

Geese in the Wadden Sea: an effect of grazing on habitat preference

Maarten J.J.E. Loonen and Daan Bos

Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, NL-9750 AA Haren, The Netherlands (e-mail: m.j.j.e.loonen@biol.rug.nl, d.bos@biol.rug.nl)

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Abstract

Field experiments with manipulations of vegetation plots and experiments with captive geese have tested habitat preference of geese. Barnacle geese and brent geese prefer salt marshes grazed by livestock over ungrazed salt marshes. This is shown on various sites, in experiments where livestock grazing has been manipulated. The geese show the highest grazing pressure on short vegetation, with little obstruction of tall unpalatable plant species. On agricultural fields, grazing is also important to facilitate goose usage. In the month of May, in the period of rapid grass growth, brent geese are clearly favouring the shortest canopy. Sheep will keep the vegetation short, but also grazing by the geese themselves will increase later usage by geese. Geese reject tall vegetation because the revenues, expressed as intake of nutrients are smaller per unit feeding time. In an undisturbed habitat, geese will be able to concentrate in a small area and manage their own food supply. In a disturbed habitat geese will rely on sheep grazing for optimal feeding conditions.

Introduction

Understanding habitat selection is of vital importance for the management of wild animal populations. It offers tools for improving feeding conditions or redirecting the distribution of animals. The latter has become an important issue in goose management. Goose numbers have increased tremendously in the last decades (Madsen et al., 1999) and the resulting increase in use of agricultural fields causes economic losses and has intensified the conflict between nature conservationists and farmers (Van Eerden, 1990). The reduction of damage to agricultural grasslands and crops has become an important management goal, which can be made effective by directing the geese to less-expensive crops or to

increase their usage of nature reserves (Vickery et al., 1994).

Habitat selection will be a trade-off between optimal foraging conditions and predation risk. Hunting and scaring are effective ways to change the distribution of the geese, but these methods disturb other wildlife and are time-consuming. Optimizing foraging conditions and luring geese to special areas is an alternative and this paper examines the potential for this method based on grazing management.

In the Wadden Sea, brent geese (*Branta b. bernicla*) and barnacle geese (*Branta leucopsis*) are the most numerous goose species, feeding both on salt marshes and agricultural grass fields. Both species are protected and shooting is not allowed. In October, both species

arrive from their Arctic breeding grounds in the Wadden Sea. In the end of April, the barnacle geese leave for their spring staging sites in the Baltic, while the brent geese stay in the Wadden Sea until the end of May. In this period, the Wadden Sea harbours almost the entire flyway population and the brent geese directly compete with the farmers for the first harvest of their grass.

Geese are highly selective herbivores. Their relatively simple digestive tract forces them to select for nutritious, high protein food. Habitat selection of these free-flying wild herbivores has often been explained by differences in quality and digestibility of their food. What will happen when the goose habitat changes due to a change in management?

For many centuries, salt marshes have been grazed by livestock (Behre, 1985). The last decade, this is quickly changing. The economical value of the salt marshes became less and nature conservation bodies took over the management. New approaches were formulated for the management with more emphasis on a reduction of human influence. Large areas of salt marsh along the Wadden Sea have become ungrazed by livestock. This change in management has a strong effect on vegetation structure and composition, while the consequences for the geese are still poorly understood. Will the area become less profitable for the geese?

Also on agricultural grasslands, grazing by livestock potentially affects goose usage. On Ameland, many brent geese are staging on agricultural fields until their departure to the breeding grounds in the end of May, while on Schiermonnikoog the geese leave the ungrazed polder at the end of April to continue feeding on the salt marsh. In the period 1980-1990 on Ameland, both the number of brent geese and the number of

sheep tripled, while the number of cattle showed a slight reduction. Do sheep facilitate for brent geese?

This paper aims to study the effect of previous grazing on habitat use of the geese. The first part considers salt marsh vegetation grazed by livestock. The second part will study the effect of livestock grazing on goose grazing in agricultural grasslands. The final part will evaluate the effect of previous goose grazing on preference by geese for agricultural grasslands. The effects are studied by experimentally manipulating the vegetation and monitoring the effect on the grazing pressure of geese.

Material and Methods

Dropping counts

Grazing pressure of geese can be estimated by counting the amount of droppings in a given area. Geese defaecate every 4-6 minutes and the amount of droppings produced is a good measure for the total time spent in an area (Owen, 1971). In this study, grazing pressure was measured in 4 m² circular plots, permanently marked with one stick. Plots were visited within 14 days intervals and all droppings were counted and removed. In most weather conditions, droppings will remain intact and well recognisable on the vegetation for a period of at least 14 days. Droppings in drift lines (caused by flooding) or on small heaps (produced by sleeping birds) were neglected. Droppings of Greylag Geese (*Anser anser*) and Wigeon (*Anas penelope*) could be differentiated from droppings of Barnacle Geese and Brent Geese by their size. Droppings from the latter two species were difficult to separate, but on many occasions the presence of a species could be determined through observations.

Vegetation height

Vegetation biomass and structure is heavily influenced by a herbivore. Vegetation height was used as an index for biomass. Within the same vegetation type, this measure correlates very well with biomass (Hassall et al., 2001). Vegetation height was measured to the nearest 0.5 cm using a sward stick: a polystyrene disc of 24 gram and a diameter of 20 cm, sliding along a graduated stick. The mean of five or six measurements was calculated for each plot.

Salt marshes

Goose grazing was studied on salt marshes along the Groningen coast and on the island of Schiermonnikoog, The Netherlands, and in the Leybucht, Germany.

The Groningen coast is a mainland salt marsh: man-made with a thick clay layer. Different farmers own parcels perpendicular to the dike, and grazing pressure of cattle, sheep and horses varies even in neighbouring parcels. Three neighbouring fields were selected, differing in vegetation cover of *Atriplex portulacoides*, a small woody shrub of 30 to 50 centimetres height. The presence of this plant is dependent on the grazing pressure of livestock (Jensen, 1985, Bakker & Bos, 2002). Grazing pressure of the geese was measured from October to December 1996 by weekly dropping counts in six permanent quadrats within each field. No livestock was present on the marsh in this period.

The Leybucht is a mainland salt marsh in NW Germany. It used to be heavily grazed by cattle, but since 1983, this management is gradually abandoned in favour of an ungrazed marsh. In this area large experimental areas were established in 1980 to study the effect of cattle grazing (Andresen et al., 1990, Bakker & Bos, 2002). Three fenced areas of 100 * 700 m² with densities of 0, 0.5

and 1 cow per hectare were placed in an large salt marsh where 2 cows per hectare were grazing. Grazing occurred each year until 1999, from the end of May to the end of October. In spring 1999, all treatments were ungrazed. On 21 May 1999, droppings were counted along 4 transects intersecting all treatments at the same elevation. Per transect, five dropping plots of 4 m² were counted in each treatment, resulting in 20 plots per treatment. For each plot, the dominant plant species was noted. Vegetation height was measured five times per plot and averaged to one value. In this area, barnacle geese are the dominant goose species.

The Schiermonnikoog marsh is an island salt marsh. It is naturally formed on a sandy soil and the clay layer thickness is much smaller than on the mainland salt marshes. Clay layer thickness varies with elevational height and age of the salt marsh (Olf et al., 1997, Van Wijnen & Bakker, 1997). Vegetation development differs between island and mainland salt marshes due to the difference in soil types. Our study area on the marsh of Schiermonnikoog is cattle-grazed since 1972. In 1997 an area of 60 by 60 meter was fenced off for cattle. During the period when geese were present, no cattle grazed on the salt marsh. The fences were removed from the beginning of November to the middle of May, to have no obstructions for the geese. Both barnacle and brent geese use this marsh intensively. Plots were equally divided inside and outside the enclosure and in two vegetation communities dominated by *Festuca rubra* and *Puccinellia maritima*. In total 24 permanent dropping plots were counted at regular intervals.

Agricultural fields

The effect of previous grazing on agricultural fields was studied on the Dutch Wadden Sea islands of Ameland,

Schiermonnikoog and Texel. On Ameland, brent geese are staging, while barnacle geese are relatively rare. The majority of geese continues foraging on agricultural fields until their departure in the end of May. On Ameland sheep graze parts of these fields. They graze the whole year round, moved between different parcels by the farmer. Cattle are only allowed to graze outside after mid May. We selected 12 parcels, six grazed by sheep during winter and spring and six ungrazed. In each parcel, five permanent dropping plots were placed on a transect perpendicular to the dike. Droppings were counted at weekly intervals.

On Schiermonnikoog production of grass for cattle is the dominant management type. In early spring both barnacle and brent geese stage in the agricultural fields. Both species shift to the salt marsh during spring, barnacle geese usually a month earlier than brent geese (Boudewijn, 1994, Prins & Ydenberg, 1985). The barnacle geese leave the island at the end of April, while the brent geese stage another month almost exclusively on the salt marsh.

In 1999 preference for sheep-grazed areas was tested experimentally. In a large cattle-grazed field, an area of 1 ha was fenced off and grazed by 9 sheep and 6 lambs throughout March, April and May. To maintain vegetation height, grazing intensity was increased over the season by gradually reducing the area of the enclosure. The fence became a border between sheep-grazed vegetation and ungrazed vegetation, because cattle did not enter the field during the study period. A pair of captive brent geese was used to study foraging preference. The geese were caught on Texel in 1990 and kept in captivity at the Biological Centre in Haren. The animal experiments were conducted under permit no. BG07697/2382. The captive geese were allowed to graze in cages of 4x4 m², made of nylon netting 2 m in height. Ungrazed and sheep-grazed vegetation were equally

present in the cage. The amount of feeding on each half was quantified for a period of two hours. Alternating the cage was built on the east and west boundary of the sheep-grazed area, with the sheep-grazed side respectively in the west and the east of the cage. Drinking water was provided ad libitum in the middle of the cage. After two weeks allowing the geese to adjust to the experimental set-up, 11 trials in total were made in the period from 7 April till 22 May. In between trials, supplemental food pellets were provided to the geese, while they remained in the cage on the study site.

In 2000 the effect of previous goose grazing on habitat preference of brent geese was studied in the nature reserve Zeeburg on Texel. The reserve is grazed with sheep and cattle during summer, but the cattle are not entering the fields as long as the geese are present. Brent geese stay in the area usually until the middle of May. On a field intensively grazed by brent geese 28 exclosures of 4*4 m² were built. On 4 different dates, we constructed 7 exclosures respectively 6 weeks, 4 weeks, 2 weeks and one week before the start of the experiment on 7 May 2000. In these exclosures, the vegetation could develop without grazing, while the brent geese grazed the surroundings. Together with a serie of control-plots in the remainder of the field, there were 5 treatments, differing in biomass, with 7 replicates per treatment. All exclosures were removed on 7 May. Wild geese could feed on all treatments, differing in vegetation height and biomass.

From each replicate, a small sample of fresh leaf tips, which mimicked goose grazing, was taken for nitrogen analyses and a turf of 10 x 10 cm² was taken for measuring intake rate. The sample for the nitrogen analysis was dried at 60° for 48 h. Total elemental nitrogen was measured with an automated element analyser (Interscience EA 1110). Intake rate was measured in an

Figure 1. Grazing pressure of geese on salt marshes along the coast of Groningen, The Netherlands. Based on dropping counts, grazing pressure declines with increasing cover of *Atriplex portulacoides*, a plant unpalatable for geese and increasing in cover when salt marshes become ungrazed by livestock.

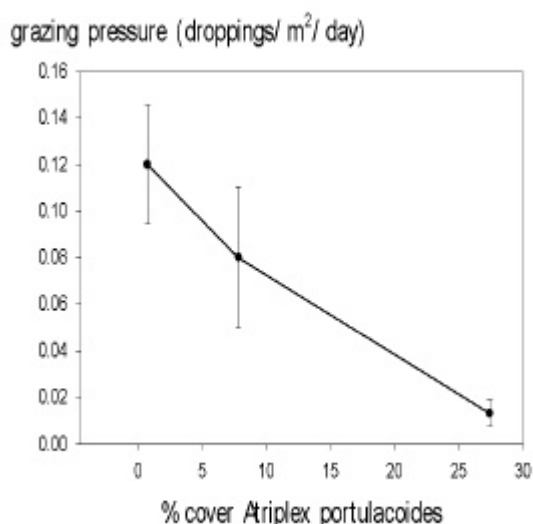
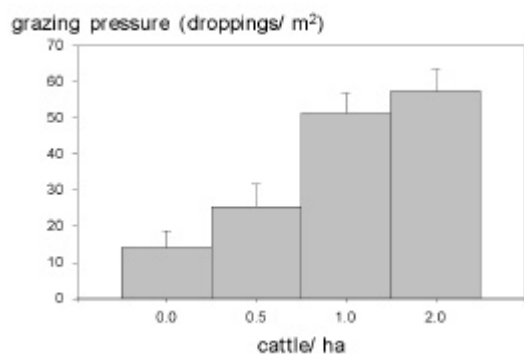


Figure 2. Grazing pressure of geese, based on dropping counts, in experimental areas in the Leybucht, Germany, grazed with different stocking rates of cattle. Goose usage increases with stocking rate.



experiment with 3 captive brent geese (permission no. BG07697/2382). One goose was allowed to feed on a turf for a maximum of approx. 50 pecks. The feeding was taped on video and the number of pecks and the feeding time were measured. The amount of vegetation

removed was calculated as the weight loss of the turf during the trial after correction for evaporative water loss during the trial. By dividing the amount of vegetation removed by the total feeding time, intake rate could be calculated.

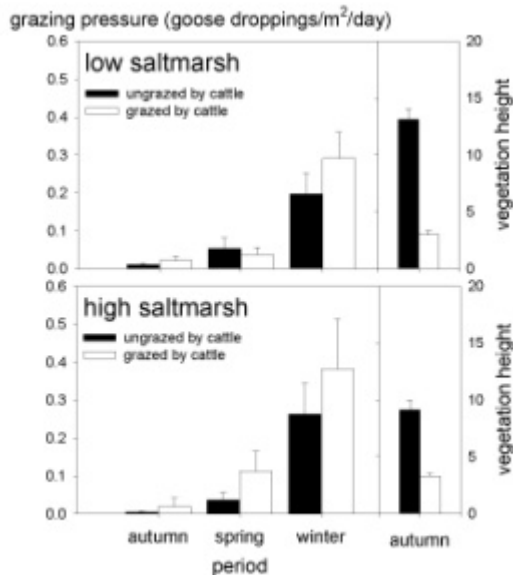
Results

Salt marshes

On the Groningen coastal salt marshes, three adjacent fields differed as a result of differences in grazing pressure of livestock. Vegetation cover of *Atriplex portulacoides* varied from 0 to 28 percent. There was a steep decline in grazing pressure with increasing cover of *A. portulacoides* (Fig. 1). The geese preferred the shortest vegetation with no inedible plants present.

In the experimental enclosures on the Leybucht salt marsh, goose dropping densities showed a strong correlation with grazing pressure of cattle during grazing summer. The highest goose grazing pressure was found in the control area, which was heaviest grazed by cattle (Fig. 2). Only four plant species were recorded as dominant species in any of the dropping plots. *Elymus athericus* was the tallest with an average height of 29.7 ± 2.5 cm ($n=21$). It occurred in the two enclosures with the lowest grazing pressure of livestock (see also Bakker & Bos, 2002). In only three out of these 21 plots, droppings were found. The average density was 0.1 goose dropping/m² for all *Elymus* plots. Dropping plots dominated by *Agrostis stolonifera* and *Puccinellia maritima* had a goose dropping density of 23.4 ± 9.5 ($n=25$) and 11.0 ± 0.2 droppings/m² ($n=34$) respectively. Vegetation height was 4.8 ± 0.9 cm in the *Agrostis* plots and 3.8 ± 0.4 cm in the *Puccinellia* plots. Dropping plots dominated by *Agrostis* occurred in all treatments equally (in order of increasing

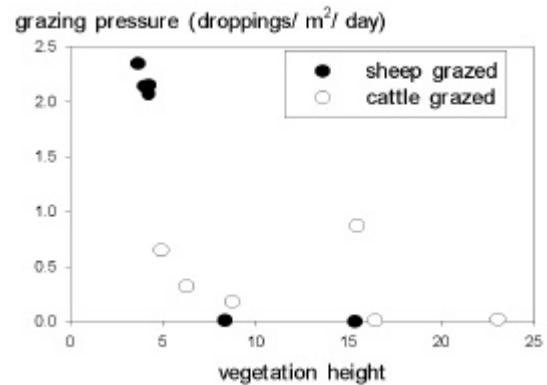
Figure 3. A comparison of areas inside and outside a large cattle enclosure on the salt marsh of Schiermonnikoog, The Netherlands. Grazing pressure increases over the season. In the cattle-grazed control, more droppings are found than inside the enclosure.



cattle grazing pressure: 6, 5, 7, 7), while dropping plots dominated by *Puccinellia* where found more often in treatments with more livestock grazing (1, 7, 13, 13). Within plots dominated by these species, there were negative relations between vegetation height and livestock grazing pressure (*Elymus*: $F_{1,19}=5.00$ $p=0.04$; *Agrostis*: $F_{1,23}=10.19$ $p<0.01$; *Puccinellia*: $F_{1,32}=4.79$ $p=0.04$) and between dropping density and livestock grazing (*Elymus*: $F_{1,19}=6.88$ $p=0.02$; *Agrostis*: $F_{1,23}=25.88$ $p<0.001$; *Puccinellia*: $F_{1,32}=4.79$ $p=0.04$).

In the period from 1997 until 1999 the vegetation type in the enclosure on Schiermonnikoog did not change dramatically, though there was a significant effect of the enclosure on vegetation height (Fig. 3, repeated measurement ANOVA of 6 vegetation height measurements per plot on 12 Oct 1999: $F_{1,22}=82.80$, $p<0.001$). The geese showed a preference for the grazed vegetation (repeated measurement

Figure 4. Sheep-grazed fields on Ameland, The Netherlands, have a higher grazing pressure of brent geese in May than cattle-grazed (=ungrazed) fields. Highest grazing pressure is measured on the shortest vegetation.



ANOVA of 23 measurements per plot: $F_{1,22}=6.22$, $p=0.021$). More geese are grazing on the cattle-grazed vegetation, both in the low salt marsh and the high salt marsh (Fig. 3).

Agricultural grasslands

In spring 1998 a detailed comparison was made between cattle and sheep-grazed fields on Ameland. In the beginning of the season all fields were had a short vegetation with an average vegetation height of 2.8 ± 0.2 cm ($n=12$). Goose droppings were found in all fields and daily grazing pressure gradually increased over spring. However in May, geese concentrated in four fields only. These fields were all sheep grazed (Fig. 4). The frequency with which parcels remain to be visited intensively by geese is unequal for sheep-grazed and ungrazed parcels ($\chi^2 = 5.06$, $P<0.05$). The descriptive study revealed some problems with the experimental set-up. There was considerable variation between fields in soil type, reseeding and the use of artificial fertiliser. Also cattle-grazed fields are actually ungrazed during the goose season while the cattle enters the field only after the middle of May. In

Figure 5. The increase in vegetation height in two experimental plots at Schiermonnikoog, The Netherlands, over spring. The ungrazed plot increases exponentially in the beginning of May, while the sheep-grazed plot remains at a low vegetation height. Goose preference is tested in these plots with a pair of captive geese.

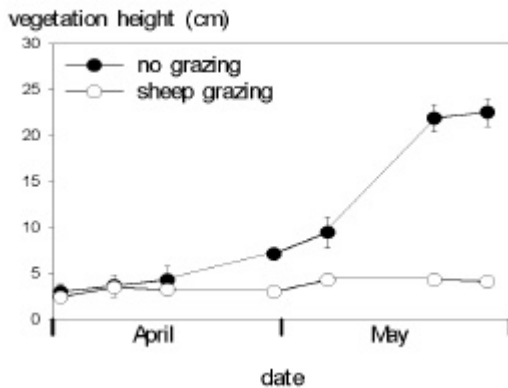
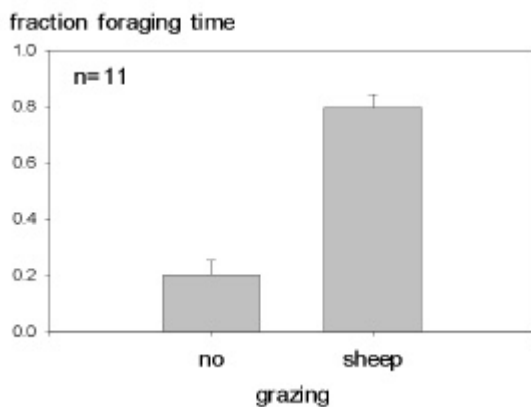


Figure 6. A pair of brent geese favours the shorter vegetation and spends most of its foraging time in the sheep-grazed half of the cage.



contrast, sheep are left outside most of the year. Consequently, the comparison between cattle-grazed and sheep-grazed is more a comparison between ungrazed and grazed by livestock. However, geese also affect this comparison by their own grazing, keeping the vegetation of some fields in a short preferred stage.

With an experiment on Schiermonnikoog, the preference for

sheep-grazed areas was tested without these confounding factors. Fig. 5 shows the development of the vegetation height in the sheep-grazed and the ungrazed area. Especially in the middle of May, there is a rapid increase in biomass in the ungrazed area. The sheep kept their vegetation short at a height of 4 cm. Two captive geese were given a choice between the grazed and ungrazed vegetation. In all cases, the geese fed most of their time on the sheep-grazed area, showing again a clear preference for short vegetation (Fig. 6).

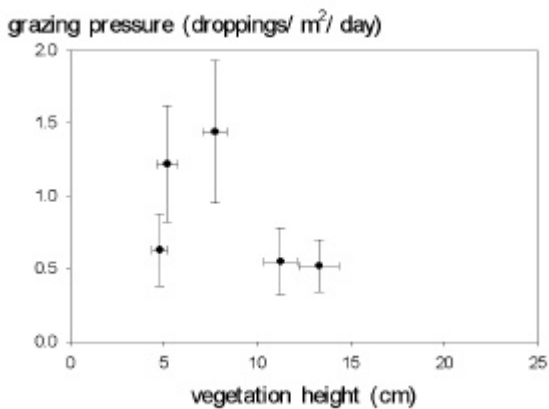
Can geese improve their future feeding sites by their own grazing? Wild geese in the reserve Zeeburg were offered plots excluded from goose grazing for various periods. The plots differed in vegetation height due to this manipulation. The geese showed a preference for the plots, which had been excluded one and two weeks (Fig. 7). The treatment without enclosure was not preferred, probably because it resembled the heavily grazed environment. The plots, which had been excluded 4 and 6 weeks, where the vegetation had reached a height of more than 10 centimetres, had a low number of goose droppings. Geese clearly rejected the plots with high standing crop.

Discussion

Grazing increases the utilisation by geese

Areas grazed by livestock are preferred over ungrazed vegetation. This was true for salt marshes and agricultural fields. On the salt marshes of the Hamburger Hallig in Schleswig Holstein, Germany, Stock & Hofeditz (2002) also found a lower grazing pressure of Barnacle Geese after the cessation of sheep grazing. This effect was more profound in autumn than in spring. Our study along the Groningen coast was also in autumn, but in the enclosure studies in the Leybucht and on

Figure 7. On agricultural fields, the functional response of Brent geese is an optimum curve. The highest grazing pressure is found in vegetation plots which have been excluded for 1 or 2 weeks. Vegetation plots which have been excluded for zero, 4 and 6 weeks are less intensively used. The rejection of the plots with the tallest vegetation has important consequences for habitat selection in May (see text).



Schiermonnikoog we found positive correlations between goose usage and cattle grazing in spring. On agricultural grasslands at Ameland and Schiermonnikoog, sheep-grazed areas are preferred by Brent geese in the month of May. All fields in our study are intensively used by farmers and are heavily fertilised. Ungrazed areas have higher biomass and taller vegetation, but there is no difference in species composition or the amount of dead material. In spring, grass production increases with date, but sheep can keep the vegetation short, at a vegetation height which is more suitable for the geese. The effect was detected only in the month of May, when Brent geese are still present and grass production is high.

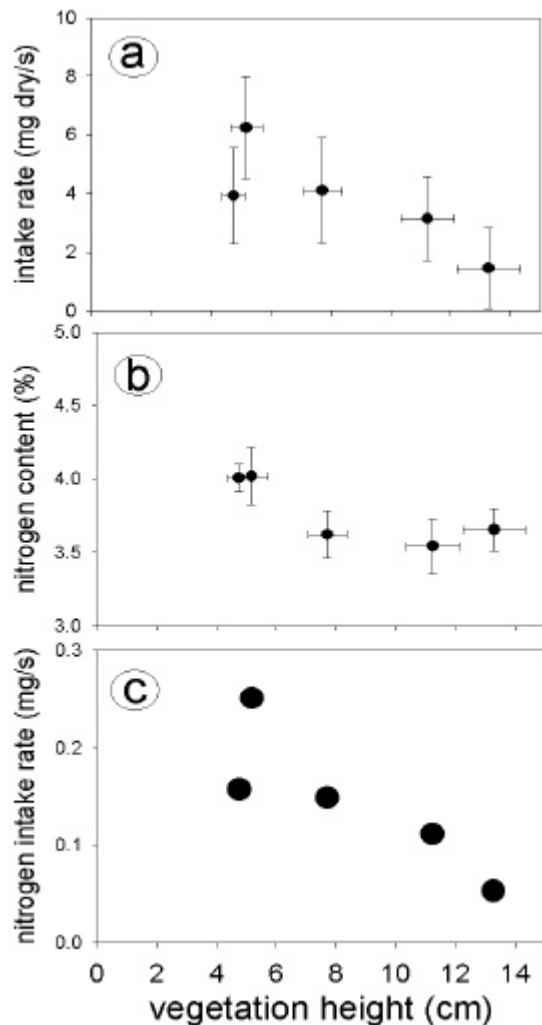
Livestock grazing affects the vegetation composition, the structure of the vegetation and the nutrient content. On the high salt marsh, without livestock, first *Aster tripolium* and *Artemisia maritima* and later *Elymus athericus* take over (Kiehl et al., 2000). On the low

marsh the spread of *Atriplex portulacoides* makes the area less attractive (Jensen, 1985; Roozen & Westhoff; 1985, Bakker & Bos, 2002). These species are less palatable for geese and make a taller vegetation structure. Van der Wal (2000b) tested the effect of an increasing cover of *Atriplex portulacoides* experimentally on Schiermonnikoog during spring. He manipulated the amount of *Atriplex* and found more geese grazing when *Atriplex* was removed and fewer geese when *Atriplex* bushes were planted. Taller vegetation makes walking more difficult and predator detection will be hampered as well. Usually, nutrient content is higher in grazed vegetation (Drent & Prins, 1987 and Fig. 8b). The age of the leaves is younger and there is less dead material. The rate of foraging can thus be enhanced as the density of suitable bites is higher in grazed vegetation.

Geese select for the highest intake rate of nutrients (Riddington et al., 1997). Both the nutrient content of the food and the instantaneous intake rate are important. Instantaneous intake rate is also dependent on vegetation height. Intake rate increases with grass height in a range of 2 to 6 cm (Hassal et al., 2001). However, our results show a negative relation between intake rate and vegetation height when height increases from 5 to 14 cm (Fig. 8). The intake rate of nutrients as a function of biomass has a maximum for Brent geese when vegetation height ranges between 5 and 6 cm. Taller vegetation should be abandoned in favour of this optimal height. A similar functional response has been found in wigeon (Durant, 2001) and barnacle geese (Van der Wal et al., 1998) although the optimum is probably depending on the size of the animal or more specific the size of the bill (Durant, 2001).

Not only livestock grazing, but also goose grazing can keep the vegetation in a preferred stage. The

Figure 8. The effect of vegetation height on intake rate (a), nitrogen content (b) and nitrogen intake rate (c). Vegetation height was manipulated by varying the time period over which the vegetation was excluded from goose grazing. Intake rate was measured with captive geese feeding on a vegetation turf. Each data point consists of 7 replicas.



experiment on Texel showed that the vegetation height in the goose-grazed area stayed only 4.7 ± 0.38 cm ($n=7$), while the excluded vegetation reached a height of 13.3 ± 1.05 cm ($n=7$) in the same period. Stahl (2001) showed that previous goose grazing by barnacle geese may facilitate later use by brent geese on the saltmarsh. Undisturbed grazing by large goose flocks seems a prerequisite

for this process. In the nature reserve Zeeburg on Texel, where we did our experiment, geese are left undisturbed. In our year of study on Ameland geese were disturbed by farmers, which probably increased their dependence on sheep-grazed parcels. A recent increase of grazing pressure of brent geese in the agricultural fields of Schiermonnikoog coincided with a local ban of disturbance.

In order to keep the vegetation short in these highly productive grasslands in May, the geese abandon some of the grazed parcels and concentrate in fewer areas to compensate for the increase in grass growth rate (Spaans & Postma, 2001). In the end of May, the brent geese will migrate to their breeding grounds and leave the vegetation ungrazed. Without other herbivores or farmers mowing the fields, the geese don't manage to keep the vegetation in an optimal stage. For salt marsh vegetation this was shown in the present study by a comparison of different sites with and without livestock grazing. Van der Wal et al (2000a) showed the same effect in a time series of three areas on Schiermonnikoog.

In our study we did not find any evidence, that there is a difference in this trend between island and mainland salt marshes. Mainland salt marshes are more productive due to the thicker clay layer. But also on the saltmarsh of Schiermonnikoog, grazing pressure of geese declined when the vegetation was no longer grazed by cattle during the summer.

Is there an effect of changes in management on the brent goose population?

Since 1970, almost all goose populations in the world have increased enormously (Madsen et al., 1999). A reduction in the hunting pressure and an increase in the availability of nitrogen rich vegetation, due to the use of artificial fertiliser and

acid rain, were the main factors which made this increase possible (Ebbinge, 1985, 1991; Van Eerden et al., 1996; Abraham et al., 1997). The population of brent geese reached a maximum size of 314,000 birds in 1991/1992. However, since then the population has decreased. In the Netherlands, the maximum number of brent geese counted decreased from 113,599 in May 1991 (Koffijberg et al., 1997) to 51,000 in May 1999 (SOVON Ganzen- en Zwanenwerkgroep, 2000). The estimate for the world population of dark-bellied brent geese is now 181,000 birds, 58% of the recent population maximum (SOVON Ganzen- en Zwanenwerkgroep, 2000).

This paper and Stock & Hofeditz (2002) show clearly that goose-grazing pressure on salt marshes declined after cessation of grazing by livestock. In 1990, livestock grazed 75% of all salt marshes in the Wadden Sea. In 1998, this had decreased to 56% (de Jong et al., 1999). However, a direct link between the declining brent goose population and the change in salt-marsh management cannot be substantiated.

Ganter et al. (1997) examined fitness parameters of individually marked brent geese after salt marsh loss. They found a slight reduction in breeding success and survival of displaced birds compared with a control group, but these results were not significant. They argue that there were enough alternative feeding areas available for the displaced geese when the salt marsh was lost due to embankment.

An effect of habitat loss on population numbers depends on the presence of alternative feeding areas. These alternative feeding areas could be seagrass beds, other salt marshes and agricultural fields.

Seagrass beds in the Wadden Sea are traditional habitat. The sudden reduction of this habitat in the 1930s, played an important role in an earlier population crash of brent geese (Madsen

et al., 1999). The area covered with seagrass is still declining in the Wadden Sea (Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, 1998) and seagrass in this area is nowadays hardly used by brent geese in spring. It seems no alternative feeding area for displaced individuals.

Natural salt marshes, not grazed by livestock, can accommodate brent geese in their early succession stage (Olf et al., 1997). Van der Wal (2000b) showed that brent goose grazing on Schiermonnikoog is highest on salt marshes, which are about 15 years old. When these marshes had not been grazed by wild hares, he showed with enclosure studies that a vegetation type with *Atriplex portulacoides* would develop earlier and this would shorten the window of goose usage. Salt marsh development is still occurring on Schiermonnikoog in The Netherlands, and on Trischen, in the Leybucht and along the coast of Schleswig-Holstein in Germany. The grazing pressure by brent geese on the salt marshes in the Wadden Sea varies. For the salt marshes on Terschelling and Schiermonnikoog in The Netherlands and Langli in Denmark, the present goose numbers seem close to the maximum (Ebbinge, 1992, Madsen et al., 1999). Brent geese use man-made mainland salt marshes less heavily (Prop, 1997). These areas could sustain higher number of geese, if there are no constraints, which cause the lower brent goose grazing pressure. In general, the main-land salt marshes are more productive, which can make it more difficult to keep the vegetation short. Also the timing of growth and the phenology of the nutrient content of the vegetation may be different. The number of geese present in the Wadden Sea are not only based on the local food availability (Prop & Deerenberg, 1991) but is also timed with food availability in other spring staging sites and the breeding grounds for these migrating species.

There are still many agricultural fields in the Wadden Sea area, which are potential feeding areas for brent geese. The geese depend on short vegetation. Undisturbed sites with a heavy goose grazing pressure or sheep-grazed fields can accommodate extra geese, but this will affect the yield of the farmers and continue the conflict between farmers and nature conservation unless appropriate compensation schemes are in place.

Prop & Black (1999) raised another important issue. They found that barnacle geese feeding on agricultural fields became fat, but lacked protein reserves essential for successful breeding. Spaans & Postma (2001), however, did not find any difference in breeding success between geese feeding on agricultural land compared to geese feeding on natural marshes. These differences are difficult to detect. The breeding success of brent geese is highly variable and only one out of three years is a successful breeding year. There is also a possibility that geese after feeding on agricultural grassland, supplement their diet with feeding in other habitats both within the Wadden Sea and during their next stop in the White Sea. Studies on habitat utilisation of individual marked geese throughout the flyway in relation with fattening rate and reproductive

success are needed to link changes in habitat with population dynamics.

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References

- Abraham KF, Jefferies RL, Rockwell RF and MacInnes CD (1997) Why are there so many white geese in North America? In: Ratti, J (ed.). Proc. 7th International waterfowl symposium, Memphis Tennessee.
- Andresen H, Bakker JP, Brongers M, Heydemann B and Irmeler U (1990) Long-term changes of salt marsh communities by cattle grazing. *Vegetatio* 89: 137-148.
- Bakker JP, Bos D and De Vries Y (2002) To graze or not to graze, that is the question. In: Wolff WJ, Essink, K, Kellermann, A and van Leeuwe MA, (eds) Proc. 10th International Scientific Wadden Sea Symposium Groningen. Ministry of Agriculture, Nature Management and Fisheries, The Hague
- Behre KE (1985) Die ursprüngliche Vegetation in den Deutschen Marschgebieten und deren Veränderung durch prähistorische Besiedlung und Meeresspiegelbewegungen. *Verhandlungen der Gesellschaft für Ökologie* 13: 85-95
- Boudewijn T (1984) The role of digestibility in the selection of spring feeding sites by Brent Geese. *Wildfowl* 35: 97-105
- de Jong F, Bakker JF, van Berkel CJM, Dankers NMJA, Dahl K, Gätje C, Marencic H and Potel P (1999) Wadden Sea Quality Status Report. Wadden Sea Ecosystem No. 9; Wilhelmshaven Germany:

- Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Quality Status Report Group.
- Drent RH and Prins, HTT (1987) The herbivore as a prisoner of its food supply. In: van Andel J, Bakker JP and Snaydon RW (eds) *Disturbance in Grasslands*: 131-148. Dr. W. Junk, Dordrecht.
- Durant D (2001) Patterns and processes underlying the differences in the use of swards by grazing Anatidae. Ph.D. thesis Université de la Rochelle.
- Ebbinge BS (1985) Factors determining the population size of arctic-breeding geese wintering in western Europe. *Ardea* 73: 121-128.
- Ebbinge BS (1991) The impact of hunting on mortality rates and spatial distribution of geese wintering in the Western Palearctic. *Ardea* 79:197-210.
- Ebbinge BS (1992) Regulation of numbers of Dark-bellied Brent Geese *Branta bernicla bernicla* on spring staging sites. *Ardea* 80: 203-228.
- Ganter B, Prokosch P and Ebbinge B (1997) Effect of salt marsh loss on the dispersal and fitness parameters of dark-bellied brent geese. *Aquatic Conserv.: Mar. Freshw. Ecosyst.* 7: 141-151.
- Hassall M, Riddington R and Helden A (2001) Foraging behaviour of brent geese, *Branta b. bernicla*, on grasslands: effects of sward length and nitrogen content. *Oecologia* 127: 97-104.
- Jensen A (1985) The effect of cattle and sheep grazing on salt-marsh vegetation at Skallingen, Denmark. *Vegetatio* 60: 37-48.
- Kiehl K, Schröder H, Bredemeier B & Wiggershaus A (2000) Der Einfluss von Extensivierung und Beweidungsaufgabe auf Artenzusammensetzung und Struktur der Vegetation. In: Stock Mand Kiehl K (eds) *Die Salzwiesen der Hamburger Hallig*: 34-42. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning.
- Koffijberg K, Voslamber B and van Winden E (1997) Ganzen en zwanen in Nederland: overzicht van pleisterplaatsen in de periode 1985-94. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
- Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer (1998) *Umweltatlas Wattenmeer*.
- Madsen J, Cracknell G and Fox AD (eds.) (1999) *Goose populations of the western Palearctic. A review of status and distribution*. Wetlands International Publ. No. 48. Wetlands International, Wageningen, The Netherlands. National Environmental Research Institute, Rönne, Denmark.
- Oloff H, de Leeuw J, Bakker JP, Platerink RJ, van Wijnen HJ and de Munck W (1997) Vegetation succession and herbivory in a salt marsh: Changes induced by sea level rise and silt deposition along an elevational gradient. *Journal of Ecology* 85: 799-814
- Owen M (1971) The selection of feeding site by white-fronted geese at the New grounds, Slimbridge. *J. Appl. Ecol.* 9: 385-398.
- Prins HHT and Ydenberg RC (1985): Vegetation growth and a seasonal habitat shift of the barnacle goose (*Branta leucopsis*). *Oecologia* 66: 122-125
- Prop J (1997) Management and carrying capacity of salt marshes. In: van Nugteren J (ed.) *Dark-bellied Brent Goose Branta bernicla bernicla*. Flyway management plan. National Reference Centre for Nature Management, Wageningen.
- Prop J and Black JM (1998) Food intake, body reserves and reproductive success of barnacle geese *Branta leucopsis* staging in different habitats. In: Mehlum F, Black JM and Madsen J (eds.) *Research on arctic geese*. Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 23-26 September 1997. Norsk Polarinstitut Skrifter 200: 175-194.
- Prop J and Deerenberg C (1991) Spring staging in brent geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* 87: 19-28.
- Riddington R, Hassall M and Lane SJ (1997) The selection of grass swards by brent geese *Branta b. bernicla*: Interactions between food quality and quantity. *Biological Conservation* 81: 153-160
- Roosen AJM and Westhoff V (1985) A study on long-term salt marsh succession using permanent plots. *Vegetatio* 61: 23-32
- Rösner H-U and Stock M (1994) Numbers, recent changes, seasonal development and spatial distribution of Dark-bellied Brent Geese in Schleswig-Holstein. In: van Nugteren, J. (ed.) *Brent geese in the Wadden Sea*: 69-85. Dutch Society for the Preservation of the Wadden Sea, Harlingen
- SOVON Ganzen- en Zwanenwerkgroep (2000) *Ganzen- en zwanentellingen in Nederland in 1998/99*. SOVON monitoringsrapport 2000/03, RIZA-rapport BM99.15, Expertisecentrum LNV coproductie 33. SOVON

- Vogelonderzoek Nederland, Beek-Ubbergen.
- Spaans B and Postma P (2001) Inland pastures are an appropriate alternative for salt-marshes as a feeding area for spring-fattening Dark-bellied Brent Geese *Branta bernicla*. *Ardea* 89: 427-440
- Stahl J (2001) Limits to the co-occurrence of avian herbivores. How geese share scarce resources. Ph. D. thesis, University of Groningen.
- Stock M and Hofeditz F (2002) Impact of sheep grazing on habitat utilisation of Barnacle Geese (*Branta leucopsis*) on salt marshes – implications for management. In: Wolff, WJ, Essink K, Kellermann A, and van Leeuwe MA (eds.) Proceedings 10th International Scientific Wadden Sea Symposium, Groningen. Ministry of Agriculture, Nature Management and Fisheries, The Hague.
- van der Wal R, van de Koppel J and Sagel M (1998) On the relation between herbivore foraging efficiency and plant standing crop: An experiment with barnacle geese. *Oikos* 82: 123-130.
- van der Wal R, van Lieshout S, Bos D and Drent RH (2000a) Are spring staging brent geese evicted by vegetation succession? *Ecography* 23: 60-69
- van der Wal R, van Wijnen H, van Wieren S, Beucher O and Bos D (2000b) On facilitation between herbivores: How Brent Geese profit from brown hares. *Ecology* 81: 969-980
- van Eerden MR (1990): The solution of goose damage problems in The Netherlands, with special reference to compensation schemes. *Ibis* 132: 253-261
- van Eerden MR, Zijlstra M, van Roomen M and Timmerman A (1996) The response of Anatidae to changes in agricultural practice: long term shifts in the carrying capacity of wintering waterfowl. *Gibier Faune Sauvage, Game Wildl.* 13: 681-706.
- van Wijnen H and Bakker JP (1997) Nitrogen accumulation and plant species replacement in three salt marsh systems in the Wadden Sea. *Journal of Coastal Conservation* : 19-26
- Vickery JA, Sutherland WJ and Lane SJ (1994) The management of grass pastures for brent geese. *Journal of Applied Ecology* 31: 282-290

