence of these factors on grazing pressure could be determined. As mentioned before, an increase in plant standing crop may result in an increase in the proportion of standing dead material (Bakker *et al.* 1984; Bazely & Jefferies 1986). In contradiction, we found that plots with an increased plant standing crop (biomass enhanced plots) had a decreased proportion of cover of dead standing material (Fig 7), which may be due to short time scale we are looking on (about four weeks).

During the whole study period grazing pressure was highest on plots that were enhanced in both quality and biomass (BQ), while unmanipulated control (C) plots were least visited. Most of the variance in grazing pressure was explained by treatment (C, B, Q & BQ). When controlling for treatment forage availability (biomass) explained only a small part of the variance, while forage quality (nitrogen content) did not have a significant effect. Therefore, it seems that the distribution of geese over the plots is mostly influenced by the treatments *within* replicates, rather than by the forage availability and quality *between* replicates (Fig 11, *see also* Fig 9). The strong effect of treatment on the presence of geese may be caused by the clear differences between plots with respect to forage availability and quality. In this experiment it seems that goose presence is only determined by treatments, but it is likely that food availability and food quality are underlying parameters that determine the grazing pressure on a plot.

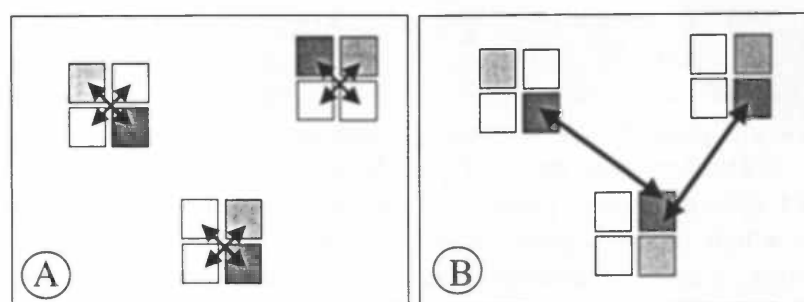


Fig 11. (A) The choice of the geese for plots within a replicate. (B) The choice of the geese for food availability and food quality between replicates.

For dark-bellied brent geese grazing on an unfertilised vegetation it has been shown that the negative relationship between sward height and grazing intensity is caused by

the negative correlation between sward height and nitrogen content. Elimination of this relationship by application of fertiliser led to a higher preference for longer swards (Hassall *et al.* 2001; Riddington *et al.* 1997). These results correspond with the results we found for the barnacle geese on Gotland. In a natural unfertilised situation more geese were present in the areas with low biomass (salt marsh), whereas on the experimental plots grazing pressure was higher on plots with a high biomass *and* high quality (BQ).

The results presented here show which treatments attract most geese and how geese distribute themselves over different treatments, but we do not gain insight in the preference of individuals for a vegetation parameter, represented here by quality or quantity. Carrying capacity might be an important factor determining the number of geese visiting a plot. The plot with the highest carrying capacity might therefore be the plot visited most, but is not necessarily the most preferred plot (Fig 12).

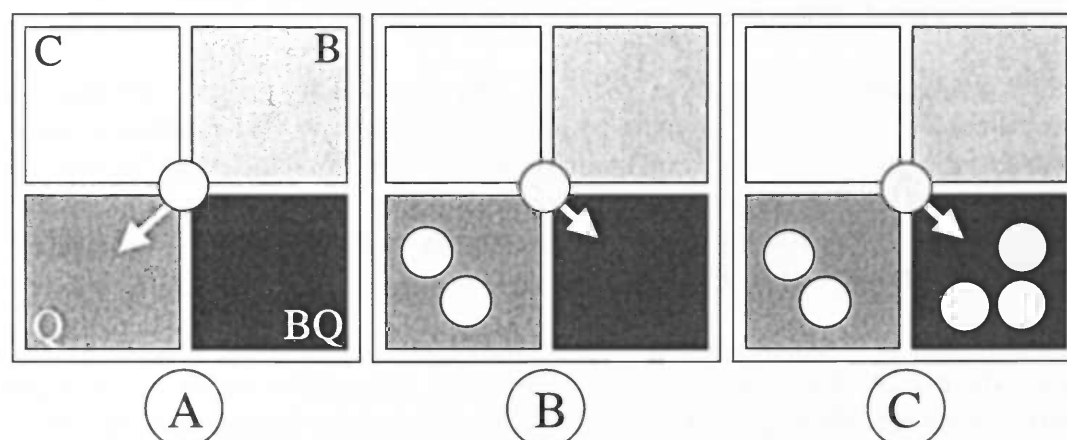


Fig 12. A scheme of the possible distribution pattern of the geese over the experimental plots. Picture A, B & C represent successive time periods. (A) Geese first arriving or being most dominant choose most preferred plots. (B) Geese choose the second-best plots when the most preferred are occupied or depleted. (C) Geese continue choosing the second-best plots until they are occupied or depleted. The second-best plots can be the most visited plot if they have a higher carrying capacity.

Biomass on Q-plots was lower than the biomass BQ-plots, whereas quality did not differ significantly. BQ-plots, which presumably had a higher carrying capacity, i.e. higher biomass, were visited most. Although the BQ-plots had the highest grazing pressure, the Q-plots, might have been the most preferred plots. It has been shown that nutrient intake rates decline with increased levels of standing crop (Bos *et al.* 2002b) and geese might have maximised their nitrogen intake rate on Q-plots as a result of a shorter sward. The relatively high goose numbers on the salt marsh of Gotland could have caused depletion of the most preferred plots, indicated by a clearly visible decrease in biomass a couple of days after opening the experimental plots for geese. Furthermore, the differences in grazing pressure between plots levelled off (Fig 10) which indicates that the grazing pressure decreases when treatment effect dilutes over time, e.g. biomass is grazed down.

Measurements on the individual choice of a goose will yield valuable information on which food parameters are important for patch and habitat preference on different stepping stones along the East Atlantic Flyway. The relative importance of food parameters for patch choice could be investigated by observing individual geese on the experimental plots. (1) Patch choice can be determined by observing the choice of

the first individual wild geese using the experimental plots, i.e. when no depletion has taken place (Fig 12A). (2) Alternatively, a choice-experiment can be carried out with captive geese. Observations of patch can be made and intake rate on different treatments can then be measured.

Riddington *et al.* 1997 proposed that intake rate of nitrogen is the main factor that determines patch choice by geese. It would be interesting to investigate whether geese maximise their nutrient intake by making different choices along the flyway and over the season. According to the optimal foraging theory it is assumed that geese are able to distinguish between quality and quantity of forage (Krebs & Davies 1978). Geese are able to distinguish between grass species, select plant parts with high nutrient contents and maximise the total intake of nitrogen (Nyeland Kristiansen *et al.* 2000). The hypothesis is that quality of forage becomes more important through the season due to seasonal decline, whereas biomass becomes less limiting due to over abundance. Forage quality might be more important in determining patch preference in temperate breeding areas (Baltic sea & Dutch Delta area), because nitrogen content is at a lower level (Appendix 2, Fig 15).

Geese distinguish between plots (or high and low quality vegetation) based on parameters that are "visible" to them by sight, taste, smell etc. The nitrogen content is related to the greenness of the vegetation (Bos *et al.* 2002b), which may be one of the parameters "visible" to geese. For future research it can be interesting to measure the greenness of a plot and relate this to the nitrogen content of the forage and the presence (or preference) of the geese.

Results found on Gotland correspond with the results found at the Russian breeding sites, where plots that were enhanced in biomass and quality received the highest grazing pressure (Havinga 2003). On Schiermonnikoog the highest grazing pressure was measured on quality enhanced (Q) plots, whereas biomass enhanced plots (B & BQ) seemed to be avoided (Lubbe 2003). One important factor explaining the difference with the island Schiermonnikoog is the management regime of the salt marsh. On Schiermonnikoog the experiment was carried out in an ungrazed salt marsh, where biomass of food plants and dead standing material remained higher throughout winter (van der Graaf, unpublished data). These factors might influence the presence of geese.

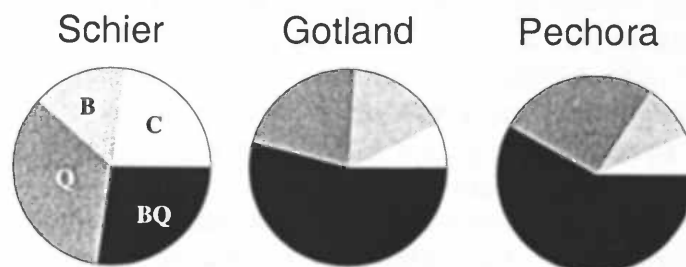


Fig 13. Relative grazing pressure on the experimental plots in the three different areas along the flyway.

Acknowledgements

Julia, thanks a lot for the great time on Gotland. I enjoyed the field work, all the nice trips and of course the ice creams very much! Many thanks go to Julia Stahl and Sandra van der Graaf for their great supervision. I learned very much from all the discussions about analyses and interpretation of the data, you were always there when I had questions and problems. I would like to thank Henk van der Jeugd for counting goose droppings in July when I already returned to the Netherlands, we would have missed a nice point in our graph! Also lots of thanks for all the discussions and useful comments. Finally I would like to thank Kjell Larsson, for the possibility of staying at his place, and all the other people in Sigsarve, for the nice field season: Julia, Kjell, Henk, Annika, Thor, Richard and Peter. Financial support for this study was provided by the European Science Foundation. The research I carried out was embedded within a project entitled 'Trapped between landscape change and physiological constraints - The role of coastal stepping stones for the migration of Arctic geese' granted as a Post-Doc Fellowship to Dr. Julia Stahl by the Deutsche Forschungsgemeinschaft.

Appendices

Appendix 1: Forage availability along the flyway

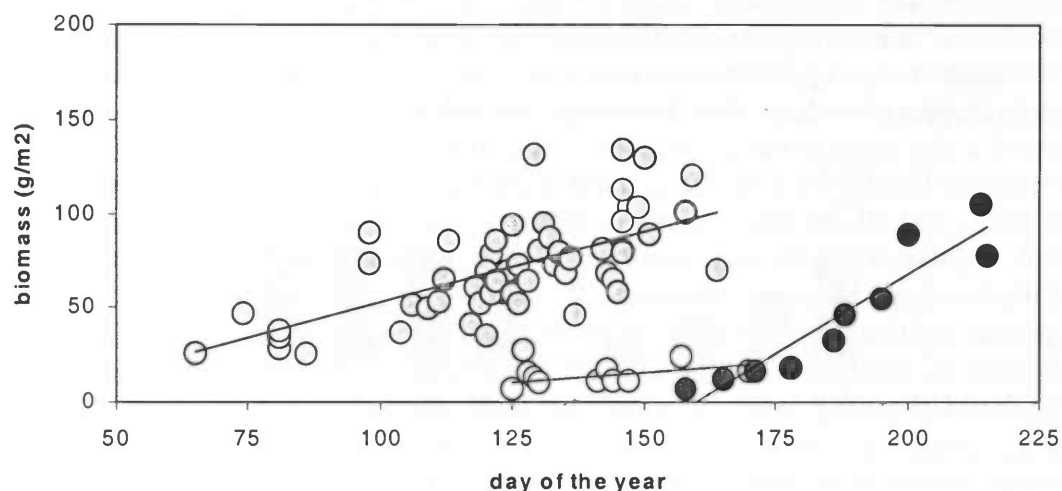


Fig 14. Forage availability (biomass in gram dry weight per m²) in different areas along the East Atlantic Flyway. Different colours represent different areas along the flyway: grey = Schiermonnikoog (the Netherlands); white = Gotland (Sweden); black = Tobseda (Russia). (van der Graaf 2004)

Appendix 2: Forage quality along the flyway

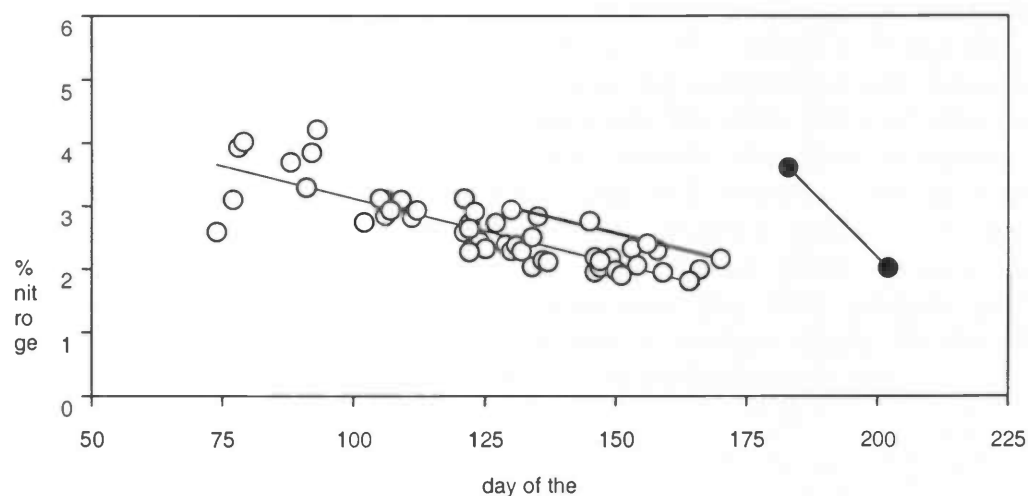


Fig 15. Forage quality (% Nitrogen) in different areas along the East Atlantic Flyway. Different colours represent different areas along the flyway: grey = Schiermonnikoog (the Netherlands); white = Gotland (Sweden); black = Tobseda (Russia). (van der Graaf 2004).

Appendix 3: Production measurements

We attempted to measure production of *Festuca sp.* on Gotland this year (Table 1). Per transect one small enclosure was placed near the transect. Every second week tiller densities of *Festuca sp.* were counted (20 times per enclosure) and one sample of 50 tillers was collected. Biomass was calculated by multiplying the number of tillers per m² and the weight of one tiller. The difference between the biomass on the transect and the biomass in the enclosure was the production. This method turned out to be inapplicable for calculating the production. Negative production values were retrieved very often, which might be due to the size of the enclosure and the inhomogeneity of the vegetation. We now assume that production enclosures were too small. Due to low grazing pressure on the grassland the differences between production enclosures and the transect might be too small to detect. For future research on Gotland it is very important to obtain a reliable production measurement, because Food availability is an important factor determining the preference of geese. A better measure for production is obtained when the production enclosures are not replaced every second week after measuring the biomass. When the enclosure is maintained the whole study period ("permanent" production enclosure) at exactly the same place the biomass change can be traced. This avoids additional variation due to inhomogeneous vegetation. The increase in biomass per gram standing biomass can be calculated (productivity). Due to the positive effect of grazing on vegetation growth production measurements in "permanent" production enclosures might underestimate real production.

Table 1. Production values per area for the different habitats over time. GB = Grötlingboud, HU = Hummelbosholm, NH = Närsholmen. Values displayed in bold are the values measured in the salt marsh areas.

Area	Day no	Transect	Production (gr dry/day)	SE
GB	130	salt marsh	x	x
GB	144	salt marsh	0.37	0.08
GB	143	grassland	-0.11	0.36
GB	157	salt marsh	0.42	0.10
GB	156	grassland	0.04	0.21
HU	128	salt marsh	x	x
HU	141	salt marsh	0.25	0.23
HU	141	grassland	-0.35	0.56
HU	154	salt marsh	0.63	0.15
HU	155	grassland	0.76	0.27
HU	168	salt marsh	-0.13	0.51
HU	168	grassland	-0.32	0.18
NH	129	salt marsh	x	x
NH	144	salt marsh	0.12	0.21
NH	144	grassland	0.01	0.03
NH	158	salt marsh	-0.12	0.33

Appendix 4: Indications for goose preference

Based on the results of this project we cannot draw conclusions on goose preferences for the food parameters quality and quantity. I will here try to evaluate the preference of the geese on Gotland, based on the collected data. The number of droppings on a plot corrected for the forage supply (# droppings/gram nitrogen.m⁻²) indicate a possible preference of the geese (Fig 16). If the number of droppings corrected for the forage supply is not equal on all plots, we can assume a preference for certain plots.

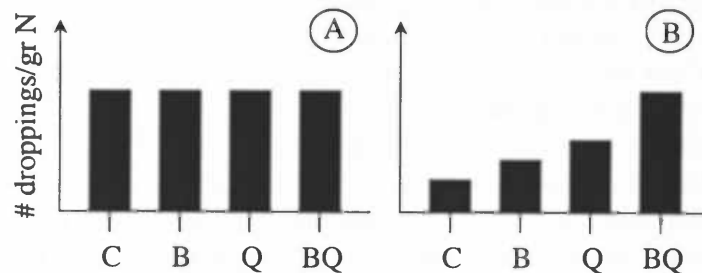


Fig 16. Measuring preference - 2 hypothetical alternatives: (A) The number of droppings per gram Nitrogen on all treatments if the presence of geese is completely dependent on the carrying capacity of a plot (here defined as nitrogen supply). (B) The number of droppings per gram Nitrogen on all treatments if the presence of geese is not completely dependent on the carrying capacity, but also on the preference for certain treatments.

The number of droppings corrected for the carrying capacity (Fig 17) did not differ significantly for set 1 ($F_{3,15}=1.42$, $p=0.276$), which might indicate that the distribution pattern of droppings was determined by the carrying capacity of the plot rather than by the preference of individual geese. For set 2 the number of droppings was highest on BQ-plots and lowest on C-plots ($F_{3,15}=19.65$, $p<0.001$), which indicates that the presence of geese is not only determined by the carrying capacity of a plot. According to these results there is an indication that geese prefer BQ-plots above all others and C-plots are least preferred, although it is still possible that prior occupancy or depletion influence the results. Comparing set 1 and set 2, preference seemed to shift throughout the season. For set 1 no differences in dropping numbers were found between treatments, whereas in set 2 BQ-plots were preferred. Quality declines when the vegetation is growing and therefore preference may shift towards quality enhanced plots. Carrying capacity is described here as nitrogen-supply, but the same trend are shown when carrying capacity is defined as the biomass per plot.

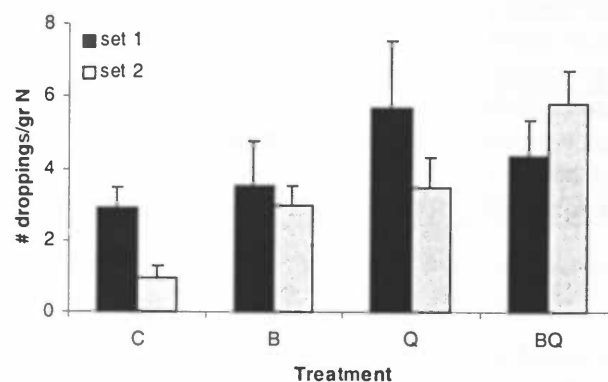


Fig 17. The number of droppings per gram Nitrogen.m⁻² for all treatments. On the y-axis the number of droppings, on the x-axis the different treatments.

References

- Bakker, J. P., de Leeuw, J., & van Wieren, S. E. (1984) Micro-patterns in grassland vegetation created and sustained by sheep-grazing. *Vegetatio*, **55**: 153-161.
- Bazely, D. R. & Jefferies, R. L. (1986) Changes in the composition of salt-marsh communities in response to the removal of a grazer. *Journal of Ecology*, **74**: 693-706.
- Bos, D., Bakker, J. P., de Vries, Y., & van Lieshout, S. (2002a) Long-term vegetation changes in experimentally grazed and ungrazed back-barrier marshes in the Wadden Sea. *Applied vegetation science*, **5**: 45-54.
- Bos, D. (2002) Grazing in coastal grasslands, Brent Geese and facilitation by herbivory. *PhD thesis*, University of Groningen, the Netherlands.
- Bos, D., Rubinigg, M., & Stahl, J. (2002b) The relative importance of food biomass and quality for patch and habitat choice in brent geese, in: *Grazing in coastal grasslands: brent geese and facilitation by herbivory. PhD thesis*, 23-41. University of Groningen, The Netherlands.
- Cooch, E. G., Lank, D. B., Rockwell, R. F., & Cooke, F. (1991) Long-term decline in body size in a snow goose population: evidence of environmental degradation? *Journal of Animal Ecology*, **60**: 483-496.
- Crawley, M. J. (1983) *Herbivory: the dynamics of animal-plant interactions*, Blackwell, Oxford.
- Drent, R. H. & Prins, H. H. Th. (1987) The herbivore as a prisoner of its food supply, in: van Andel, J., Bakker, J. P., and Snayden, R. W. (eds.), *Disturbance in grasslands*, 131-147. Dr. W. Junk publishers, Dordrecht.
- Ebbinge, B. S. & Spaans, B. (1995) The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied brent geese *Branta b. bernicla* in the high Arctic. *Journal of Avian Biology*, **26**: 105-113.
- Ebbinge, B. S. & van Biezen, J. B. (1987) Estimation of annual survival rates using resightings of individually marked barnacle geese *Branta leucopsis*, wintering in the Netherlands and northern Germany. *Acta Ornithologica*, **23**: 101-114.
- Forslund, P. & Larsson, K. (1991) Breeding range expansion of the barnacle goose *Branta leucopsis* in the Baltic area. *Ardea*, **79**: 343-346.
- Fox, A. D., Kristiansen, J. N., Stroud, D. A., & Boyd, H. (1998) The effects of stimulated spring goose grazing on the growth rate and protein content of *Phleum pratense* leaves. *Oecologia*, **116**: 154-159.
- Ganter, B., Larsson, K., Syroechkovsky, E. V., Litvin, K. E., Leita, A., & Madsen, J. (1999) Barnacle goose *Branta leucopsis*: Russia/Baltic, in: Madsen, J., Cracknell, G., and Fox, T. (eds.), *Goose populations of the western palearctic; a review of status and distribution*, 270-283. Wetlands international publication no. 48; Wageningen.
- Grant, S. A. (1981) Sward components, in: Hodgson, J., Baker, R. D., Davies, A., Laidlaw, A. S., and Leaver, J. D. (eds.), *Sward measurement handbook*, 71-92. British grassland society, Hurley.
- Hassall, M., Riddington, R., & Helden, A. (2001) Foraging behaviour of brent geese, *Branta b. bernicla*, on grasslands: effects of sward length and nitrogen content. *Oecologia*, **127**: 97-104.
- Havinga, R. M. (2003) What does Barnie want for dinner? *Student report*, University of Groningen (in press).

- Karasov, W. H. (1990) Digestion in birds: chemical and physiological determinants and ecological implications. *Studies in Avian Biology*, **13**: 391-415.
- Klimkowska, A. (2003) Geese on a green wave; weather parameters and seasonal changes in food availability and food quality in relation to the barnacle goose (*Branta leucopsis*) migration along the East Atlantic flyway. *Report*, RIZA (Lelystad) & RuG (Groningen).
- Krebs, J. R. & Davies, N. B. (1978) *Behavioural ecology, an evolutionary approach*, Blackwell sciences, Oxford.
- Larsson, K. & Forslund, P. (1991) Environmentally induced morphological variation in the barnacle goose *Branta leucopsis*. *Journal of Evolutionary Biology*, **4**: 619-636.
- Larsson, K. & Forslund, P. (1994) Population dynamics of the barnacle goose *Branta leucopsis* in the Baltic area: density-dependent effects on reproduction. *Journal of Animal Ecology*, **63**: 954-962.
- Larsson, K., Forslund, P., Gustafsson, L., & Ebbinge, B. S. (1988) From the high Arctic to the Baltic: the successful establishment of a barnacle goose *Branta leucopsis* population on Gotland, Sweden. *Ornis Scandinavia*, **19**: 182-189.
- Larsson, K. & van der Jeugd, H. P. (1998) Continuing growth of the Baltic barnacle goose population: number of individuals and reproductive success in different colonies, in: Mehlum, F., Black, J., and Madsen, J. (eds.), *Research on Arctic geese. Proceedings of the Svalbard goose symposium, Oslo, Norway.*, 213-219. *Norsk Polarinstitutt Skrifter* **200**,
- Larsson, K., van der Jeugd, H. P., van der Veen, I., & Forslund, P. (1998) Body size declines despite positive directional selection on heritable size traits in a barnacle goose population. *Evolution*, **52**: 1169-1184.
- Loonen, M. J. J. E., Larsson, K., van der Veen, I., & Forslund, P. (1997) Timing of wing moult and growth of young in arctic and temperate breeding barnacle geese, in: *Goose breeding ecology: overcoming successive hurdles to raise goslings. PhD Thesis*, 136-153. University of Groningen, The Netherlands.
- Lubbe, G. (2003) Competitie voor *Festuca* tussen brandganzen en hazen: de rol van biomassa en kwaliteit. *Student report*, van Hall instituut, Leeuwarden, the Netherlands & University of Groningen, the Netherlands.
- Manseau, M & Gauthier, G. (1993) Interactions between greater snow geese and their rearing habitat. *Ecology*, **74**: 2045-2055.
- Nyeland Kristiansen, J., Fox, T. A. D., & Nachman, G. (2000) Intake by shoot selection among herbivorous geese. *Ardea*, **88**: 119-125.
- Oloff, H., de Leeuw, J., Bakker, J. P., Platerink, R. J., van Wijnen, H. J., & de Munck, W. (1997) Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. *Journal of Ecology*, **85**: 799-814.
- Owen, M. (1980) Movements and migration, in: *Wild geese of the world*, 97-110. Batsford, London.
- Prins, H. H. Th. & Ydenberg, R. C. (1985) Vegetation growth and a seasonal habitat shift of the barnacle goose *Branta leucopsis*. *Oecologia*, **66**: 122-125.
- Prop, J. & Deerenberg, C. (1991) Spring staging Brent Geese *Branta bernicla*: feeding constraints and the impact on the accumulation of body reserves. *Oecologia*, **87**: 19-28.

- Prop, J., van Eerden, M. R., & Drent, R. H. (1984) Reproductive succes of the Barnacle Goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, western Spitsbergen. *Norsk Polarinstitution Skrifter*, **181**: 110-121.
- Prop, J. & Vulink, T. (1992) Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. *Functional Ecology*, **6**: 180-189.
- Riddington, R., Hassall, M., & Lane, S. J. (1997) The selection of grass swards by brent geese *Branta b. bernicla*: interactions between food quality and quantity. *Biological Conservation*, **81**: 153-160.
- Summers, R. W. & Critchley, C. N. R. (1990) Use of grassland and field selection by brent geese *Branta b. bernicla*. *Journal of Applied Ecology*, **27**: 834-836.
- Ulyatt, M. J. (1981) The feeding value of temperate pastures, in: Morley, F. W. H. (eds.), *Grazing animals*, 125-141. Elsevier, Amsterdam.
- van der Graaf, A. J. (2004) Foraging choices of Barnacle geese along the flyway - from temperate to Arctic. *Presentation workshop Coastal Ecology (Antwerp)*,
- van der Jeugd, H. P. & Larsson, K. (1998) Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledgling characteristics. *Journal of Animal Ecology*, **67**: 953-966.
- van der Jeugd, H. P., Olthoff, M. P., & Stahl, J. (2001) Breeding range translations into staging site choice: Baltic and Arctic barnacle geese *Branta leucopsis* use different habitats at a Dutch Wadden sea island. *Ardea*, **89**: 253-265.
- van der Veen, I. (1994) Temperate breeding in barnacle geese *Branta leucopsis*: factors affecting growth and quality of food on Gotland, Sweden. *Student report*, University of Groningen, the Netherlands.
- Wright, R. F., Alewell, C., Cullen, J., Evans, C. D., Marchetto, A., Moldan, F., Prechtel, A., & Rogora, M. (2001) Trends in nitrogen deposition and leaching in acid-sensitive streams in Europe. *Hydrology and Earth System Sciences*, **5**: 299-310.
- Ydenberg, R. C. & Prins, H. H. Th. (1981) Spring grazing and the manipulation of food quality by barnacle geese. *Journal of Applied Ecology*, **18**: 443-453.
- Zar, J. H. (1999) *Biostatistical analysis*, 4th edition, Prentice Hall, New Jersey.