# Surfing on a green wave – how plant growth drives spring migration in the Barnacle Goose *Branta leucopsis*

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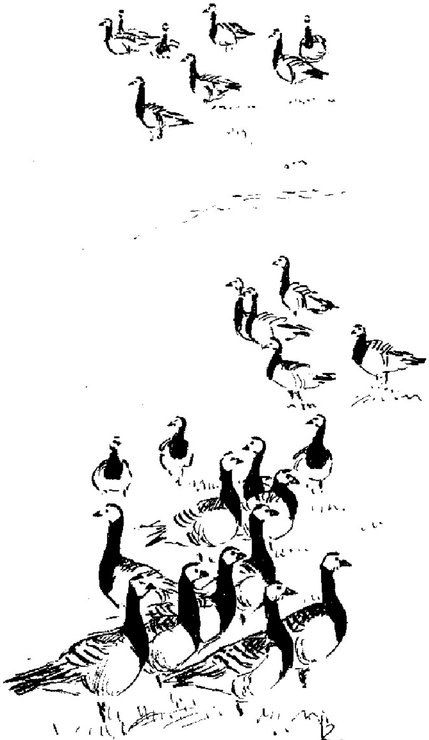
The nutritional quality of forage plants varies in space and time. This variation is presumed to drive the annual migration of herbivore species which follow peaks in the availability of high quality forage between sites. The green-wave hypothesis predicts that during spring migration to northern breeding 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 *Branta leucopsis* 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 saltmarsh 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 in one measure, the nutrient biomass. For all sites, nutrient biomass 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 nutrient biomass. At the Russian breeding site, geese arrive prior to the flush of spring growth of forage plants and profit from the peak in nutrient biomass when the goslings hatch and adult birds start moulting. We conclude that spring nutrient biomass is a key factor driving the timing of the annual northern migration of avian herbivores



Key words: Arctic breeding, forage quality, nutrient intake, plant biomass, spring staging, stopover sites

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## INTRODUCTION

Though 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 & Jones 1997), particularly in response to seasonal changes. Herbivores frequently migrate between sites following local peaks in the nutritional quality of forage plants. A well-known example is the annual migration of the Wildebeest *Connochaetes taurines* in the Serengeti-ecosystem in East Africa (McNaughton 1979). Wildebeest migrate in the wet season from the woodlands in the North to the plains in the South where seasonal rains initiate the growth of green swards. After the wet season they return to the woodlands where overall annual 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 that represents spring growth, i.e. Red Deer *Cervus elaphus* (Albon & 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 1970s (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. Fig. 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 stopovers at coastal sites in areas of the Baltic and White Seas, *en route* to the breeding grounds in northern Russia (Ganter *et al.* 1999). Traditionally, breeding sites were restricted to Novaya Zemlya and Vaigach islands, but in recent decades their breeding range has expanded west to the Archangelsk region (Filchagov & 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 & 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). Monocotyledonous plants grow from a basal meristem, enabling sequential harvest 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, plant tissues become more fibrous, with lower protein contents, hence, nutritional quality decreases. Moreover, as the plants continue to grow, the structurally tall swards become increasingly difficult for the geese to graze. Many studies demonstrated that geese and other small herbivores prefer vegetation of low or intermediate heights (Lang & Black 2001, Durant *et al.* 2003, van de Koppel *et al.* 1996, van der Wal *et al.* 1998). 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

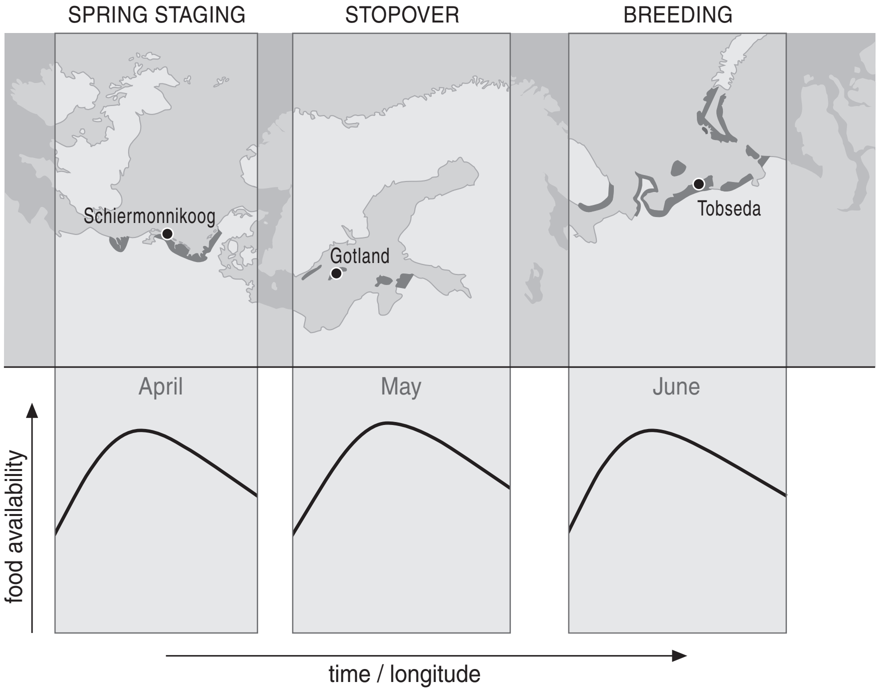

**Figure 1.** A schematic overview of the green wave hypothesis (Drent et al. 1978, Owen 1980), modified for the flyway of the Russian population of Barnacle Geese. Breeding sites are given with dark grey shading. The three study sites are indicated on the map; Schiermonnikoog – a Wadden Sea staging site, Gotland – a Baltic Stopover site and Tobseda – a Russian breeding site.

intake, instead of total biomass intake (Durant *et al.* 2004, Teunissen *et al.* 1985). Besides separate measures of biomass (g dry weight of green leaves $m^{-2}$) and nutritional quality (measured as the nitrogen content of leaf tips, %), we will concentrate on the measure of nutrient biomass (measured as nitrogen biomass, in $g\,N\,m^{-2}$) 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. Assuming that forage decisions in small herbivores are based on the combined influence of plant quality and biomass, we adjust the hypothesis to predict that there are waves of nutrient 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 (Fig. 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 nutritional quality at these 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 southwestern-most study site is the salt marsh on the island of Schiermonnikoog 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 & Stahl 2003), part of the salt marsh is grazed by cattle in summer. 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 stopover. The third study site is a breeding site in the Pechora Delta in northern Russia next to the abandoned village of Tobseda (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 1500 breeding pairs of geese (van der Jeugd *et al.* 2003, van der Graaf *et al.* 2004).

Vegetation structure at all three sites is similar; canopy is low, due to summer-grazing by livestock in the Wadden Sea and Baltic Sea site, whereas canopy remains low at the Russian breeding grounds through environmental constraints.

### Migration dynamics

At the Wadden Sea staging site and the Baltic stopover site in 2004 and on Russian breeding site in 2003 we assessed goose grazing pressure, based on faecal counts. Goose droppings were counted along transects consisting of 5 inconspicuous marking sticks at intervals of 10 m. At the Wadden Sea, Baltic Sea and Russian sites we established 10, 10 and 7 replicated transects, respectively, in areas with suitable vegetation. Every 10 days droppings were counted and removed in a 4-m$^2$ 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 & Hofeditz 2002) and from Eemshaven, The Netherlands (1999–2002, data Kees Koffijberg –SOVON), data of both sites were combined to represent departure date from the Wadden Sea. Data on peak migration days over southern Finland was obtained from Lintukymi, the annual reports of the Kymenlaakso Birding Society (1990–2004). For both datasets, the date at which 75% of the Barnacle Geese observed at that site had travelled through (75% of total migration) was used. These data form the basis for Fig. 2B. Data on peak hatch and nest initiation were obtained from Gotland, Sweden (1985–2004, pers. comm. Henk van der Jeugd & Kjell Larsson) and Tobseda, Russia (2002–2004, pers. comm. Henk van der Jeugd & Götz Eichhorn).

### Forage biomass and quality

In 2003 and 2004 we collected data on forage biomass and nutritional quality at the three main study sites (for the Russian site only in 2003). We measured tiller density on ten marked quadrates of 5x5 cm. To measure biomass, we sampled 50 tillers from either Red Fescue (Wadden Sea staging site, Baltic stopover site) or 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 to get a measure for 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 (% of dry weight), from here on 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.

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 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 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 $R^2$ (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-samples *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 analyse 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 (Fig. 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, did grazing pressure increase 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. Fig. 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 (Figs. 3A and B). Biomass increased linearly as spring progressed in all areas. Estimates of biomass ceased around peak standing crop. 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

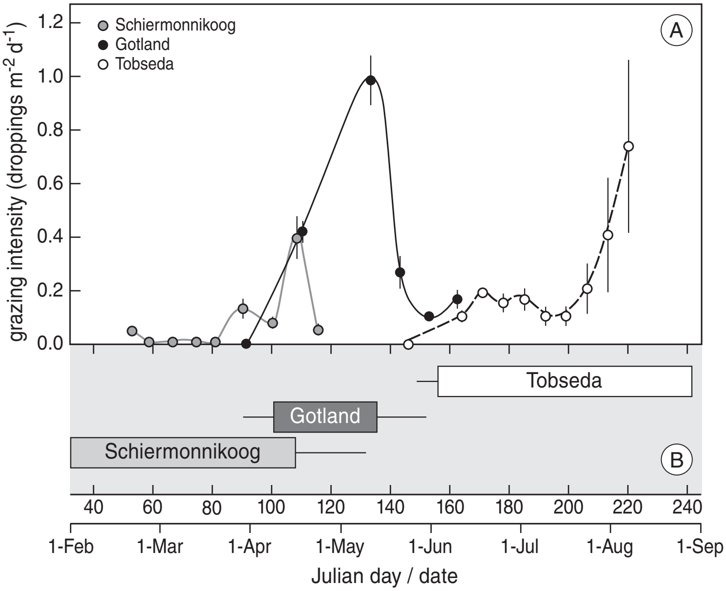

**Figure 2.** Timing of goose migration; (A) grazing pressure in the years 2003/2004 expressed as the number of droppings per m$^2$ per day for each area over the staging season and (B) staging periods as derived from observations (Schiermonnikoog, pers obs. D. Bos and J. Stahl; Gotland, pers obs. H.P. van der Jeugd and K. Larsson; Tobseda, 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.

Sea staging site, we did not find a peak within the measuring period. Table 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$^{-2}$), Fig. 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.

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 Fig. 3B.

### 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 (Fig. 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 2, comparisons 1 and 2, respectively).

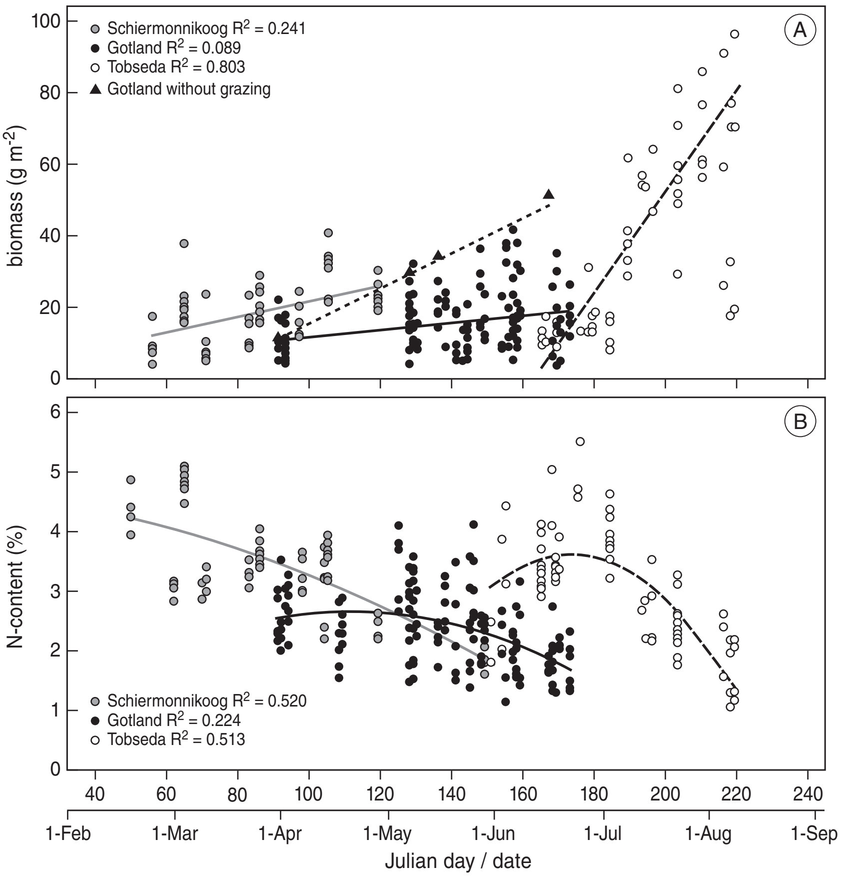

**Figure 3.** Forage biomass (g $m^{-2}$) (A) and N-content (% of dry weight of above-ground biomass) (B) between day 40 and day 220, at three sites along the flyway of the Barnacle Goose; Schiermonnikoog – a Wadden Sea staging site, Gotland – a Baltic stopover site and Tobseda – a Russian breeding site. For all regression lines $P \leq 0.001$.

**Table 1.** Regression parameters of vegetation biomass (g $m^{-2}$) and quality (g N $m^{-2}$) 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 sites. Equations for the linear and quadratic regressions are y = a + bxt and y = a + bxt + cxt$^2$, respectively.

| Biomass (Linear) | $R^2$ | *df* | *F* | *P* | a | b | |
|---|---|---|---|---|---|---|---|
| Wadden Sea staging site | 0.241 | 65 | 20.60 | < 0.001 | –0.2844 | 0.2206 | |
| Baltic stopover site | 0.089 | 129 | 12.62 | 0.001 | 1.7789 | 0.0996 | |
| Russian breeding site | 0.803 | 49 | 199.74 | < 0.001 | –230.45 | 1.4192 | |
| **Quality (Quadratic)** | $R^2$ | *df* | *F* | *P* | a | b | c |
| Wadden Sea staging site | 0.520 | 68 | 36.79 | < 0.001 | 4.7342 | –0.0053 | $-9\ E^{-05}$ |
| Baltic stopover site | 0.224 | 148 | 21.32 | < 0.001 | –0.8556 | 0.0626 | –0.0003 |
| Russian breeding site | 0.513 | 76 | 40.10 | < 0.001 | –29.001 | 0.3763 | –0.0011 |

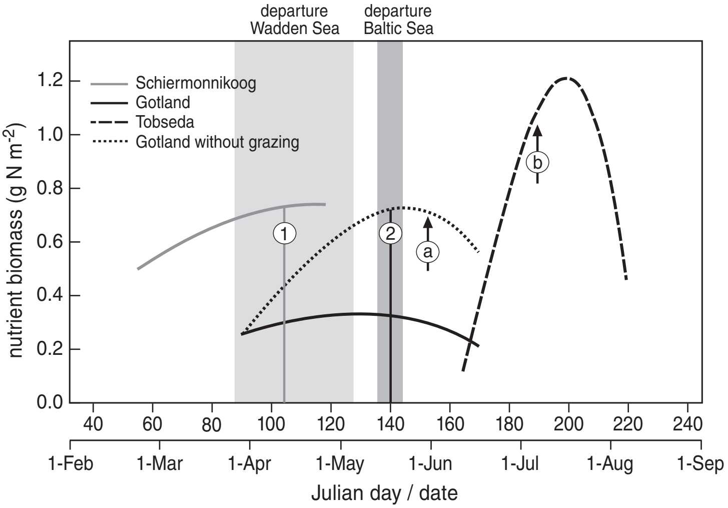

**Figure 4.** Nutrient Biomass (g N $m^{-2}$) as a combined measure of forage biomass (g $m^{-2}$) and N-content (%) at three sites along the flyway of the Barnacle Goose; Schiermonnikoog – a Wadden Sea staging site, Gotland – a Baltic Stopover site and Tobseda – a Russian breeding site. Shaded areas indicate timing of departure from the Wadden Sea (1) and Baltic Sea (2), respectively. Drop lines indicate the average departure date. Arrows indicate peak hatch date at the Baltic Sea (a) and the Russian breeding ground (b), respectively.

**Table 2.** Mean plant biomass (g $m^{-2}$) and quality (g N $m^{-2}$) for three study sites at different times in spring 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).

| Site | Average ± SE | | | Equal variances assumed | *t* | *df* | *P* |
|---|---|---|---|---|---|---|---|
| | Wadden Sea staging | Baltic stopover | Russian breeding | | | | |
| **Biomass** | | | | | | | |
| 1 | 15.68 ± 1.61 | 10.66 ± 1.15 | | Y | 2.43 | 25 | 0.022 |
| 2 | 27.21 ± 1.50 | 15.25 ± 1.22 | | Y | 6.18 | 44 | < 0.001 |
| 3 | | 14.67 ± 1.02 | 12.47 ± 0.89 | N | 1.62 | 34.74 | 0.114 |
| 4 | | 20.25 ± 2.45 | 48.42 ± 3.51 | Y | –6.81 | 25 | < 0.001 |
| **Quality** | | | | | | | |
| 1 | 3.61 ± 0.12 | 2.63 ± 0.10 | | Y | 6.28 | 34 | < 0.001 |
| 2 | 2.86 ± 0.04 | 2.63 ± 0.11 | | N | 1.94 | 54.41 | 0.058 |
| 3 | | 2.43 ± 0.09 | 3.38 ± 0.13 | Y | –6.13 | 68 | < 0.001 |
| 4 | | 2.35 ± 0.12 | 2.59 ± 0.14 | Y | –1.14 | 41 | 0.263 |

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 – 3 June, day 154) and arrive on the breeding grounds (27 May – 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 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 2, comparison 4).

## DISCUSSION

### A green wave?

This study demonstrates that nutrient biomass occurred in successive waves along the spring flyway of herbivorous waterfowl as they progress their migration. This may help to explain 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 increases 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 biomass. Nutritional quality and quantity of the forage are combined based on a calculation of nutrient biomass per unit areas (g N $m^{-2}$). At each site we found a maximum value of nutrient biomass during spring (Fig. 4). We expect the same holds for other stopover sites along the migration route of the geese; additional important stopover sites between the Baltic stopover 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

The geese left their winter and spring staging sites in the Wadden Sea when the nutrient biomass (g N $m^{-2}$) reached a peak (Figs 2 and 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 would remain 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 Fig. 2) prevented biomass accumulation. The dotted line in Fig. 4 represents the nutrient biomass 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 nutrient 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 (Fig. 3). However, the biomass available to goslings and moulting adult birds was much higher at the Russian breeding site compared to that in Gotland. Nutrient biomass, 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 to benefit gosling rearing later in the season.

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## SAMENVATTING

Planten die door herbivoren worden gegeten, zijn zowel in de tijd als in de ruimte heterogeen verdeeld. Deze heterogeniteit is waarschijnlijk de oorzaak van het jaarlijkse trekpatroon van veel herbivoren. Deze volgen de pieken van optimale voedselbeschikbaarheid in de verschillende gebieden. De 'groene-golfhypothese' stelt dat ganzen en andere herbivore watervogels tijdens hun trek naar de noordelijke broedgebieden, een klimatologische gradiënt volgen, waarbij ze in elk gebied waar ze pleisteren, voordeel halen uit de voorjaarsgroei van hun voedselplanten. We testten een van de aannames van de groene-golfhypothese, namelijk dat er van de gematigde wintergebieden tot de arctische broedgebieden opeenvolgende golven van voedselbeschikbaarheid zijn. We gebruikten de trekroute van de Brandgans als model om gegevens van voedselplanten te vergelijken met de timing van de voorjaarstrek. We hebben in drie kweldergebieden langs de traditionele trekroute van de Brandgans gegevens verzameld over de biomassa en kwaliteit van de voedselplanten: in een gematigd overwinteringsgebied in het waddengebied, een pleistergebied in het Baltische gebied en in het Russische, subarctische, broedgebied. In alle gebieden was er een optimumcurve van voedselbiomassa en voedselkwaliteit, met een vroege piek in kwaliteit en een toename van biomassa gedurende de gehele voorjaarsperiode. Overal lijkt de combinatie van biomassa en kwaliteit (stikstofbiomassa) de beste voorspeller van de timing van de trek. In het Baltische gebied was de biomassa van het voedsel heel laag vergeleken met die in de andere gebieden. Een vergelijking van experimenteel onbegraasde proefvlakken met naburige begraasde vlakken liet echter zien dat de hoge begrazingsdruk in het begin van het groeiseizoen de accumulatie van biomassa verhindert. In het Russische broedgebied arriveren de ganzen vóór de voedselpiek. In plaats daarvan profiteren de ganzen van de piek in stikstofbeschikbaarheid als de jongen zijn uitgekomen en de volwassen ganzen in de rui zijn. Onze gegevens laten zien dat de beschikbaarheid van voedsel in het voorjaar een van de belangrijkste bepalende factoren kan zijn voor de timing van de jaarlijkse voorjaarstrek van herbivore watervogels.

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