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Short-term and long-term facilitation of goose grazing by livestock in the Dutch Wadden Sea area

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Abstract. We studied the impact of livestock grazing on the distribution of *Branta bernicla bernicla (*Dark-bellied Brent goose) in the Dutch Wadden Sea during spring. It was hypothesized that livestock facilitate short-term (within-season) grazing for geese as well as long-term (over years). Therefore we measured grazing pressure by geese in salt marsh and polder areas that were either grazed (spring-grazed) or ungrazed during spring (summer-grazed). Additionally, we carried out a preference experiment with captive geese to test the preference between spring-grazed and summer-grazed polder swards. We furthermore compared patterns of use by geese between long-term ungrazed and grazed salt marshes.

In May, there is a difference in grazing pressure by geese between polder pastures that are grazed or ungrazed during spring. In this month, the ungrazed polder pastures are abandoned and the geese shift to either the grazed polder pastures or to the salt marsh. Vegetation in the polder that had been spring-grazed had a lower canopy height and a higher tiller density than summer-grazed vegetation. The captive geese in the preference experiment showed a clear preference for vegetation that had been spring-grazed by sheep over ungrazed vegetation. Goose grazing pressure was negatively correlated to canopy height, both on the polder and on the salt marsh. Within the plant communities dominated by *Festuca rubra* and *Puccinellia maritima*, marshes that were intensively grazed by livestock generally had higher grazing pressure by geese than long-term ungrazed or lightly grazed salt marshes.

Keywords: Barnacle geese; *Branta bernicla bernicla*; *Branta leucopsis*; Dark-bellied Brent goose; Herbivory; Polder; Salt marsh; Succession

Nomenclature: van der Meijden (1990).

Introduction

Salt marshes and agricultural pastures in embanked (polder) areas in the Dutch Wadden Sea are important spring-staging areas for *Branta bernicla bernicla* (Dark-bellied Brent goose; Brent goose hereafter) and *Branta leucopsis* (Barnacle goose) (Madsen et al. 1999). The birds traditionally shift in between these two main habitats as the season progresses (Prins & Ydenberg 1985; Bos 2002). The feeding conditions during spring are of crucial importance for reproduction at the Arctic breeding sites, as breeding success depends upon the rate of fat storage during spring (Ebbinge & Spaans 1995). Management of the coastal areas by grazing with livestock during summer affects the feeding conditions for Brent goose in winter (Vickery et al. 1994), and on salt marshes long-term effects of grazing by livestock on habitat choice were observed for Barnacle goose (Aerts et al. 1996). In this study we shall examine to what extent livestock grazing affects the habitat use by geese within a single spring season, as well as in the long term. Our focus is on the Brent goose, but because the two species co-occur in some of our study areas in early spring we are not always able to distinguish between them.

Within-season grazing facilitation

On the island of Schiermonnikoog, Brent geese shift between agricultural pasture and salt marsh in mid-April. Traditionally, the shift is explained by a relative change in quality of the vegetation on both the polder and the salt marsh. The onset of spring growth of the vegetation is later on the salt marsh compared to that in the polder. Therefore, in mid-April the quality of the salt-marsh grasses, notably *Festuca rubra* and *Puccinellia maritima* rises, whereas that of the polder grasses decreases (Boudewijn 1984; Prins & Ydenberg 1985). Also the sward of the polder gets taller, which causes handling problems for the geese (Bos 2002). There appears to be a limit to the number of geese on the salt marsh of Schiermonnikoog, as the spring-staging population on this island has remained stable (at about 2000-3000 animals) for over 25 years, despite a rapid increase in total Brent goose numbers in The Netherlands since 1980 (van der Wal et al. 2000). On the neighbouring island of Ameland, however, the spring-staging population of Brent geese has continued to increase the past 25 years from ca. 4000 to about 20 000 birds, most of which remain foraging in the polder during the entire spring period (Kersten et al. 1997). The question rises why the polder on Ameland remains attractive for the geese throughout April and May, whereas the polder on Schiermonnikoog is abandoned during these months. We hypothesize that this has to do with the difference in grazing management. On Schiermonnikoog cattle graze the polder from May onwards. These cattle-grazed pastures thus remain ungrazed throughout most of the spring-staging period of the geese. In contrast, on Ameland part of the polder is grazed by sheep the year round. We suppose that grazing by sheep maintains the sward at a height and quality that is preferred by the geese (Hassall et al. 2001). This process of one herbivore creating attractive swards for another herbivore, is known as grazing facilitation. The best known example of grazing facilitation is the enhancement of plant production caused by the grazing of wildebeest in the Serengeti (McNaughton 1979). In general, grazing causes a higher quality of the vegetation, due to the increased production of fresh new leaves or tillers, that are of high quality, and a reduction of the standing dead and litter biomass (Fox et al. 1998; Mayhew & Houston 1999; van de Koppel et al. 1996).

Grazing facilitation over multiple years

The process of facilitation is relevant at short time scales (within growing seasons), but is also important at longer time scales. Grazing by cattle, for example, strongly affects the vegetation composition on salt marshes in Europe, with serious consequences for geese. Under ungrazed conditions, salt-marsh vegetation changes due to natural succession, and tall plant species that are unpalatable to geese ultimately will dominate the marsh (Roozen & Westhoff 1985; Jensen 1985; Olff et al. 1997; van Wijnen & Bakker 1997). Livestock grazing favours short palatable grasses, such as *Puccinellia maritima* on the lower parts of the salt marsh and *Festuca rubra* on the high marsh (Kiehl et al. 1996). Results from several studies suggest that Brent and Barnacle geese prefer these intensively grazed areas over ungrazed areas (Ebbinge & Boudewijn 1984; Aerts et al. 1996; Stock & Hofeditz 2000).

Hypotheses

To test our hypothesis that livestock grazing facilitates goose grazing within one spring season, we compared goose grazing pressure and vegetation parameters for spring- and summer-grazed sites on both the polder and salt marsh of Ameland and Schiermonnikoog. Secondly, we compared grazing pressure by geese and vegetation parameters between marshes, at four different locations, that were intensively grazed by livestock in summer, lightly grazed or long-term ungrazed, to test the hypothesis that livestock grazing facilitates goose grazing in the long run. Finally, a complementary approach was followed by setting up a small-scale preference experiment on Schiermonnikoog, in which captive geese were offered a choice between patches that were either ungrazed or previously grazed by sheep.

Methods

Study area

This study was performed at four study sites along the Dutch Wadden Sea (Fig. 1); the islands of Ameland (53°27' N; 5°50' E) and Schiermonnikoog (53°30' N; 6°10' E), and two sites at the mainland coast referred to as Noord Friesland (53°23' N; 5°50' E) and Groninger kust (53°25' N; 6°25' E).

Both islands have a polder and a salt marsh, part of which is grazed by livestock. The embanked polder areas contain intensively grazed and fertilized (up to 400 kg N $ha^{-1}.yr^{-1}$) pasture, protected by a seawall. The vegetation consists mainly of agricultural grass species such as *Lolium perenne* and *Poa* spp. The polder of Ameland (2000 ha) is much larger than the polder of Schiermonnikoog (265 ha). Only the eastern part of the polder of Ameland (240 ha) was used for this study. The

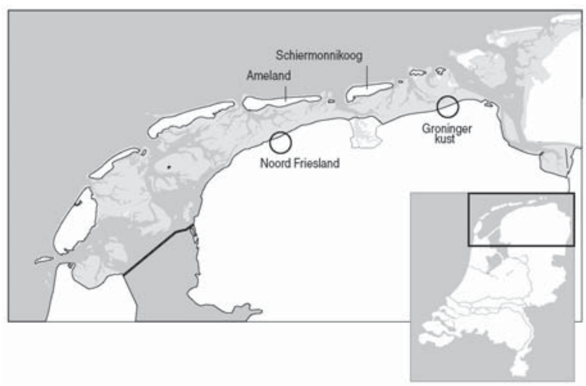

Fig. 1. Location of the study sites.

polder of Schiermonnikoog is grazed by cattle between May and November; the polder of Ameland has additional year-round sheep grazing. In both polder areas, farmers attempt to scare geese from their land. The grazed salt marsh of Ameland contains one part (300 ha) that is spring-grazed by sheep from mid-April onwards and from the end of May onwards also by cattle, and a second part (50 ha) that is only summer-grazed by cattle. Both areas are grazed at a stocking rate of 0.5 Livestock Unit per hectare (LU.ha^{-1}). One LU refers to one adult cow or 10 sheep. The spring-grazed part is lightly fertilized (100 kg-N.ha^{-1}.yr^{-1}). The vegetation on both sites, which are only separated by a gully, is a mixture of *Puccinellia maritima* and *Festuca rubra*. The ungrazed salt marsh of Ameland (100 ha) is less than 70 yr old. The grazed salt marsh of Schiermonnikoog (185 ha) is only summer-grazed by cattle at 0.5 LU.ha^{-1}, from the end of May onwards, and is unfertilized. The long-term ungrazed salt marsh of Schiermonnikoog (1450 ha) is characterized by an age gradient from West (ca. 100 yr old) to East (still growing). In addition to 2000 Brent geese, ca. 6000 Barnacle geese use the marsh on Schiermonnikoog. On Ameland ca. 20 000 Brent geese stay in spring, whereas the number of Barnacle geese is negligible. Brent geese leave the spring feeding grounds in late May, while the majority of Barnacle geese departs during April (Madsen et al. 1999).

To compare marshes with different livestock grazing regimes, we additionally collected data from two salt-marsh sites at the Dutch mainland coast, Noord Friesland and Groninger kust (Fig. 1). The marshes we compared within these study sites differ from each other in stocking rate and will be referred to as either lightly or intensively grazed. Noord Friesland is used by ca. 24 000 Brent geese and 36 000 Barnacle geese in spring. The major part of the marsh (1400 ha) is intensively grazed with cattle and sheep during summer at 1-2 LU.ha^{-1}. Ca. 300ha of the marsh at Noord Friesland are lightly grazed at 0.4 LU.ha^{-1}. Adjacent to the marsh there are also large areas (1000 ha) of agricultural grassland that are occasionally flooded during winter (summer polders), which are heavily utilized by Barnacle, but hardly by Brent geese. The Groninger kust is used by ca. 3800 Brent and 4500 Barnacle geese in spring. The marsh (1600 ha) is grazed with cattle, sheep or horses and along the entire coast intensively (ca.1 LU.ha^{-1}), lightly (ca. 0.5 LU ha^{1}) and ungrazed marshes alternate each other.

Site selection

In order to compare effects of livestock grazing on the distribution of geese, we selected sites with different grazing management in which dropping counts and vegetation measurements were performed along fixed transects. On the polder areas, pastures were classified as spring-grazed if any (sheep) grazing had been going on during the spring-staging period, and summer-grazed when they had not been grazed during this period (March-May). In the polder of Ameland six spring- and six summer-grazed pastures were selected. In the polder of Schiermonnikoog only five summer-grazed pastures were selected, as no livestock grazing occurred here before the end of the spring-staging period. On the salt marsh of Ameland we sampled in both parts of the grazed salt marsh, the part that is only grazed by cattle and thus remains ungrazed during the spring-staging season of the geese, and the part that is also grazed by sheep and thus grazed during the spring-staging season. We will refer to these parts as summer-grazed and spring-grazed, respectively ($n = 2\times 6$). Finally, we established transects in the *Festuca rubra* community of the long-term ungrazed salt marsh of Ameland (n = 6), the *Puccinellia maritima* and *Festuca rubra* community of the summer-grazed ($n = 2 \times 6$) and the long-term ungrazed (age 10-50 yr, $n = 2 \times 6$) salt marshes of Schiermonnikoog, the *Puccinellia maritima* and *Festuca rubra* community of the intensively grazed ($n = 2 \times 6$) and the lightly grazed ($n = 2 \times 6$) salt marshes of the Groninger kust and the *Puccinellia* community of the intensively grazed (n = 9) and the lightly grazed (n = 5) salt marshes of Noord Friesland (Table 1).

Dropping counts

At each selected site we established one transect. Each transect consisted of five plots (4 m^2), with a distance between plots of about 10 m. From the begin-

Table 1. Characterization of the transects used in this study on the different locations. Unless otherwise noted all areas are summer-grazed only. For a description of the vegetation types, and the composition of the lightly-grazed marsh on Ameland, see Methods.

	Schiermonnikoog	Ameland	Groninger kust	Noord Friesland
Polder	Summer-grazed	Summer-grazed; spring-grazed	-	-
Lightly grazed marsh	*Festuca; Puccinellia*	Summer-grazed; spring-grazed	*Festuca; Puccinellia*	*Puccinellia*
Intensively grazed marsh	-	-	*Festuca; Puccinellia*	*Puccinellia*
Ungrazed marsh	*Festuca; Puccinellia*	*Festuca*	-	-

ning of March until the end of May 1998, goose droppings were counted and removed from all plots weekly. The number of droppings was used to calculate the goose grazing pressure as the total number of droppings per m^2 per day.

Vegetation parameters

In May 1998 vegetation composition was assessed, applying visual cover estimates of dead material, bare ground and plant species in every plot. Tiller density was measured in April 1998 on the salt marsh and polder of Ameland. Tiller density was measured by counting the number of tillers in a 5 cm × 5 cm area, repeated 10 times at random within each transect. Canopy height was measured monthly, by dropping a polystyrene disk (24 g, diameter 20 cm) along a calibrated sward stick. This was randomly repeated six times in every plot. At the end of April, samples of leaf tips of forage grasses were taken from every transect on Ameland, to measure forage quality. The samples were washed, air-dried at 70 ºC and nitrogen content was measured using an automated CNHS-analyser (Interscience EA 1110).

Information on overall vegetation composition of salt marshes, in terms of the cover of plant communities for the different grazing regimes, was derived from GIS vegetation maps. These maps refer to the same marshes in which our transects are located. For comparison we additionally included a 110-ha stretch of marsh at Noord Friesland, which has been ungrazed for more than 20 yr. The maps, kindly provided by Rijkwaterstaat (Monitoring programme, Ministry of Transport and Public Affairs), were all derived from interpretation of aerial photographs in combination with a field survey. The scale of mapping is 1:10000 and the date of mapping varies between 1988 and 1995. The legend units for each map were aggregated to plant communities at the level of the association, according to Schaminée et al. (1998).

Preference experiment

In the spring of 1999 a preference experiment with a pair of captive Brent geese was carried out, in order to test the preference for vegetation that was previously grazed by sheep or left ungrazed. The site was situated in the polder of Schiermonnikoog, where the pastures are usually grazed only in the summer (by cattle). An enclosed area (ca. 1 ha) of polder pasture was grazed by nine sheep and five lambs from 15 March onwards, while the surrounding sward remained ungrazed during spring. The stocking rate of sheep was gradually increased over the season by reducing the area of the enclosure to maintain sward height at 3-5 cm. During the period from 15 April until 21 May, 11 feeding trials (each lasting 3 hr) were performed with a pair of captive Brent geese that was offered the choice between feeding in grazed or ungrazed swards. For this purpose, a cage of nylon netting (4 m × 4 m) was placed on the vegetation, so that half of the cage included previously ungrazed swards and the other half the swards recently grazed by sheep. Prior to each feeding trial canopy height and nitrogen content of leaftips were measured as described above. The geese were observed from a hide for a minimum of 9 bouts of 10 min and time spent foraging in each part of the cage was recorded for both geese. At the end of the trial all droppings were counted for both parts separately. For each trial the birds were moved to a different place. Preference was calculated as the percentage of time the two geese species spent foraging in each treatment as related to the total time spent foraging. As it is likely that the geese were not acting independently of each other, the results were pooled in the analysis. Observation bouts of 10 min with no feeding at all were discarded and during each trial the geese foraged at least 10% of the time. The geese had unlimited access to fresh water, which was placed in a tray in the middle of the cage. When not used in the feeding trials, the geese were maintained at polder swards on site and supplementary fed with waterfowl pellets (Anseres II). The experiments with geese were approved by the Dutch commission for use of experimental animals (DEC), licence nr. BG07697/2382.

Statistics

All parameters met the statistical assumption of normality (Kolmogorov-Smirnov test: $P > 0.05$). For all comparisons, except canopy height and goose grazing pressure, an ANOVA followed by a Scheffé's post-hoc test was used. Canopy height on each transect was calculated as the mean of the 30 measurements per transect. Canopy height and grazing pressure, data that were collected each month and each week, respectively, were analysed using Repeated Measurements ANOVA. To improve the equality of variances a square-root transformation, $X' = \sqrt{X + 0.5}$, was conducted for grazing pressure and canopy height (Zar 1996). An arcsine-square root transformation was conducted for percentage values (Zar 1996). Correlations were determined using the Pearson correlation coefficient. All tests were carried out using SPSS 10.1 for Windows. Standard errors are given unless otherwise noted.

Results

Polder

The difference between the summer- and spring-grazed areas is most pronounced in May; the polder area of Schiermonnikoog and the summer-grazed polder areas on Ameland are abandoned, whereas goose grazing pressure rises on the spring-grazed polder areas on Ameland (Fig. 2). Only in this month there is a significant difference in goose grazing pressure between the spring-grazed and the summer-grazed polder areas of Ameland (Table 2, Repeated Measurements Anova with three repetitions, week 19-21, $F_{1,10} = 13.8$, $P = 0.04$). In fact, within the pastures that we sampled, all goose grazing in the polder was concentrated on four spring-grazed pastures, while two spring-grazed pastures and six summer-grazed pastures were not visited by the geese in May. This proportion is significantly different from a random choice of four pastures out of 12 (contingency test $\chi_c^2 = 5.06$, $P < 0.05$).

On average over the entire spring staging season of 1998 there were no significant differences in canopy height and tiller density between the spring- and summer-grazed polder areas of Ameland (Table 2). For nitrogen content we found a higher value in summer-grazed than in spring-grazed swards. We also found a significant negative correlation between average canopy height and average goose grazing pressure on the polder of Ameland over the whole season as well as in May (Pearson correlation = –0.69; $P = 0.013$; $n = 12$ and Pearson correlation = –0.68; $P = 0.014$; $n = 12$).

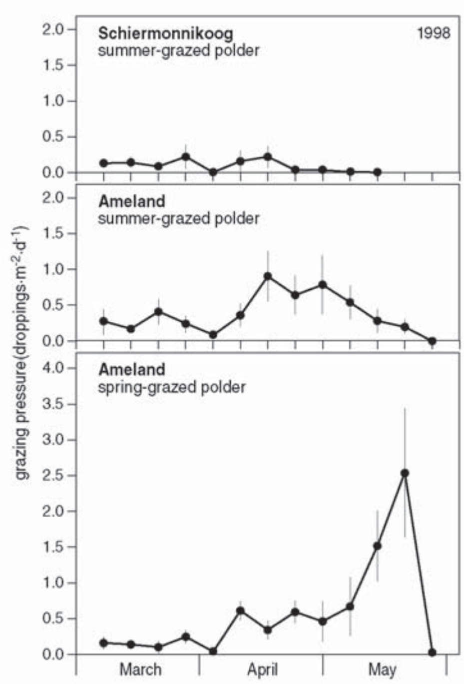

Fig. 2. Goose grazing pressure for different grazing regimes in the polder of Schiermonnikoog and Ameland over the spring season of 1998 (mean ± se).

Preference experiment

The grazing treatment with sheep had a significant influence on canopy height and biomass. These parameters were also highly correlated (Pearson 0.95; $n = 22$; $P < 0.001$). Canopy height increased significantly over time from 3.4 to 23 cm in the ungrazed vegetation (Ancova, interaction day × treatment, $F_{1,18} = 67.5$; $P < 0.001$) and remained constant at 4 ± 0.1 cm in the grazed vegetation. The nitrogen content of the sward declined over time (linear regression $F_{1,18} = 19.1$; $P < 0.001$), irrespective of the treatment (linear regression $F_{1,18} = 0.079$; n.s.). The geese had a clear preference for grazed over ungrazed vegetation, as measured with observational data (T-test; $t = 5.4$; $P < 0.001$) and dropping-counts (T-test; $t = 4.5$; $P = 0.001$). The geese foraged ca. 80% of the time on the grazed vegetation and only 20% of the time in the ungrazed vegetation. There was no significant effect of the time of testing through the

Table 2. Vegetation and grazing parameters (mean ± se) for the polders of Ameland and Schiermonnikoog. Values for Schiermonnikoog are given for comparison, but differences are not tested. Significant differences ($P < 0.05$) between values for spring- and summer-grazed areas in the polder of Ameland are indicated with different letters. Spring averages are for the months of March until May.

		Grazing management polder					
		Ameland Summer-grazed		Ameland Spring-grazed		Schiermonnikoog Summer-grazed	
		Mean	se	Mean	se	Mean	se
Spring goose grazing pressure	Spring average	0.40	0.11[a]	0.62	0.17[a]	0.10	0.05
(no. droppings.m^{-2}.day^{-1})	May	0.34	0.14[a]	1.58	0.51[b]	0.008	0.05
Canopy height (cm)	Spring average	6.66	1.02[a]	4.09	0.66[a*]	6.10	0.32
	May	12.64	2.80[a]	6.53	1.91[a]	9.9	1.6 (*n*=3)
Tiller density (10^3 tiller.m^{-2})		14.88	1.67[a]	17.85	0.81[a]		
Live material (%)		99.5	0.28[a]	98.9	0.45[a]		
Nitrogen content (%; end of April)		4.67	0.24[a]	3.97	0.14[b]	4.50	0.59

* $P = 0.055$

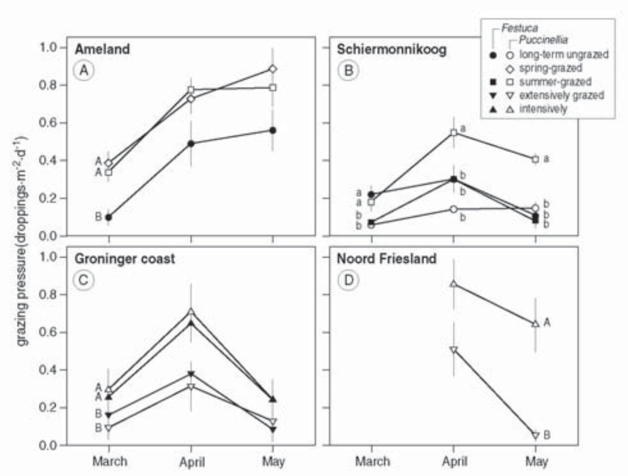

Fig. 3. Comparison of goose grazing pressure on *Puccinellia* and *Festuca* communities at different salt-marsh sites for different livestock-grazing management regimes; **A.** Ameland; **B.** Schiermonnikoog; **C.** Groninger kust; **D.** Noord Friesland. Significant effects of grazing treatment within each study area are indicated using different capital letters. On Schiermonnikoog a significant interaction was found; significant differences are therefore indicated per month with lower case letters.

season, nor was there an effect of time during the trials. Percentage foraging time did not differ between the two geese (mean = 32.7%, paired *t*-test; $t = -1.0$; n.s.) and the geese did not differ either in preference for any of the treatments (contingency test, $\chi^2 = 1.04$; n.s.).

Salt marsh

On the salt marsh of Ameland canopy height was significantly lower and tiller density significantly higher on the spring-grazed part than on the summer-grazed part, whereas no differences were found in vegetation composition (Table 3A) between those two parts. Grazing pressure increased continually during spring (Fig. 3), with no difference between the spring-grazed and the summer-grazed part. Similarly, on all salt marshes and all grazing regimes that we sampled, goose grazing pressure increases during the months of March and April (Fig. 3). In contrast, in May grazing pressure continues to rise on the marsh of Ameland, whereas it decreases at all other locations after the Barnacle geese have left for their Arctic breeding grounds.

At each site, there are significant differences between livestock grazing regimes in terms of goose grazing pressure and vegetation parameters (Tables 3 A-D). Lightly grazed marshes at Noord Friesland have a lower goose grazing pressure than intensively grazed marshes (Table 3C, Fig. 3, Repeated Measurements ANOVA grazing regime: $F_{1,25} = 10.6$, $P = 0.003$) and data from the Groninger kust give the same result (Table 3D, Fig. 3, Repeated measurements ANOVA grazing regime: $F_{1,23} = 5.6$; $P = 0.026$). The long-term ungrazed marsh on Ameland has a lower goose grazing pressure than both parts of the grazed marsh (Table 3A), although this comparison is confounded by differences in fertilization

Table 3. Vegetation and grazing parameters (mean ± se) for **A.** The grazed and long-term ungrazed salt marshes of Ameland. **B.** Schiermonnikoog. **C.** The *Puccinellia*- dominated salt marsh of Noord Friesland, and **D.** The salt marsh of the Groninger kust. GP = spring goose grazing pressure (no. dropping.m^{-2} day^{-1}), CH = canopy height (cm), TD = tiller density (10^3 tiller.m^{-2}), C-L = cover of live material (%), C-EG = cover of edible grasses (%), C-EP = cover of edible plants (%), C-TP = cover of tall plant species (%), N = nitrogen content. Significant differences ($P < 0.05$) within a site are indicated with different letters. The category edible grasses includes *Puccinellia maritima, Festuca rubra, Juncus gerardi* and *Poa* spp. Edible plants include all edible grasses and *Plantago maritima* and *Triglochin maritima*. Tall plant species include *Elymus athericus, Artemisia maritima* and *Atriplex portulacoides*.

A. Ameland	GP		CH		TD		C-L		C-EG		C-EP		C-TP		N	
	Mean	se	Mean	se	Mean	se	Mean	se	Mean	se	Mean	se	Mean	se	Mean	se
Summer-grazed	0.63	0.06 a	3.54	0.20 a	23.17	1.40 a	80.5	1.89 a	64.9	5.40 a			0.07	0.04 a		
Spring-grazed	0.65	0.06 a	1.59	0.34 b	32.15	3.28 b	84.1	1.07 a	49.67	10.58 a			0.01	0.01 a		
Long-term ungrazed	0.37	0.07 b	5.61	0.86 c	8.08	0.86 c	60.2	2.59 b	45	0.01 a			0.06	0.03 a		
B. Schiermonnikoog																
Puccinellia Grazed	0.38	0.03 a	2.8	0.1 a	19.16	2.48 a			47.0	4.6 a			1.6	0.5 a	3.5	0.2 a
Long-term ungrazed	0.11	0.01 b	5.7	0.2 b	6.84	1.08 b			5.7	1.0 b			2.8	1.0 a	3.4	0.0 a
Festuca Grazed	0.15	0.04 b	3.7	0.1 a	27.88	2.56 a			80.3	1.7 a			2.9	0.7 a	2.5	0.2 a
Long-term ungrazed	0.21	0.02 b	7.3	0.3 b	16.36	1.28 b			57.0	4.8 b			24.2	6.2 b	2.4	0.1 a
C. Noord Friesland																
Heavily grazed	0.8	0.1 a	4.2	0.4 a					57.5	6.8 a	80.8	4.2 a	2.7	0.6 a		
Lightly grazed	0.3	0.1 b	17.1	4.8 b					49.8	4.9 a	49.8	4.9 b	12.2	10.3 a		
D. Groninger kust																
Puccinellia Heavily grazed	0.4	0.1 q	4.3	0.6 a					48.3	2.1 a			6.1	0.9 a		
Lightly grazed	0.2	0.1 b	9.8	1.1 b					45.3	3.3 a			19.8	3.7 b		
Festuca Heavily grazed	0.4	0.1 a	4.5	0.6 a					52.8	3.2 a			8.6	2.2 a		
Lightly grazed	0.2	0.1 b	6.6	0.6 b					57.2	1.9 a			15.4	2.2 b		

and plant community. At Schiermonnikoog, the effect of grazing regime is significant (Table 3B, Repeated measures ANOVA grazing regime: $F_{1,20}$ = 5.8, P = 0.025), and the long-term ungrazed marsh has significant lower grazing pressure than the summer-grazed marsh for the *Puccinellia* community for each month (Fig. 3). However, there was also a significant interaction between plant community and grazing regime (Repeated measures ANOVA plant community × grazing regime: $F_{1,20}$ = 33.4, P < 0.001). This interaction was caused by the fact that the grazing pressure in March on the *Festuca* community was higher in the long-term ungrazed marsh than in the grazed salt marsh. Canopy height and goose grazing pressure are negatively correlated at the transect-level on the salt marshes of Ameland (Pearson r = –0.71; P = 0.001; n = 18), Noord Friesland (Pearson r = –0.53; P = 0.04; n = 14) and the Groninger kust (Pearson r = –0.66; P < 0.001; n = 26), while on Schiermonnikoog this overall correlation was not significant (Pearson r = –0.29; n.s.; n = 24). With reduced stocking rates of livestock, or without livestock grazing, both plant communities develop a taller canopy in each of the study areas. Additionally in most of the comparisons, reduced stocking rates result in a lower cover of plant species that are palatable for geese (Table 3 A-D).

The differences in vegetation composition between marshes with different grazing regime are also found at the level of plant communities. From the vegetation maps it appears that on Ameland and Noord Friesland, plant communities with short vegetation are more abundant on the grazed than on the ungrazed salt marsh (>95% versus 60% short vegetation, i.e Festucetum, Puccinellietum and Juncetum, Table 4). At the older long-term ungrazed salt marsh of Schiermonnikoog less than 30% of the area consists of plant communities suitable for geese, compared to 50% for the grazed marsh and 76% for the young long-term ungrazed marsh.

Discussion

Within-season facilitative effects of livestock

Our data from the polder of Ameland and from the preference experiment suggest that, towards the end of spring, geese prefer vegetation that has previously been grazed by livestock. In May, spring-grazed swards in the polder of Ameland were lower in canopy height and higher in tiller density than swards that had been ungrazed during spring, however, these differences were not significant (Table 2). For nitrogen content we even found the opposite of our hypothesis: the nitrogen content was higher in the summer-grazed areas. However, in this comparison we used the six pastures that had been spring-grazed, but two of these pastures were not visited by the geese in May. When these two spring-grazed areas are excluded from the analysis, there is a significant difference in canopy height in May (summer-grazed mean ± se = 12.64 ± 2.80 cm, spring-grazed = 3.86 ± 0.15 cm; t_8 = 2.927; P = 0.019) and no difference in nitrogen content (summer grazed mean ± se = 4.67 ± 0.24%; spring-grazed = 4.05 ± 0.18%; t_8=1.842; P = 0.103).

We also observed no effect of previous grazing on nitrogen content in the preference experiment on the polder of Schiermonnikoog in 1999. However, the observed patch choice of the captive geese in the grazing experiment is in line with data from previous studies which show that geese discard tall, ungrazed swards (Summers & Critchley 1990), as such swards in general are characterized by a higher fibre content (Boudewijn 1984; Demment & van Soest 1985), a lower nitrogen concentration (Hassall et al. 2001) and a lower tiller density (Vickery et al. 1994). Besides effects of forage maturation on food quality, goose intake rates of biomass can become depressed at higher levels of canopy

Table 4. Cover of plant communities for different livestock grazing regimes above the pioneer zone on the salt marshes of Ameland, Schiermonnikoog and Noord Friesland (in percentages). Communities that are especially relevant for geese are indicated with an asterix. Tall vegetation refers to the sum of the cover of plant communities with a tall canopy. Short vegetation is defined by the combined cover of *Festucetum*, *Puccinellietum* and *Juncetum*. Data are derived from vegetation maps.

Location	Grazing regime	Age	*Puccinellietum**	*Festucetum* *	*Juncetum*	*Atripli-Elytrichietum*	*Artemisietum*	*Halimionetum*	Tall vegetation	Short vegetation
Ameland	Grazed	Old	7	92	0	2	0	0	2	98
	Ungrazed	Young	17	43	0	38	2	0	40	60
Schiermonnikoog	Grazed	Old	5	22	22	26	21	3	50	50
	Ungrazed	Old	9	8	13	37	19	14	71	29
	Ungrazed	Intermediate	10	19	20	18	19	13	51	49
	Ungrazed	Young	52	20	4	9	4	10	24	76
Noord Friesland	Grazed		87	3	6	2	3	0	5	95
	Lightly grazed		67	14	14	4	0	2	6	94
	Ungrazed		60	0	0	28	0	12	40	60

height due to problems with handling the long leaves (Bos 2002). In addition, increased levels of dead biomass could depress the intake rate of biomass at higher levels of standing crop (van der Wal et al. 1998), but this effect is negligible in intensively managed agricultural swards where the amount of dead biomass is small. Furthermore, taller swards may increase the costs of locomotion or decrease predator detection. Over spring, primary production is increasing rapidly and towards the end of the spring-staging period of the geese the differences between spring-grazed and summer-grazed swards will become exceedingly pronounced. We propose this as the reason for the high goose grazing pressure in sheep-grazed polder swards in May on Ameland, whereas it was negligible in swards that had been ungrazed during spring on Ameland and Schiermonnikoog (Fig. 2) in 1998. Taking the preference experiment on Schiermonnikoog as an additional line of evidence, we can conclude that, within a growing season, livestock facilitates goose grazing.

Within-season facilitative effects of goose grazing

Even in the absence of livestock, grazing facilitation by geese and other herbivorous wildfowl can be observed. In the Hudson Bay Area (Canada) *Chen caerulescens caerulescens* (Lesser snow goose) enhance production and quality of salt-marsh vegetation through increased nitrogen cycling mediated by faeces deposition (Hik & Jefferies 1990). Fox et al. (1998) showed that spring-grazing *Anser albifrons flavirostris* (Greenland white-fronted goose) improved the nitrogen content of *Phleum pratense* and the amount of tissue available for geese, excluding an effect of faeces. Also Wigeon were found to increase protein content and quality (Mayhew & Houston 1999). Different studies suggest that herbivorous birds adopt a rotational grazing strategy, returning to a previously grazed spot when the yield in terms of biomass or protein content is highest (Drent & van der Wal 1999; Mayhew & Houston 1999). However, Hutchings & Gordon (2001) question whether the observed grazing pattern is a strategy or merely a consequence of short-term individual decisions. Also in polder areas in The Netherlands, geese were shown to be able to maintain a suitable sward by repeated grazing. The 100-ha Brent goose reserve at Zeeburg on the Wadden island of Texel, 53º05' N, 4º50' E) consists of intensively managed agricultural pastures and supports ca. 10 000 geese during winter and spring until the second half of May. At Zeeburg the grazing pressure by Brent geese depends on primary production and the geese concentrate their grazing in a restricted area, abandoning more and more fields as the spring season progresses (Spaans & Postma 2001). This concentration of grazing on a restricted area when levels of primary production increase is of crucial importance for maintaining a short and suitable sward. Experiments with exclosures in pastures that were intensively utilized by geese in this reserve confirmed that temporarily ungrazed patches (> 4-8 wk) get abandoned (Bos 2002). At the time of our study, on both Ameland and Schiermonnikoog the geese were actively chased away by farmers when foraging on their land, thus keeping the geese from concentrating in one area and maintaining the sward in a short condition.

Between the spring- and summer-grazed parts of the salt marsh on Ameland we found differences in canopy height and tiller density, but no difference in vegetation composition or goose grazing pressure. This might be related to a difference between salt marsh and polder in the level of primary production, which is lower on the salt marsh compared to agricultural pastures, due to differences in fertilization, water availability and salt stress. In combination with lower levels of disturbance on the salt marsh, the geese may be able to cope with the primary production themselves, and to maintain a suitable sward by intensifying their grazing pressure over the course of the season (Fig. 3).

Long-term effects of livestock grazing on salt marshes

In the absence of livestock grazing, natural succession leads to changes in vegetation composition (Olff et al. 1997; Table 3 A-D) and grazing pressure by geese (Fig. 3; Aerts et al. 1996). In our comparison of grazing regimes we have sampled plant communities that are known to be utilized by geese, the *Puccinellietum* and the *Festucetum*. Even within these communities differences in species composition can be pronounced. Long-term ungrazed marsh develops a taller sward and often has higher cover of plant species that are unpalatable for geese, whereas livestock grazing favours short and palatable grass species (Table 3 A-D). This was also found by Stock & Hofeditz (2000) in a comparison between sheep-grazed salt marsh and marsh that had been ungrazed for 9 yr on the Hamburger Hallig, Germany. Grazing pressure by geese is significantly higher in the more intensively grazed situation for most of the comparisons we made, except for the *Festuca* community on Schiermonnikoog (Fig. 3). Moreover we found that, without livestock grazing, the total surface cover of plant communities that are suitable for geese decreases (see Table 4; Andresen et al. 1990; Bakker et al. 2002). Productive long-term ungrazed marshes quickly become unsuitable as a habitat for small herbivores over the years, due to natural succession (Aerts et al. 1996; Bergmann & Borbach-Jaene 2001; Bos 2002). On the barrier marshes this process takes several decades (van de Koppel et al. 1996; Olff et al. 1997), and this explains why the old ungrazed marsh on Schiermonnikoog has much larger cover of communities with tall canopy than the young ungrazed marsh (Table 4). The declining suitability of ungrazed marsh for small herbivores is a compound effect of the increase in canopy height, dead biomass and cover of tall unpalatable plant species coinciding with decreased tiller density, cover and biomass of forage species. Together these changes are likely to result in reduced intake rates of biomass for the small herbivores, and reduced average forage quality.

Implications for management

By the end of spring, primary production has reached high levels on polder areas along the Wadden Sea, such that virtually unlimited numbers of birds could be sustained if only biomass were important. However, forage maturation effects and increasing leaf lengths diminish the suitability of swards for geese, where standing biomass accumulates. These effects can be counteracted by continuous grazing of the sward during spring, either by livestock or by geese themselves. Especially the latter scenario requires undisturbed conditions, as human disturbance was shown to severely constrain the use of inland feeding areas (Bos 2002). Thus, appropriate management can strongly enhance the capacity of highly productive inland feeding areas by maintaining a short sward and keeping low levels of disturbance, as for example shown by Spaans & Postma (2001). Note, however, that maintaining a short sward is not a panacea, as forage availability might be limiting under conditions of low primary productivity (Hassall et al. 2001). For inland feeding areas on the winter grounds, managed to accommodate as many geese as possible, it is, therefore, more effective to provide swards of intermediate canopy height in order to strike a balance between forage availability and forage quality (Riddington et al. 1997). Finally, as pointed out by Prop & Black (1997), there is reason to assume that agricultural grassland may not satisfy all nutritional requirements of Brent geese and Barnacle geese in spring, potentially affecting subsequent reproduction. The use of inland feeding areas as a management tool to support the population of Brent geese should, therefore, be treated with caution. It is more appropriate to try and maintain or even enhance the capacity of natural habitat to support the geese in spring.

Livestock grazing on salt marshes improves the feeding conditions for geese, with the highest goose grazing pressure in areas where stocking rates are highest. Brent geese and Barnacle geese rely upon young or grazed salt marshes during spring, as undisturbed natural succession leads to a declining suitability of the habitat for these small herbivores (van de Koppel et al. 1996). Because young marsh is relatively rare, there is an argument to maintain considerable areas of marsh under grazing in the Wadden Sea, in order to support current numbers of geese in the Wadden Sea in spring (Bos 2002). However, livestock grazing also affects other taxa that are characteristic of salt marshes, such as breeding birds (Norris et al. 1998), insect fauna (Andresen et al. 1990) and of course plants (Bakker et al. 2002), and management should not entirely be guided by the needs of single species. A more exhaustive discussion on this issue is presented elsewhere (Bakker et al. in press), but the central tenet for us is that goose grazing management should be guided by clearly defined ecological objectives and a continuous monitoring of developments.

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