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

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## Summary

1. Overlap in habitat use between herbivores can result in facilitative interactions, through enhancement of forage quality, as well as competitive interactions. The latter result from either interference or indirectly from resource depletion.

2. We investigated competitive and facilitative interactions between wild Barnacle and Brent Geese and European Brown Hares on a salt marsh in the Dutch Wadden Sea. In a multifactorial experimental design, we manipulated biomass and quality of grass swards and determined foraging preferences of the wild herbivores.

3. We found that both Barnacle and Brent Geese select plots with plants that have a higher nitrogen content. Barnacle Geese avoid plots with high plant biomass.

4. Hares prefer the combination of high biomass with high plant quality, when geese are absent. However, in the natural situation with geese present, hares select high biomass swards.

5. Grazing increases the quality of the vegetation within one season. Geese mainly select plots that have been previously grazed by either geese or hares within the same season.

6. We conclude that indirect competition through forage depletion by large numbers of geese in spring plays a significant role determining the foraging choices of hares, while Barnacle Geese profit from grazing facilitation by other small herbivores which prevents the maturation of forage tissues.

*Key-words:* barnacle goose, brent goose, European brown hare, grazing, salt marsh

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## Introduction

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

Two constraints on rates of nutrient uptake in herbivores are the short-term rate of food intake, mainly influenced by forage availability, and the long-term rate of energy assimilation, mainly characterized by processing constraints that reflect forage quality (Wilmschurst, Fryxell & Hudson 1995). Besides plant phenological changes, food plant availability and nutritional quality also depend on the manipulation of the foraging environment by the herbivores themselves (Drent & Van der Wal 1999). The maintenance of grazing lawns brought about by events of cyclic grazing (McNaughton 1984) is one example of maximizing intake per unit time (reviewed in Drent & Van der Wal 1999). Foraging herbivores can either physically change the structure of a plant community (trampling or selective grazing) or can modify plant phenology as a consequence of consumption, which often indirectly changes the chemical composition of tissues (Arsenault & Owen-Smith 2002). We use the term herbivore

facilitation when the foraging opportunities of one species are enhanced indirectly by the feeding activities of another. In contrast, depletion of resources, interference and resource competition between consumer species negatively affect resource acquisition by a particular herbivore species, potentially influencing foraging choices, and inducing resource partitioning by different herbivores (Belovsky 1984; Gordon & Illius 1989; Edwards, Croft & Dawson 1996; Murray & Illius 2000).

The close interplay of facilitative and competitive interactions between herbivores has long been neglected and experimental field studies remain scarce (Van der Wal, Kunst & Drent 1998a; Van der Wal *et al.* 2000b). Overlap in habitat use, sharing of food plants and limited food supply, which are generally described as necessary prerequisites for resource competition (De Boer & Prins 1990), are also prerequisites for facilitation in a system where one herbivore species has a beneficial effect upon another. We suggest that the timing of overlap in plant use by different herbivores in connection with seasonal patterns of plant phenology can lead to either competition or facilitation. The African savannahs with their collection of large, mainly migratory, ungulate grazers are an example of a system where both competitive and facilitative interactions between herbivores occur (De Boer & Prins 1990; Sinclair 1995; Van de Koppel & Prins 1998; Prins & Olf 1999).

In the present study we report on temperate salt marshes, where there is the potential for interactions between three herbivore species with strong temporal and spatial overlap. Barnacle Geese, *Branta leucopsis*, and Dark-Bellied Brent Geese, *Branta bernicla bernicla*, use coastal salt marshes in the Dutch, German and Danish Wadden Sea during spring fattening, accumulating energy reserves essential for successful migration and subsequent reproduction at Arctic breeding sites (Ebbinge & Spaans 1995). On natural salt marshes European Brown Hares, *Lepus europaeus*, are the only other important vertebrate herbivore, which, in contrast to staging geese, use the salt marsh year round. Migratory geese are among those herbivores, for which the terrestrial green world is far from being universally edible or universally nutritious, and the birds show a high degree of dependency on forage of superior quality (e.g. Prop & Deerenberg 1991). For this reason, geese are particularly selective in their habitat choices (Van der Graaf *et al.* 2006b), and we predict that they are sensitive to alterations in food availability and quality imposed by interactions with other herbivores using the same forage. Recent studies provide evidence for direct interference and food competition between Brown Hares and Brent Geese during spring (Van der Wal *et al.* 1998a), as well as for indirect, long-term facilitation by hares for Brent Geese through selective removal of woody plant material in winter (Van der Wal *et al.* 2000b). In this study we focus both on competitive (i.e. removal of potential forage by preceding grazers) and facilitative

(i.e. grazing lawns maintained by predecessors) interactions. For our study site we find that the vegetation is not affected by nitrogen addition through dropping deposition (A. J. Van der Graaf, unpublished data).

With a multifactorial experimental approach, we manipulated biomass and quality of forage grass swards in the field. Subsequently we monitored the use of these plots by wild geese and hares. The experiments allowed us to investigate the reaction of small herbivores to the main forage parameters which are biomass availability and forage quality. Based on their dependence on high-quality forage (Prop & Vulink 1992), we expect that geese prefer plots with increased quality. Hares can cope with less nutritious food (Kuijper, Van Wieren & Bakker 2004). For hares, we therefore hypothesize that they select plots with high biomass even with a lower nutritional value. In particular, we aimed to gain insights into the interactions of geese and hares on a common food source in the spring period. We expect the relationship between these vertebrate herbivores to be competitive when resident hares and staging geese jointly use *Festuca rubra* as forage, especially during March, April and May, the spring staging period of the migratory geese. These competitive interactions may result in one of the herbivores accepting suboptimal foraging conditions.

## Methods

### STUDY AREA

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

Three experimental studies were conducted during the spring of 1997, 2002 and 2003. The study area on the higher marsh was approximately 30 years of age (as described by Van der Wal *et al.* 1998a) and is one of the salt-marsh areas most intensively grazed by small herbivores in spring (Van de Koppel *et al.* 1996). The vegetation was dominated by dense swards of *Festuca*

*rubra* (average cover value 72%); *Juncus gerardi* was present in shallow depressions (average cover value 18%). Emerging stems of the shrub *Artemisia maritima*, can locally dominate the plant community during summer, but average cover was only 2% during spring. *Festuca rubra* accounts for 90% of the diet in staging Barnacle Geese (Van der Wal, Van de Koppel & Sagel 1998b), 53% of the diet in staging Brent Geese (Van der Wal *et al.* 2000a) and 51% of the estimated spring diet of hares in the study area (Van der Wal *et al.* 1998a).

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

#### TESTING FORAGE CHOICES IN RELATION TO DIFFERENT COMPETITIVE SCENARIOS (MAIN EXPERIMENT)

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

The enclosures were established for 2 weeks and then removed. This event is called *start of the experiment*. Upon removal, we imposed two different competitive scenarios: five replicates (each containing four plots representing the four treatments) were completely opened for herbivore access, so both geese and hares could graze in these plots. On the other five replicates selective goose enclosures were erected. The goose enclosures allowed hares to graze the plot but effectively excluded geese. The enclosures were constructed from bamboo sticks connected by horizontal ropes at different heights (10 cm and 50 cm). The four treat-

ments within one replicate were separated by approximately 3 m and replicates were spaced approximately 150 m apart. In order to quantify foraging choices of both herbivore species we counted the number of droppings of both hares and geese on the plots. Sward heights are generally lower than 7.5 cm in our study area (Van der Graaf *et al.* 2002) and provide no shelter from predators. In the following we therefore use dropping numbers as an indicator of grazing pressure. Droppings were counted before opening the treatments to grazing, as a measure of grazing pressure before the start of the experiment, and again 3 weeks after the start of the experiment. At the start of the experiments, no droppings were recorded in the enclosures.

At the start of the experiment biomass and forage quality were measured. In order to leave the sward undisturbed we applied a non-destructive technique to measure biomass by multiplying average tiller weight with average tiller density. Tiller density was measured on 20 randomly placed quadrats of 5 cm × 5 cm on each individual plot. In these quadrats we counted all tillers of *Festuca rubra*. Tiller weight was determined by clipping 50 tillers of *Festuca rubra* at ground level from each plot. In order to obtain a representative sample of tillers, a point was randomly selected within each plot and all tillers around this point were collected until a sample of 50 tillers was achieved. These tillers were dried at 60 °C for 48 h and weighed. In addition, samples of approximately 4 g of fresh *Festuca* tips (2 cm) were collected on each plot. Plant material was washed, dried at 60 °C for 48 h and ground to a fine powder. As a measure of forage quality, total nitrogen content of the plant tissue was determined using an automated CHNS analyser (automated element analysis, Interscience EA 1110, New York).

#### ADDITIONAL EXPERIMENTS

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

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

In 2002 we created 10 replicates, each consisting of four experimental plots. Each replicate consisted of a natural grazed plot (grazed by wild geese and hares), a plot on which grazing by geese was excluded (goose

closure), a plot on which grazing by both geese and hares was excluded (full enclosure) and a plot on which grazing by captive geese was applied (two geese in a holding pen for 24 h). Grazing pressure applied by the captive geese closely mimicked the natural cumulative grazing pressure of the site during that period in spring (natural vs experimental grazing pressure, mean  $\pm$  SE:  $2.85 \pm 0.54$  vs  $3.06 \pm 0.29$ ). These treatments created a range of amounts of plant biomass and of tissues with different nitrogen contents on *Festuca* swards (in total 40 plots of 4 m  $\times$  4 m). The plots were opened to wild Barnacle Geese and hares at the start of the experiment in the first week of April 2002. At that time in spring, Brent Geese rarely forage on *Festuca* swards and the measured response of goose grazing pressure therefore represents the grazing pressure of Barnacle Goose only. Plot selection, enclosure design and fertilizer application followed the same protocol as described in the previous paragraph for the main experiment. Grazing with captive geese was conducted under licence of the ethical committee for use of experimental animals of the University of Groningen (DEC RuG, licence number 2734).

In the additional experiments, forage biomass and quality were measured at the start of the experiment following the protocol described for the main experiment. At the start of both additional experiments, goose and hare droppings were counted on all plots and removed. The foraging choice of wild geese and hares was monitored, based on weekly dropping counts for a period of 3 weeks after the start of the experiment. For the analyses, cumulative dropping numbers for 3 weeks were linked to values of biomass and forage quality of each individual plot. In our analyses, we do not examine the experimental history of the plots, since this was merely the means of creating a range of values of biomass and forage quality. We will relate directly grazing pressure to differences in biomass and forage quality that were created from the different treatments. Replicates ( $N = 48$  for 1997 and  $N = 40$  for 2002) and date (first week of May and first week of April for 1997 and 2002, respectively) were included as factors in the statistical model, given below.

In order to measure herbivore responses in the main as well as the additional experiments, we deliberately used cumulative dropping numbers for 3-week periods instead of weekly counts. We chose to use a 3-week period to ensure that all experimental blocks (each containing the four treatments) were actually detected by the herbivores, as zero values contain no information whether a treatment was not preferred, or simply not found and therefore not used in a particular week.

#### STATISTICS

For all analyses, we log-transformed ( $\log(x + 1)$ ) data of the dropping count to meet normality.

In the analysis of herbivore responses in the main experiment in 2003, we used a univariate ANOVA with

fertilization and enclosure as fixed factors, and replicate nested within the starting date of the experiment as random factor. From now on, we will refer to the set of replicates started on the same date as set. To test the effects of the treatments on *Festuca* biomass and nitrogen content we used a multivariate ANOVA with the same factors as mentioned above.

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

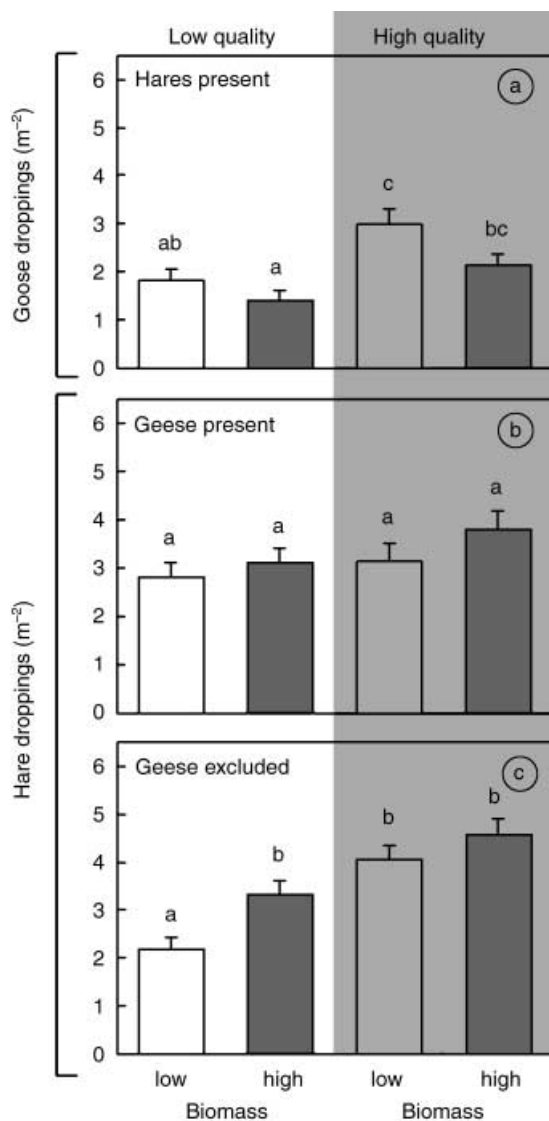
For the comparison of goose and hare droppings before (preceding grazing pressure) and after (foraging choice) the start of the experiments we used a Pearson correlation coefficient.

#### Results

Our results of the vegetation measurements clearly indicate that the enclosure treatment created a sward with increased biomass and that the fertilization treatment increased the nutritional quality of the forage plants (Table 1). Fertilization did not increase biomass, nor did enclosures affect forage quality (Table 1). These data from our main experiment in 2003 demonstrated clear foraging choices by the Barnacle

**Table 1.** Quantity and nitrogen content of biomass of *Festuca rubra* as created by the different treatments (fertilizer application and enclosed from grazing by geese and hares), at the start of the main experiment, given as mean  $\pm$  SE for each treatment and summarized for three sets in mid-February, early March and early April 2003 on the salt marsh of Schiermonnikoog. A results of a multivariate ANOVA in B. Treatments: bq – low biomass, low quality, Bq – high biomass, low quality, bQ – low biomass, high quality, BQ – high biomass, high quality

A		Biomass		Quality (% N)	
Treatment	N	(g dry weight m <sup>-2</sup> )			
bq	30	24.2 $\pm$ 1.3		3.38 $\pm$ 0.68	
Bq	30	26.7 $\pm$ 1.3		3.35 $\pm$ 0.69	
bQ	30	24.3 $\pm$ 0.9		4.66 $\pm$ 1.09	
BQ	30	27.2 $\pm$ 1.4		4.66 $\pm$ 1.08	
B		Biomass		Quality	
	df	F	P	F	P
Fertilization	1	0.011	0.917	187.633	<0.001
Enclosure	1	6.520	0.012	0.074	0.786
Fert. * Excl.	1	0.000	0.997	0.080	0.778
Replica (Set)	29	1.939	0.010	6.197	<0.001
Error	86				



**Fig. 1.** Use of the different treatments, created in the main experiment, by either geese (a), hares in a natural situation where geese are present (b) and in a situation where geese are excluded (c) on the salt marsh of Schiermonnikoog. Shown is the mean  $\pm$  SE, summarized for three sets in mid-February, early March and early April 2003. Different letters denote significantly different values (Tukey LSD test).

Geese: they preferred fertilized plots above non-fertilized plots and they avoided previously ungrazed (excluded) plots (Fig. 1a, Table 2). We conclude that the geese prefer forage of high nutritional quality in combination with low or moderate above-ground biomass levels.

Hares showed no preference for any treatment when plots were simultaneously used by geese (Fig. 1b, Table 2), which simulates the natural spring grazing situation. However, we detect a non-significant trend towards a preference of previously excluded plots with higher levels of biomass ( $P = 0.069$ , Table 2). When geese were excluded and hares were the only grazers on the plots, hares preferentially foraged on plots with high biomass and with shoots of high nutritional quality (Fig. 1c,

**Table 2.** Results of a univariate ANOVA testing the response of (A) Barnacle Geese (with hares present), (B) Brown Hares (with geese present) and (C) Brown Hares (with geese absent) to the treatments applied to swards of *Festuca rubra* in the main experiment in 2003 (fertilizer application and excluded from grazing by geese and hares) on the salt marsh of Schiermonnikoog,  $N = 60$ . Sets 1–3 were opened, respectively, in mid-February, early March and early April 2003

	Parameter estimate	df	F	P
<b>A. Goose droppings – with hares present</b>				
Fertilization	+0.123	1	20.424	<0.001
Exclosure	-0.076	1	7.859	0.008
Replica (Set)		14	19.949	<0.001
Error		43		
<b>B. Hare droppings – with geese present</b>				
Fertilization	NS	1	0.376	0.543
Exclosure	NS	1	3.482	0.069
Replica (Set)		14	20.338	<0.001
Error		43		
<b>C. Hare droppings – without geese</b>				
Fertilization	+0.171	1	21.980	<0.001
Exclosure	+0.091	1	6.200	0.017
Replica (Set)		14	7.102	<0.001
Error		43		

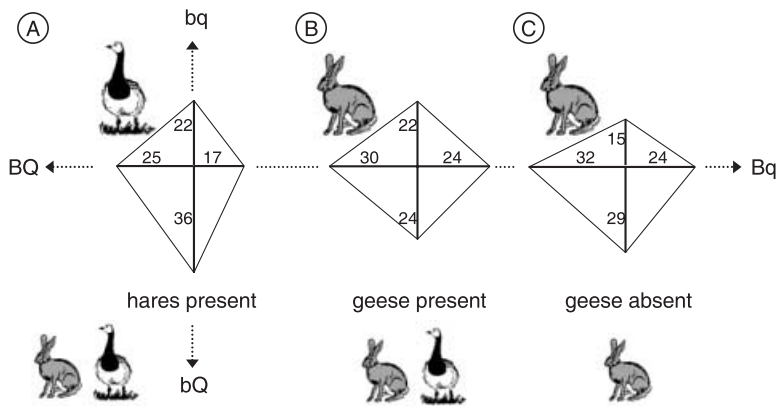
Table 2). Forage choices of the hares thus shifted in the absence of direct competition with geese as shown in Fig. 2, which depicts the relative preference of the herbivores for plants subject to the different treatments. In contrast to Fig. 1, this figure allows a direct comparison of the two herbivore species as it presents relative values of forage choices and demonstrates the differences in preference for quality and biomass parameters between geese and hares.

#### REACTION OF OTHER HERBIVORES AS MEASURED BY THEIR PREFERENCE FOR THE QUALITY AND QUANTITY OF BIOMASS

We amalgamated data from all experiments to relate the quantity and quality of biomass to food choice by geese and hares. We tested the foraging responses of the herbivores over a wider range of biomass amounts, which also differed in nutritional quality. Both Barnacle (data from 2002 and 2003,  $N = 80$ ) and Brent Geese (data from 1997 only,  $N = 48$ ) preferred plots with highly nutritious plants (Table 3). Hares preferred plots with high biomass when geese were present in the area (data from all years,  $N = 128$ ), but plots with highly nutritious plants when geese were absent (data only from 2003,  $N = 60$ , Table 3).

#### REACTION ON OTHER HERBIVORES MEASURED VIA DROPPINGS

We used a Pearson correlation to relate goose and hare grazing pressure at the start of the three experiments with cumulative grazing pressure. Hares avoided plots



**Fig. 2.** Relative grazing pressure of Barnacle Geese (left), Brown Hares with geese present (middle) and Brown Hares with geese absent (right) on the different treatments of the main experiment, summarized for three sets in mid-February, early March and early April 2003 on the salt marsh of Schiermonnikoog (mean values of Fig. 1), given as profile plots; the lengths of each arm of the cross inside the polygon represents the contribution of each treatment to the total grazing pressure. Small numbers give percentage shares. The total length of all arms represents the total grazing pressure accumulated on all treatments, set at 100%.

that had previously been grazed by either hares or Barnacle Geese, while Barnacle Geese preferred these plots (Table 4). Combined results of all experiments indicate that nutritional quality of a plot increased with increased goose grazing (univariate ANOVA, goose droppings:  $F_{1,58} = 12.026$ ,  $P = 0.001$ ; hare droppings:  $F_{1,58} = 0.511$ , NS; replicate (set)  $F_{42,58} = 10.730$ ,  $P < 0.001$ ), while biomass declined with previous grazing (univariate

ANOVA, goose droppings:  $F_{1,74} = 7.810$ ,  $P = 0.007$ ; hare droppings:  $F_{1,74} = 4.371$ ,  $P = 0.040$ ; replicate (set)  $F_{47,74} = 3.039$ ,  $P < 0.001$ ). This again demonstrates that, within a given biomass range, the Barnacle Geese selectively chose plots with low biomass which had been grazed previously, but which offered forage tissue of increased quality. Hares avoided previously grazed plots.

## Discussion

### FORAGE CHOICE BY GEESE

All our experimental data indicate that both Barnacle and Brent Geese prefer plots with a nutrient-rich sward (Fig. 1, Table 3). Additionally, we found that Barnacle Geese avoid plots with high biomass. This finding is supported by the significant positive correlation between the grazing pressure of the Barnacle Goose during the experiment and the previous history of grazing by hares and Barnacle Geese on the experimental plots (Table 4). Forage quality in our salt-marsh system is generally highest in the beginning of the growing season and decreases rapidly as the season progresses (Van der Graaf *et al.* 2006b). However, continuous grazing can retard this seasonal decline. Grazing by either hares or geese apparently improves the quality of the vegetation relative to an ungrazed area and makes these plots particularly attractive for foraging geese (Ydenberg & Prins 1981; this study). Brent Geese

**Table 3.** Response of geese and hares to the manipulation of biomass and quality on plots of *Festuca rubra* on the salt marsh of Schiermonnikoog for all experiments combined: in early May 1997 (Brent Geese, Hares – geese present), early April 2002 (Barnacle Geese, Hares – geese present) and (Barnacle Geese, Hares – geese present, Hares – geese absent). *N* is lower than the actual number of experimental plots for ‘Barnacle Geese’ and ‘Hares – geese present’ as quality samples were collected for only part of the plots in 2002

	Barnacle Geese			Brent Geese			Hares – geese absent			Hares –geese present		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Biomass	1	0.140	0.709	1	0.549	0.463	1	19.888	<0.001	1	1.229	0.274
Quality	1	12.185	0.001	1	4.290	0.045	1	0.092	0.763	1	6.107	0.018
Replicate (Set)	19	8.707	<0.001	7	13.311	<0.001	27	9.348	<0.001	14	3.797	<0.001
Error	58			38			98			42		

**Table 4.** Pearson correlation between grazing pressure of Brown Hares and Barnacle and Brent Geese before the start of the experiments and grazing pressure 3 weeks after the start of the experiments on the salt marsh of Schiermonnikoog, for all experiments combined: early May 1997 (Brent Goose, Hare), early April 2002 (Barnacle Goose, Hare) and (Barnacle Goose, Hare)

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

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

prefer high-quality plots (Table 3), although, unlike the Barnacle Geese, they do not favour previously grazed vegetation (Table 4).

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

#### FORAGE CHOICE BY HARES

For hares, we detected a subtle interplay of foraging choice with concurrent goose grazing. When given a free choice in the absence of goose grazing, hares chose to forage on plots that combine biomass of high quality and quantity. However, when geese are present, as in the spring situation at our study site, hares chose high biomass plots, which are avoided by geese (Table 3).

Van der Wal *et al.* (1998a) provided descriptive and experimental evidence that hares avoid salt-marsh sites that have been previously grazed by Brent Geese. The authors argued against the occurrence of direct competition between geese and hares, since both species forage at different times within a day (i.e. hares feed mainly at dawn and dusk and geese during the daylight period). We witnessed a strong negative correlation between hare foraging choices and previous grazing by either geese or hares in our study (Table 4). Based on these experimental data, we conclude that resource competition as a result of depletion of favourable plots by large numbers of spring staging geese is driving forage patch choice in hares on the salt marsh.

#### A SUBTLE BALANCE BETWEEN RESOURCE COMPETITION AND GRAZING FACILITATION

Grazing by both geese and hares leads to an increased quality of vegetation. This facilitative process, in which grazing of one herbivore induces a subsequent increase in quality of forage tissue through the production of new tissue within one season, has been found in previous studies at our salt-marsh site (Ydenberg & Prins 1981; Van der Graaf, Stahl & Bakker 2005), and has been demonstrated for herbivore–plant interactions in a variety of ecosystems (McNaughton 1984; Gordon 1988; Hobbs *et al.* 1996; Ruess *et al.* 1997; Fox *et al.* 1998; Green & Detling 2000). Under these circumstances, herbivores profit from the increased tissue quality as a result of an elevated rate of nutrient intake.

However, when the forage resource is used concurrently by more than one herbivore species, we expect a shift towards less-preferred plots by one species to avoid resource competition. In our experimental study, hares avoided plots that were favoured by geese. A distinct foraging choice of hares manifested itself only

in a situation where concurrent goose grazing had been excluded experimentally. We interpret this as an indication of resource competition with geese. It was suggested by Van der Wal *et al.* (1998a) that large flocks of socially foraging geese rapidly deplete preferred salt-marsh sites in spring and evict hares to alternative, less favourable foraging sites.

We can explain the observed pattern of forage choices in the small herbivores with a species-specific functional response. For smaller herbivores, several studies demonstrate a dome-shaped functional response of food intake rate vs forage biomass, a classic example of an optimality model (Fryxell 1991; Gross *et al.* 1993; Van de Koppel *et al.* 1996; Iason *et al.* 2002; Durant *et al.* 2003; Bos, Van de Koppel & Weissing 2004; Van der Graaf, Coehoorn & Stahl 2006a). The intake rate of the small herbivore increases with increasing biomass availability, beyond which intake rate declines at even higher levels of biomass. This decrease in the functional response is usually explained as a response to the handling problems of long leaves which decreases intake rate (Van der Wal *et al.* 1998b; Hassall, Riddington & Helden 2001; Durant *et al.* 2003; Bos *et al.* 2004), increased costs of locomotion and increased vigilance due to changes in the perception of predation risks (Van de Koppel *et al.* 1996). Because of their high receptiveness for short grass swards of high nutritional value (this study; Durant *et al.* 2003) we expect geese to show an optimal grazing response at low biomass levels while hares are able to cope with swards of higher biomass (Kuijper *et al.* 2004). Our experimental data demonstrate that foraging choices of sympatrically occurring small herbivores on coastal salt marshes are influenced by a complex interplay of facilitative and competitive processes.

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