



Patch choice of avian herbivores along a migration trajectory—From Temperate to Arctic

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Summary

Migratory waterfowl species seem to track temporal and spatial pulses of optimal forage availability on their way from temperate wintering to arctic breeding sites. In order to unravel the relative contribution of forage quality and forage biomass to foraging choices in avian herbivores, we experimentally manipulated biomass and quality of main forage plants through fertilisation and grazing exclusion at three sites along the flyway of barnacle geese, *Branta leucopsis*. Fertilisation increased the nitrogen content of the forage and grazing exclusion increased biomass levels. Manipulated plots were offered to wild geese in a random block experimental design and goose visitation was measured through dropping counts. At all sites there was a trend towards a higher preference of plots with increased quality and average biomass above plots with an average quality and increased biomass. Generally, geese preferred plots with highest standing crop of nitrogen. The numerical response of the geese to forage changes was supported by behavioural observations at the Baltic site. We conclude that for migrating barnacle geese the bottlenecks in the standing crop of nitrogen appear to lie in the limited biomass availability at the Baltic stopover site and the limited nutrient content of food in the Arctic breeding site, restricting the potential nutrient intake on these sites.

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Zusammenfassung

Viele pflanzenfressende Wasservogelarten scheinen entlang ihres Zugweges von gemäßigten Überwinterungs- in arktische Brutgebiete zeitlichen und räumlichen Impulsen optimaler Nahrungsverfügbarkeit zu folgen. Um den relativen Beitrag von

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Nahrungsqualität und -biomasse zur Nahrungswahl der Herbivoren zu bestimmen, haben wir entlang des Zugweges der Nonnengans, *Branta leucopsis*, Biomasse und Qualität der Hauptnahrungspflanzen experimentell manipuliert. Düngung erhöhte den Stickstoffgehalt der Nahrungspflanzen, der Ausschluß von Beweidung erhöhte das Biomasseniveau. Die manipulierten Flächen wurden durchziehenden Wildgänsen in einem random block Experimentaldesign angeboten, Gänsenutzung wurde mit Hilfe von Kotzählungen dokumentiert. In allen Gebieten wurde ein Trend zu erhöhter Präferenz von Nahrungsflächen mit erhöhter Qualität und mittlerer Biomasse im Vergleich zu Flächen mittlerer Qualität und erhöhter Biomasse festgestellt. Die Gänse bevorzugten allgemein Flächen mit höchster Stickstoffverfügbarkeit pro Oberflächeneinheit. Die numerische Reaktion der Gänse auf Nahrungsveränderungen wurde durch Verhaltensbeobachtungen in einem der Untersuchungsgebiete unterstützt. Wir folgern, dass die Limitierung von Stickstoffverfügbarkeit für ziehende Nonnengänse in den Zwischenstoppgebieten im Ostseeraum in der begrenzten Biomasseverfügbarkeit begründet liegt, während in den subarktischen Brutgebieten der Nährstoffgehalt der Pflanzen beschränkend wirkt. Beide Parameter begrenzen die Nährstoffaufnahme in den jeweiligen Gebieten

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Introduction

Avian herbivores of the Northern hemisphere breed in the Arctic and winter in more southern, temperate areas. During spring migration the birds have to balance their energy expenditure and food intake in order to build up sufficient energy reserves to be able to migrate to their breeding areas and breed successfully (Bety, Gauthier, & Giroux, 2003; Drent, Both, Green, Madsen, & Piersma, 2003; Ward et al., 2005). The birds usually migrate in several distinct steps, and refuel and rest at each stopover site (Eichhorn, Afanasyev, Drent, & Van der Jeugd, 2006; Green, Alerstam, Clausen, Drent, & Ebbinge, 2002; Nolet, Andreev, Clausen, Poot, & Wessel, 2001). Plant forage availability and quality on these sites play a crucial role for these small herbivores, as the amount of body reserves accumulated prior to migration directly influences breeding success (Ankney & MacInnes, 1978; Ebbinge & Spaans, 1995; Madsen, 2001; Prop & Black, 1998). At the breeding sites, food availability and quality influence final adult body size because of the impact on gosling growth rates (Cooch, Lank, Rockwell, & Cooke, 1991; Larsson, Van der Jeugd, Van der Veen, & Forslund, 1998; Loonen, Oosterbeek, & Drent, 1997; Sedinger, Flint, & Lindberg, 1995). Fledgling weight also influences post-fledgling survival (Loonen et al., 1997; Van der Jeugd & Larsson, 1998) and the probability of breeding for individuals that survive (Sedinger, Herzog, & Ward, 2004). It is evident that food availability and quality shape fitness and life history parameters of these avian herbivores. However, the birds are facing a dilemma on their migration, because an increase in plant biomass

frequently corresponds with a decline in food quality (Lepage, Gauthier, & Reed, 1998; Van der Graaf, Stahl, Bakker, & Drent, 2006). Several studies suggest that avian herbivores may not maximise intake as such, but instead maximise nutrient or nitrogen intake (Durant, Fritz, & Duncan, 2004; Hassall, Riddington, & Helden, 2001; Kristiansen, Fox, & Nachman, 2000; Lepage et al., 1998; Prop & Black, 1998). Assuming that protein intake is a function of food intake and that food quality declines with age of the flush of growth of spring forage, birds have two alternatives in order to obtain maximum protein intake: either forage on patches with high biomass and low quality and maximise total intake or forage on patches of vegetation with a lower biomass but higher quality. Given the digestive constraints on intake rate (Prop & Vulink, 1992; Sedinger & Raveling, 1988) and time constraints of birds during migration, we hypothesise that the latter strategy will be followed.

In this study this hypothesis was tested using the barnacle goose, *Branta leucopsis*. During their spring migration from staging sites in the European Wadden Sea to Arctic breeding sites, barnacle geese follow consecutive waves of fresh spring growth of their forage plants as they migrate northwards (Van der Graaf et al., 2006). At each stopover site, arrival is timed to maximise the profit from increased spring production of the vegetation and high initial nutritional quality of forage grasses. At the Arctic breeding sites, the peak in spring growth and quality appears to coincide with gosling hatch and it is assumed to facilitate good growth conditions for goslings. We tested forage patch choice of migrating barnacle geese at three points along the

East-Atlantic flyway of this species. Tissue quality and biomass of the main forage species were experimentally manipulated and choice of foraging patches of migrating geese was measured through dropping counts and supplementary behavioural observations at one site.

Methods

Study sites

The study was conducted at three sites representing staging, stopover and breeding areas along the East-Atlantic flyway of the barnacle goose during spring 2003 and 2004.

The western-most study site is 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). The salt marsh of the island consists of an ungrazed area and an area that is grazed by livestock from early May until late November. Both areas are intensively used by wild geese prior to migration. We chose to conduct the experiment on the livestock-grazed salt marsh, because vegetation structure here is more similar to that of the other sites. On the ungrazed marsh accumulation of litter complicates the foraging choices of the geese (Riddington, Hassall, & Lane, 1997; Summers & Critchley, 1990; Van der Wal, Van de Koppel, & Sagel, 1998). The geese leave this site towards the end of April.

The second study site is situated on the Swedish island of Gotland in the Baltic Sea. Here, thousands of geese use the narrow bands of coastal salt marshes and adjacent agricultural pastures as a stopover site during a period of about 4 weeks in April and May (Van der Graaf, Stahl, Veeneklaas, & Bakker, 2006). These marshes are grazed by livestock from early June until late October. Our study site is a salt marsh on the peninsula Grötlingbo-udd, in the south-east of Gotland (57°07'N, 18°27'E).

The third study site represents a breeding site in Northern Russia, at the Kolokolkova Bay near the abandoned village of Tobseda (68°35'N, 52°20'E). Geese arrive here by the end of May and start breeding upon arrival. Large moulting flocks gather in this area from mid-July onwards, together with family birds. All geese leave the area at the end of September. This colony holds around 1500 breeding pairs with peak hatch in early July (Van der Jeugd et al., 2003; Van der Graaf, Lavrinenko, Elsakov, Van Eerden, & Stahl, 2004). No livestock grazing is currently taking place at this site, but the area has been grazed by horses until around 1995.

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

Experimental set-up and measurements (Experiment 1)

Plant biomass was manipulated by placing temporary grazing exclosures on salt-marsh swards, thereby creating a difference in plant biomass with continuously grazed, non-fenced control plots. At the same time, forage quality was manipulated by fertilising plots with commercial granular fertiliser (NPK, 12–10–18) resulting in an experimental addition of 10 g of nitrogen per m². We used the same experimental design at the three sites. At all sites the vegetation was in an early (spring) growth stage. Additionally we calculated the standing crop of nitrogen, a combination of nitrogen content (per unit biomass) multiplied by the amount of biomass (standing crop) and expressed in gN m⁻².

Within the experimental area at each site, we created six replicate, randomly located blocks, spaced about 50 m apart from each other. Each block contained four plots (4 m × 4 m) representing the four treatments: naturally grazed, ungrazed, fertilised and ungrazed and fertilised. A treatment was randomly assigned to each plot within a block. Exclosures at the Wadden Sea staging site, the Baltic Sea stopover site and the Russian breeding site, respectively, were set-up on 20 March 2004, 4 April 2003 and 1 July 2003. After 3–4 weeks exclosures were removed, forage biomass and quality were assessed on all plots and all droppings were removed from previously grazed plots (13 April 2004, 5 May 2003 and 22 July 2003, respectively). Plots were now accessible for wild barnacle geese. This point in time is called start of the experiment throughout this paper and coincided for all areas with peak utilisation by the geese. Goose dropping accumulation was measured by dropping counts on all plots, which allowed an assessment of foraging choices of the geese. Droppings were counted as soon as all replicate blocks were visited by geese, in order to prevent differences being obscured by geese foraging on less favourite plots after the favourite plots had been depleted. For the Wadden Sea staging site this was 7 days, for the Baltic stopover site 5 days and for the Russian breeding site 4 days. Dropping counts are a much-used tool for determining grazing pressure of

geese, differences in digestibility of grasses might influence the retention time in the gut and thus the amount of droppings deposited per time unit (Hassall & Lane, 2005). Since our plots are very small we expect that retention time is the same in all plots, reflecting the average digestibility of the grasses in the entire study site. Differences between sites, however, can be caused by differences in average digestibility; hence, we only make comparisons within sites.

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

Specific tests including behavioural observations (Experiment 2)

In May 2004 the experiment was repeated with five replicates at the Baltic stopover site only, with the objective of assessing forage patch choice by the geese based on direct behavioural observations, in addition to dropping counts. Experiment 2 was conducted close to the area used for Experiment 1 in 2003. Measurements on biomass were conducted by cutting a small turf (10 cm × 10 cm), removing all above-ground biomass and sorting it into grasses and other species. The material was then dried at 60 °C for 48 h and weighed. Biomass data, therefore, comprise the weight of all grasses present. This destructive method, as opposed to the detailed non-destructive method in Experiment 1, was used because a mixed sward of several species occurred in the area of Experiment 2. Forage quality was measured following procedures used in 2003. Dropping counts were performed in the same way as in 2003. The choice experiment

was conducted in early May 2004. Corners of all experimental plots were marked by inconspicuous plastic tubes in order to be able to distinguish plots from a distance. Observations were made from a hide at a distance of about 250 m, placed on a slightly elevated position. During the first 5 days after the start of the experiment, the number of geese present on each plot of the different treatments was noted every five minutes. In addition, the number of aggressive encounters between geese on the plot and other flock members was recorded. For each plot, goose presence was calculated as the total time geese were present on a plot multiplied by the number of geese on the plot during the entire observation period. Goose presence is expressed as goose minutes. Interactions are given as the number of interactions per goose observed for each minute that geese were present on the plot. As a measure of forage intake, peck rates were collected for individual geese on all treatments. Peck rates were measured as the time needed for 50 pecks; these data were later converted to pecks per minute.

Statistical analyses

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

Results

Experimental manipulations and numerical response (Experiment 1)

On all sites exclusion of grazing increased above-ground biomass of forage plants and fertilisation

increased nitrogen content of the leaf tissue (Fig. 1, Table 1). At the Russian breeding site there was a significant interaction between grazing exclusion and fertilisation with respect to forage biomass, with the ungrazed and fertilised combination plot showing a high biomass response as

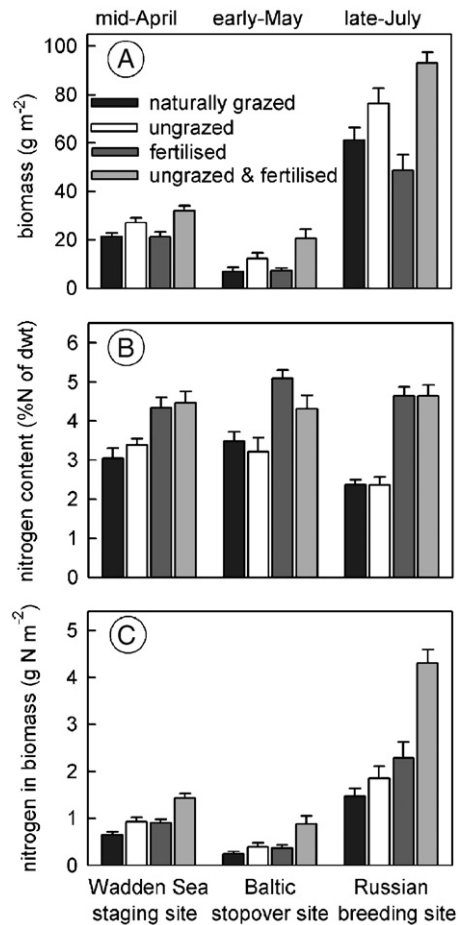


Figure 1. The effects of exclusion and fertilisation treatments at each study site on (A) leaf tissue biomass (in g m⁻²), (B) quality of forage species (%N) and (C) standing crop of nitrogen (in g N m⁻²), Experiment 1. Shown are means+SE ($n = 6$). Test results are shown in Table 1.

compared to solely ungrazed or fertilised plots. This interaction is most likely caused by a strong nutrient limitation of plant growth in this area (Van der Graaf et al., 2004), inducing not only a response of fertiliser treatment on plant quality but also on plant biomass. Because the treatments had the required effect on the vegetation from here on they will be referred to as increased quality (fertilised), increased biomass (excluded) and increased quality and biomass (fertilised and excluded).

When effects of grazing exclusion and fertilisation on subsequent dropping accumulation were tested for all sites in comparison, a strong three-way interaction was found between the two treatments and site. This interaction demonstrates that the treatments had a different effect on dropping accumulation at each site. Further analyses were therefore performed for each site separately (Table 2). At all sites along the flyway, the geese showed a strong and significant response to the experimental treatments. The significant interaction between increased biomass and increased quality for all sites combined, and for the Baltic and Russian sites separately, shows that this treatment is visited more than expected based solely on the sum of effects of the two separate treatments, which is made visible in Fig. 2. It shows the response of the geese to the experimental treatments. Values are expressed as the percentage of the total cumulative dropping accumulation per unit area in order to compare sites. All statistical tests, however, were performed based on the original data. Highest dropping accumulation occurred on plots that had been excluded and fertilised (Fig. 2). At the Wadden Sea staging site preference for plots with either increased quality only or increased biomass only was similar to the selection by the geese of naturally grazed plots. On the Baltic site both increased biomass only and increased quality are preferentially selected, while on the Russian site increased biomass only is not selected above the naturally grazed situation, in

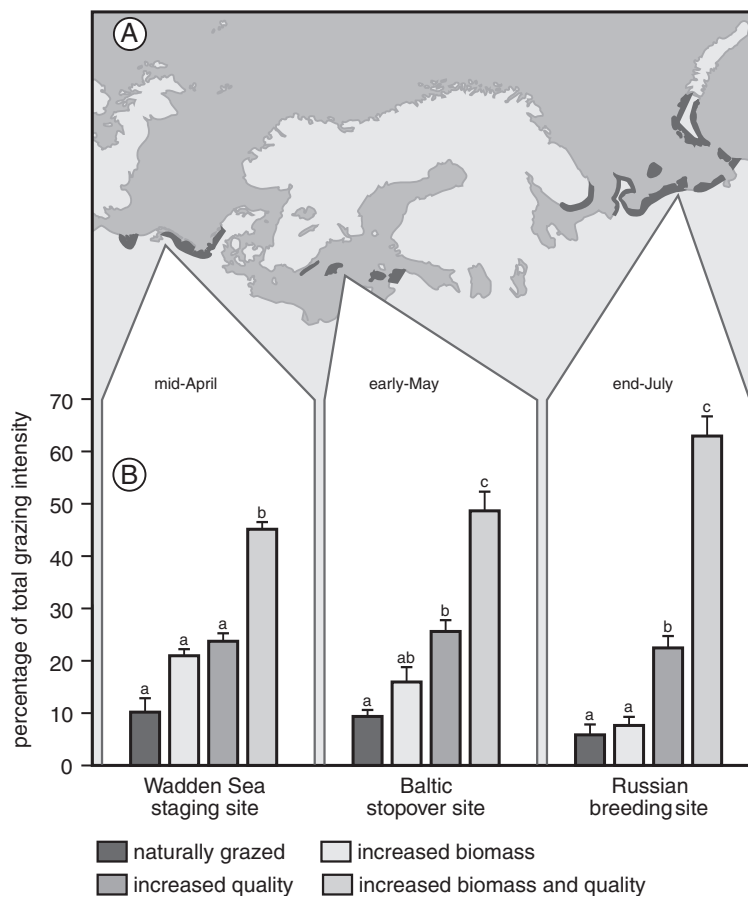
Table 1. Test results for the effects of grazing exclusion and fertilisation on tissue biomass and quality of forage species at the three study sites in Experiment 1

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

*With significant interaction of exclusion \times fertilisation on biomass: $F_{1,20} = 6.83$, $P = 0.017$. All other interactions were not significant.

Table 2. Test results for the response of goose dropping accumulation to experimentally increased biomass and quality in Experiment 1

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

**Figure 2.** (A) The flyway of the barnacle goose projected from left to right, with the three study sites. (B) The effects of increased biomass and quality on the relative dropping accumulation for each study site, Experiment 1. Shown are mean percentages+SE ($n = 6$). Different letters denote significantly different values, $P < 0.05$ Tukey LSD test.

contrast to plots of increased quality which are strongly preferred.

Combining data of all sites, there were strong correlations between forage plant biomass, forage quality and dropping accumulation. For the Wadden Sea staging site only a correlation of dropping accumulation with forage quality was observed,

while for the Baltic stopover site there was only a correlation of dropping accumulation with biomass (Table 3). Finally, at the Russian breeding site, dropping accumulation was correlated with both biomass and quality. In addition, at all three sites, there was a very strong correlation between dropping accumulation and the combined measure

Table 3. Pearson correlation between dropping accumulation and forage plant characteristics such as nitrogen content, biomass and standing crop of nitrogen in Experiment 1 ($n = 24$ for each site, $n = 72$ for all sites combined)

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

* $P \leq 0.05$.** $P \leq 0.01$.*** $P \leq 0.001$.**Table 4.** Test results for the effects of grazing enclosure and fertilisation on vegetation data and behavioural observations at the Baltic stopover site in 2004, Experiment 2

Effects of:	Biomass	Quality	Dropping accumulation	Goose presence	Aggressive interactions	Peck rate
	$F_{1,16}$	$F_{1,16}$	$F_{1,16}$	$F_{1,16}$	$U^{\#}$	$F_{1,205}$
Enclosure	51.00***	15.96***	10.13**	61.89***	100.0***	90.54***
Fertilisation	4.69*	35.70***	12.88**	33.90***	39.0	2.56
E \times F	4.85*	0.36	7.10*	13.67**	—	0.14

#Data are not normally distributed; a non-parametric Mann–Whitney U -test was used.* $P \leq 0.05$.** $P \leq 0.01$.*** $P \leq 0.001$.

of standing crop of nitrogen, which explains 35–65% of the observed variation in dropping accumulation (Table 3).

Behavioural response (Experiment 2)

In 2004 at Gotland, grazing exclusion significantly increased grass biomass (Naturally grazed, ungrazed, fertilised, ungrazed and fertilised, respectively: 28.1 ± 4.5^A , 75.1 ± 6.9^B , 27.8 ± 6.5^A and 116.6 ± 15.9^C g dwt m^{-2} ; different letters denote significant differences, post-hoc Tukey test) and experimental fertilisation increased grass quality (naturally grazed, ungrazed, fertilised, ungrazed and fertilised, respectively: 2.8 ± 0.1^{AB} , 2.1 ± 0.1^A , 4.0 ± 0.3^C and 3.2 ± 0.2^B cm) (Table 4). Dropping counts 1 week after start of the choice experiment gave similar results in 2003 and 2004 at this site (Figs. 2 and 3); plots with a combined increase of biomass and quality were preferred above all other treatments. The data from 2004 reveal a non-significant trend of greater dropping accumulation on plots with either increased quality or biomass, as compared to the naturally grazed plots. The behavioural observations indicate that geese preferred the treatment with combined high quality and high biomass (Fig. 3). Here, goose presence was higher than on all other treatments and more

aggressive interactions were observed (Table 4). Both goose presence and the number of aggressive interactions also was higher on the plots with high biomass compared to naturally grazed plots. There were no differences detected in these two parameters for plots with increased quality. Peck rate was lower on plots with increased biomass.

Discussion

Forage quality or biomass?

The great preference of geese for a combination of plant quality and biomass as seen in Figs. 2 and 3, is no surprise as these plots naturally provide forage with the highest standing crop of nitrogen. In a natural, non-experimental situation, however, there is always a trade-off between forage quality and quantity: with increasing biomass, plant quality decreases (Lepage et al., 1998; Van der Graaf et al., 2006) and digestive constraints limit an increased intake of plant material to compensate for low forage quality (Prop & Vulink et al., 1992). In this paper we, therefore, aimed to investigate the patch choice of wild geese, uncoupling biomass and quality by fertilisation and enclosure treatments. Ideally, a measure of actual intake rate would be needed to unravel whether

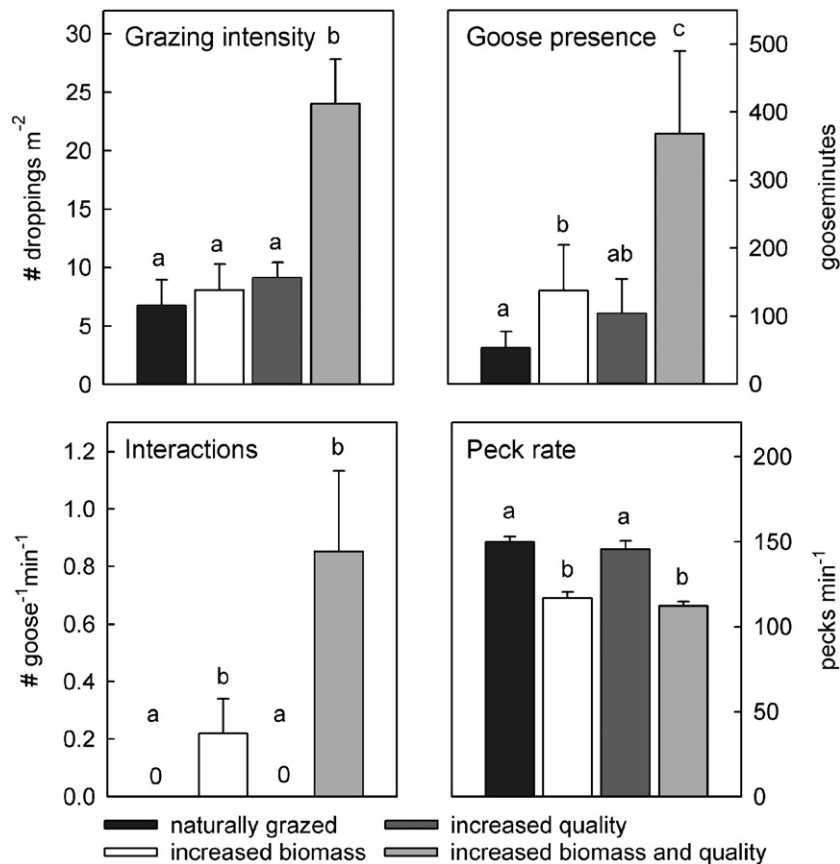


Figure 3. Behavioural observations on the use of experimental plots on the Baltic stopover site in 2004, Experiment 2. Shown are mean percentages+SE ($n = 5$). Different letters denote significant different values, $P < 0.05$ Tukey LSD test. For statistics see Table 4.

nutrient or dry matter intake is maximised. Because intake rate is a difficult measure to obtain, we circumvent this problem using treatments that either increase nutrient content (gN/g biomass) and keep biomass constant or increase biomass and keep nutrient content constant. At all sites along the goose flyway we witness a similar trend (though only significant at the Russian site); plots with increased quality and average biomass are preferred by the geese above average quality and high biomass (Fig. 2, Table 2).

It is striking that on each site the order of preference for the treatments is consistent (Fig. 2). Moreover, at each site patch choice of the geese mirrors more closely the order of standing crop of nitrogen than that of biomass (Fig. 1), which is also shown in our correlation analyses where standing crop of nitrogen consistently absorbs a higher proportion of the variance in dropping accumulation rates than biomass.

These findings are consistent with our hypothesis that selecting high-quality plants reduces the time necessary to collect sufficient body reserves and

thus potentially gives the birds the advantage of arriving earlier on the breeding sites. For the same flyway, we have shown that barnacle geese appear to follow peaks of standing crop of nitrogen along their spring migration route, the so-called “Green wave” (Van der Graaf et al., 2006). In this way the geese maximise the accumulation of body reserves during migration, while on the breeding sites the chicks can profit from the peak in standing crop of nitrogen.

Differences in site choice along the flyway

Additionally, the interactions between staging site and plant nitrogen content and forage biomass and the interaction between these measures (Table 2) indicates that patch choice differs between staging sites. We suggest that this is caused by differing limiting resources along the migration route. At the Russian breeding site overall levels of biomass are high due to low levels of goose grazing, but forage quality is low (this

study, Van der Graaf et al., 2004). Here, forage quality is the choice criterion and contributes most to the patch choice of the geese (Table 3, Fig. 2). At the Baltic stopover sites where high grazing intensities during spring migration result in comparatively low levels of biomass (Van der Graaf et al., 2006) and where overall tissue quality is high (this study), standing crop of nitrogen is highest on previously ungrazed plots with a high standing biomass. Here, barnacle geese aggressively monopolise food patches with increased biomass as our behavioural data showed (Fig. 3, Table 4). Therefore, also plots with increased biomass only are slightly preferred about control plots in this area (Fig. 2). In both these areas, the interaction between increased biomass and increased quality (Table 2) shows that the reaction of the geese towards a combination of these two parameters is significantly stronger than can be expected from a simple addition of the two single effects. At the spring staging grounds in the Wadden Sea neither biomass nor quality per se are limiting on the livestock-grazed salt marsh and probably a raised nutrient intake can be achieved by selecting plots with increased levels of either of these two parameters. In this area the preference for the combination of the two effects is not more than would be expected from an addition of the two single effects (Table 2, Fig. 2).

The bottlenecks in standing crop of nitrogen for these herbivores thus appear to lie in the limited biomass availability at the Baltic stopover site and the limited nutrient content of food in the Arctic breeding site.

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