Abstract

To Arctic breeding geese, the salt marshes of the international Wadden Sea are important spring staging areas. Many of these marshes have always been grazed with livestock (mainly cattle and sheep). To evaluate the influence of livestock grazing on composition and structure of salt-marsh communities and its consequences for habitat use by geese, a total of 17 pairs of grazed and ungrazed marshes were visited both in April and May 1999, and the accumulated grazing pressure by geese was estimated using dropping counts. We also collected such data for hare. Observed grazing pressure was related to management status and to relevant vegetation parameters.

The intensity of livestock grazing influences the vegetation on the marsh. Salt marshes that are not grazed by livestock are characterised by stands with a taller canopy, a lower cover of grasses palatable for geese, and a higher cover of plants that are unpalatable.

Overall goose dropping densities are significantly lower in ungrazed marshes compared to marshes grazed by livestock. Some ungrazed marshes had comparatively high goose grazing pressure, and these were all natural marshes on a sandy soil, or artificial mainland marshes with a recent history of intensive livestock-grazing. Goose grazing is associated with a short canopy. The plant communities with short canopy, dominated by *Agrostis stolonifera*, *Festuca rubra* and *Puccinellia maritima*, respectively, together account for 85% of all goose droppings in our data.

The sites that were not visited by geese differed very little from those that were visited, in the parameters we measured. This might indicate that there was no shortage of available habitat for spring staging geese in the Wadden Sea, in the study period.
**Introduction**

*Goose grazing, natural succession and salt-marsh management*

Salt marshes in the international Wadden Sea serve as feeding grounds for spring staging geese, preparing for migration to breeding areas in the Arctic. Barnacle Geese *Branta leucopsis* utilise the marshes mainly from February to April, with an increasing number present during May (Stock & Hofeditz 2000, Engelmoer et al. 2001), while Brent Geese *Branta b. bernicla* are mainly present from March until the end of May (Ebbing et al. 1999). Feeding conditions during this period are crucial for future reproductive success, as reproductive output of geese is strongly related to the amount of fat and protein reserves accumulated during spring (de Boer & Drent 1989, Ebbinge 1989, Prop & Black 1997). To a large extent, these feeding conditions will be determined by the vegetation composition and canopy height of the marsh, because plant species and plant parts differ in their palatability for geese. Vegetation composition is strongly related to the management of salt marshes, for example grazing with livestock (Beaftink 1977, Jensen 1985, Bakker 1989, Esselink et al. 2000, Gettner et al. 2000).

Under ungrazed conditions, salt-marsh vegetation changes due to natural succession (Jensen 1985, Roozen & Westhoff 1985, Adam 1990, Westhoff & van Oosten 1991, Bakker et al. 1993, Kiehl et al. 2000b). Continual input of nitrogen by sedimentation is put forward as the major force driving natural succession (van Wijnen & Bakker 1997). Increasing availability of nitrogen favours the growth of the later successional tall grass *Elymus athericus* at high marsh elevation and the tall forb *Atriplex portulacoides* at the lower marsh (Olff et al. 1997, van Wijnen & Bakker 1997). Both plant species are unpalatable to geese and outcompete the preferred forage species *Plantago maritima, Triglochin maritima, Puccinellia maritima* and *Festuca rubra* (Prop & Deerenberg 1991, van der Wal et al. 2000b). Subsequently, goose grazing decreases when marshes become too productive (van de Koppel et al. 1996). Grazing by hare *Lepus europaeus* has been shown to affect vegetation succession (van der Wal et al. 2000b) to a certain extent. Hare utilise the salt-marsh habitat year-round, and retard natural succession by grazing on the woody stems of *Artemisia maritima* and *A. portulacoides* in winter. Hare thus temporarily provide more suitable habitat for geese (van der Wal et al. 2000b). On the natural, livestock-ungrazed salt marsh of Schiermonnikoog it has nonetheless been observed that densities of both geese and hare decline as natural succession proceeds (van de Koppel et al. 1996).

Most of the salt marshes in the Wadden Sea have traditionally been grazed by livestock (Esselink 2000). Cattle and sheep grazing prevents accumulation of biomass. They create a short canopy and high cover of plant species that are palatable for geese and hare (Bakker et al. 1993, Olff et al. 1997), thus positively affecting the feeding conditions for geese (Aerts et al. 1996). Depending on the intensity of grazing a homogeneous sward results, dominated by few species, or a diverse vegetation pattern with alternating patches of short and tall swards (Dijkema 1983, Aerts et al. 1996, Berg et al. 1997, Kiehl 1997). In the past decade however, there has been a reduction in agricultural use along the coast of Niedersachsen, Germany (Potel & Südbeck 1994) and live-
stock grazing was stopped at 42% of the mainland marshes in Schleswig-Holstein, Germany (Stock & Kiehl 2000), as a result of policies promoting natural development of the marsh ecosystem (Kempf et al. 1987, Stock et al. 1997, Stock & Kiehl 2000). In the Netherlands and Denmark about 40% and 10% of the salt marsh area is livestock-ungrazed, respectively (Kempf et al. 1987, de Jong et al. 1999).

**Differences between marsh types**

The rate of vegetation succession, and possibly the final stages of the succession, differ between artificial mainland marshes and the natural marshes on the barrier islands of the Wadden Sea, as they differ in soil composition. The barrier marshes, or barrier-connected marshes according to de Jong et al. (1999), have a relatively thin layer of clay on top of a sandy sub-soil. In contrast, the artificial mainland marshes with sedimentation fields feature a thick layer of clay. This has important consequences for the availability of nitrogen and drainage. Marsh type is thus an important source of variation for vegetation composition and maybe also for the feeding conditions of small vertebrate herbivores, such as geese and hare.

**Objective**

In this study we will evaluate the importance of livestock grazing in explaining variability in goose utilisation relative to other sources of variation. Our basic hypothesis is that livestock grazing affects the habitat choice of Brent and Barnacle Geese. Evidence to support this hypothesis has been derived from local studies (Aerts et al. 1996, Stock & Hofeditz 2000), but the validity has not been generalised. We expect food availability to be important for the distribution of geese and we will indirectly assess food availability using parameters of vegetation composition, canopy height and tiller density. Other sources of variation that will be examined are the availability of freshwater, disturbance, the presence of hare and marsh dimensions.

**Methods**

We established 63 transects, divided over 38 study sites (see Appendix 7.1), based on the following criteria: The marsh in which the transect was placed, should have a stable and clearly defined management for at least six consecutive years. Only marshes with sufficiently large area (> 5 ha), such that a flock of geese could land without inhibition, were included. The sites were distributed over the entire Danish (n = 11), German (n = 17) and Dutch (n = 10) Wadden Sea. Twenty-two sites harboured transects in marshes with at least two different grazing regimes. Seventeen sites with paired transects were visited twice, once in April and once in May 1999, and so were some of the unpaired transects (Appendix 1). The remainder was only visited once. Several transects were known to have had a relatively recent change in management from
intensively grazed to ungrazed (< 10 years before), and these transects were treated separately. Management was subdivided in 'long term ungrazed' (> 10 years), 'short-term ungrazed' (6 - 10 years), 'extensively grazed' (≤ 4.5 sheep ha⁻¹ or > 1 cow ha⁻¹) and 'intensively grazed'. Grazed marshes were classified as being sheep- or cattle grazed. The transects on barrier marshes in our study are, with one exception, only visited by Brent Geese, while most transects on mainland marshes are utilised by Brent and Barnacle Geese.

For each management regime at each site, 1 transect was placed perpendicular to the seawall and the coastline. At fixed intervals, small plots of 4 m² were located. Twenty replicate plots per transect were sampled, equally divided over the length of the transect. The accumulated number of goose and hare droppings in these plots were counted. Goose dropping densities are a good measure of grazing intensity, as geese defecate very regularly (Owen 1971). Dropping densities and grazing pressure by hare are also correlated (Langbein et al. 1999). We did not discriminate between droppings of Brent or Barnacle Geese. Hare droppings were distinguished from rabbit faeces by shape and size. Transects from which results were likely to have been affected by flood during the preceding 14 days, which was assessed using tide tables and observations in the field, are not included in our dataset. The vegetation at each plot was classified to a plant community using a key that was based upon the salt-marsh typology from de Jong et al. (1998, see Appendix 7.2). Nomenclature of species follows van der Meijden (1990). Vegetation composition was described using five parameters: (1) percentual cover of palatable grasses (Lolium perenne, Poa spp., A. stolonifera, Puccinellia maritima and F. rubra), (2) percentual cover of tall plant species (E. athericus, A. portulacoides, A. maritima, Spartina anglica and standing dead remnants of Aster tripolium), (3) joint abundance of Plantago maritima and T. maritima (absent, present and abundant (> 3% cover)) and (4) canopy height. Canopy height was measured five times per plot to the nearest 0.5 cm using a polystyrene disc (20 cm Ø, 24 g), sliding along a graduated stick, that was randomly dropped on the vegetation. Finally, we measured (5) tiller-density in the F. rubra and Puccinellia maritima communities using a quadrat of 25 cm². A tiller was defined as a group of leaves with one meristem, often surrounded by senescing leaves. Additional plots were randomly placed in F. rubra and Puccinellia maritima communities at each transect (when present), and sampled for the parameters mentioned above, to arrive at a minimum sample size of five for these communities. For each transect, an index of disturbance was assessed covering three classes. This index was based on the distance to nearest roads, towns and recreational pressure (see Appendix 7.1). Distance to a fresh water source (km) was assessed in the field, aided by a topographical map.

Statistical analyses

Observed dropping densities were related to factors at two levels of explanation and two levels of aggregation. On the one hand, we averaged the dropping density and vegetation parameters over the 20 plots per transect and related them to livestock grazing regime, salt-marsh type (mainland versus barrier marsh) and month of sampling.
as fixed factors in a General Linear Model (GLM). In the analysis of dropping densities, we limited the selection of transects to those sites where two contrasting management regimes were sampled in either month. Transect length was included as a covariate, while site and the interaction between month of sampling and grazing regime were included as factors. Dropping density was also directly related to vegetation parameters (vegetation composition, canopy height, tiller density and combined abundance of *Plantago maritima* and *T. maritima*) using multiple regression. At a lower level of aggregation, all data were pooled per plant community and per transect, and differences between plant communities were tested. The additional plots that we had sampled were included in these analyses. Within the plant communities dominated by *Puccinellia maritima* and *F. rubra*, we also studied the effect of livestock grazing regime, salt-marsh type and month of sampling in a General Linear Model. For the analyses of dropping densities at the plant community level, only those sites were selected where geese or hare had been observed in any of the months.

The relative frequency of plant communities per transect (%) was calculated as the proportion of observations of each community on the total of 20 plots sampled. Canopy height and dropping density at the plot level were related to distance from the seawall for each grazing regime separately, while correcting for site, using General Linear Modelling. Arcsine and log-transformations were used for percentage values and canopy height respectively (Zar 1996). Non-parametric tests were employed where appropriate.

**Results**

**Effects of livestock grazing on marsh vegetation**

The vegetation composition was significantly related to livestock grazing on mainland marshes (Figure 7.1), but these differences were less pronounced on barrier marshes. Incidence of communities characterised or dominated by short grasses (*Puccinellia maritima*, *F. rubra*, *A. stolonifera* and *Juncus gerardi*) was higher at intensively grazed marshes and decreased with reduced stocking rates (GLM factor grazing, $F_{3,58} = 23.9$, $P < 0.001$). The incidence of communities dominated by tall unpalatable plants (*E. athericus*, *A. portulacoides* and *A. maritima*) increased with lower stocking rates of livestock (GLM factor grazing, $F_{3,58} = 19.7$, $P < 0.001$).

The vegetation parameters canopy height, cover of edible grasses, cover of structural elements and tiller density were strongly and significantly correlated to each other at all levels of aggregation (Pearson's correlation, all $P < 0.01$, Table 7.1). For this reason only the data for canopy height will further be presented. The canopy height of marsh vegetation strongly differed between communities (Figure 7.2A, K-W test, $\chi^2 = 75.4$, $P < 0.001$). Communities dominated by *Puccinellia maritima*, *F. rubra* and *A. stolonifera* had significantly lower canopy than communities dominated by *E. athericus*, *A. portulacoides* and *A. maritima*. But even within plant communities, a relationship was found between livestock grazing and relevant habitat parameters for
small herbivores. Under ungrazed circumstances, the communities dominated by *Puccinellia maritima* and *F. rubra* on mainland marshes, had taller canopy (Figure 7.3A, GLM, F$_{3,84} = 21.3$, $P < 0.001$). Barrier marshes had a lower canopy height for a given livestock grazing regime (Figure 7.3A, GLM, F$_{1,84} = 5.4$, $P = 0.022$). The index of combined abundance of *Plantago maritima* and *T. maritima* was higher for barrier marshes (K-W test $\chi^2 = 9.3$, $P < 0.005$) than for mainland marshes. We were not able to detect differences in the vegetation parameters studied for the two species of livestock (sheep or cattle). Canopy height significantly increased with distance from the seawall in 33% of the marshes (GLM interaction of distance and site significant), while in 54% there was no relationship. These proportions did not differ significantly between grazing regimes (contingency test, $\chi^2 = 10.3$, n.s.).

**Figure 7.1** Incidence of communities on salt marshes, grouped by height of the canopy, in relation to livestock grazing regime and marsh type. The group with short canopy includes the communities of *Puccinellia maritima, Limonium vulgare, J. gerardi, A. stolonifera* and *F. rubra*. The group with tall canopy includes the communities of *E. athericus, A. portulacoides* and *A. maritima*. See Appendix 2 for a key to identification of the communities in the field. Grazing regimes that do not share the same letter within a class of communities are significantly different from each other ($P < 0.05$).

**Table 7.1** Pearson correlation coefficients for vegetation parameters at the community level. All correlations are significant at the 0.01 level.

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<td>Cover of tall plants (TP)</td>
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<td>Cover of palatable grasses (PG)</td>
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<td>Canopy height (CH)</td>
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<td>Tiller density (TD)</td>
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Goose grazing

Grazing pressure by geese at the transect level increased significantly with the intensity of livestock grazing regime (Figure 7.4, GLM, $F_{3,60} = 5.7$, $P = 0.002$), while transect length, month of sampling, marsh type nor the interaction between grazing regime and month of sampling significantly explained any variation. Nonetheless, when testing for the effect of marsh type separately within ungrazed transects, we found that long-term ungrazed transects on the mainland had much lower dropping densities than long-term ungrazed transects on barrier marshes (0.3 ± 0.2 versus 5.2 ± 0.7; T-test, $t = 2.7$, $P = 0.03$). In April, goose dropping densities at the transect level did not differ between grazing regimes (GLM, $F_{3,21} = 1.7$, n.s.), while in May, livestock grazed marshes had significantly higher dropping densities than ungrazed marshes (GLM $F_{3,19} = 9.2$, $P = 0.001$). This finding still holds when the dataset is further limited to the 17 sites with paired transects that were visited both periods or to

Figure 7.2  A) Canopy height of salt marsh vegetation for the six plant communities that were most frequent in the dataset. Data refer to all transects. B) Grazing pressure of geese per plant community. Only data for sites that were visited by geese are used. Bars that do not share the same letter are significantly different from each other ($P < 0.05$).
the sites (n = 14) that are known to be visited by both species of geese. There were no significant differences in dropping densities by geese between transects that were grazed by cattle or sheep.

A classification into plant communities significantly explained variation in goose grazing pressure (Figure 7.2B, K-W test, \( \chi^2 = 38.1, P < 0.001 \)). The communities dominated by *Puccinellia maritima*, *F. rubra* and *A. stolonifera*, have higher utilisation by

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**Figure 7.3** The relation of livestock grazing regime and marsh type with A) canopy height, B) grazing pressure by geese and C) hare grazing pressure. Data represent the communities dominated by *Puccinellia maritima* and *F. rubra* for all sites that were visited by geese (A & B), respectively hare (C). Bars that do not share the same letter within a marsh type are significantly different (P < 0.05) from each other. Effects of marsh type were significant for all three parameters.
geese. These communities together account for 85% of all goose droppings in our data. Within plant communities, still some differences exist between levels of livestock grazing (Figure 7.3B). In the communities of *F. rubra* and *Puccinellia maritima*, the communities for which we tested these relationships, higher dropping densities were found with increased intensity of livestock grazing (GLM, $F_{3,85} = 3.6$, $P < 0.017$), with higher dropping densities at the barrier connected marshes (GLM, $F_{1,85} = 14.1$, $P < 0.001$) than at the mainland marshes.

Per transect, we summed the cover of all plant communities that are characterised by short canopy and grasses that are palatable for geese (the communities *Puccinellia maritima*, *Limonium vulgare*, *J. gerardi*, *A. stolonifera* and *F. rubra*, see Appendix 7.2 and Figure 7.1). This variable was positively related to goose dropping densities at the transect level (Figure 7.5, linear regression $R^2 = 0.1$, $P = 0.037$). Goose dropping densities at the transect level were negatively related to average canopy height ($F_{1,45} = 5.0$, $P = 0.029$) and positively related to the combined index of abundance of *Plantago maritima* or *T. maritima* ($F_{1,45} = 6.9$, $P = 0.012$). Within transects, dropping densities were negatively related to distance from the seawall in 27% of the marshes (GLM interaction of distance and site significant), but in 67% of the cases there was no relation. These proportions did not differ between grazing regimes (contingency test: $\chi^2 = 10.7$, n.s.). A visual inspection of dropping data in relation to distance from the seawall did not yield indications of a threshold level in any of the transects.

![Figure 7.4](image-url)

**Figure 7.4** Average goose grazing pressure at the transect level in relation to livestock grazing regime for all transects that were paired within the same site. Bars that do not share the same letter are significantly different from each other ($P < 0.05$).
Sites without signs of geese

Out of the 38 sites we visited, 11 sites (29%), had no goose droppings at all. This frequency did not differ significantly between island and mainland (contingency test: $\chi^2 = 3.2$, n.s.) nor between marsh type (contingency test: $\chi^2 = 1.1$, n.s.). Twenty-three percent of the transects were not visited by geese at all, and these were all positioned at the 11 sites mentioned above. The frequency of transects that were visited by geese was independent from livestock grazing regime (contingency test: $\chi^2 = 0.033$, n.s.). The height of the canopy is 3.1 cm higher ($F_{1,57} = 5.1, P = 0.027$) and tiller density is 35% lower on average (Figure 7.6, $F_{1,63} = 6.8, P = 0.01$) at these sites that are not visited by geese, after controlling for grazing regime (Figure 7.6, $F_{3,63} = 6.5, P = 0.001$). Mean grass cover, mean cover of tall plants, community composition, transect length and our indices of disturbance and freshwater availability, were not significantly different between sites that were visited by geese and sites that were not. The latter finding also held when only the sites with the highest dropping densities (>10 droppings.m$^{-2}$) were compared to sites that were not visited by geese.

Distribution of hare

Hare droppings were found in average densities that were much lower than those of geese. First of all, many more sites had no hare droppings at all (47%). These sites were found on barrier marshes as well as on mainland marshes with frequencies that did not differ significantly with marsh type (contingency test: $\chi^2 = 0.025$, n.s.). More than 40% of the transects were without hare droppings, independent from livestock
grazing regime (contingency test: $\chi^2 = 0.043$, n.s.). Average dropping densities of hare were more than ten times higher at barrier marshes than at mainland marshes (Figure 7.7, K-W test, $\chi^2 = 4.11$, $P = 0.043$), and independent from month of sampling or livestock grazing regime. Hare grazing pressure was significantly higher in the communities of *F. rubra* and *Puccinellia maritima* at the mainland marsh, compared to the other plant communities there (K-W test, $\chi^2 = 12.6$, $P = 0.027$), but the magnitude of the differences was small (0.1 droppings.m$^{-2}$). Within the barrier marshes no significant differences in hare grazing pressure were found between plant communities (K-W test,
The communities of *F. rubra* and *Puccinellia maritima* have higher hare dropping densities at barrier marshes than at the mainland for a given grazing regime (Figure 7.3C, Mann Whitney U test, \( P < 0.001 \)), and ungrazed versions of these communities at the mainland have significantly more hare droppings than grazed ones (Figure 7.3C, K-W test, \( \chi^2 = 9.9, P = 0.019 \)). In the multiple regression analysis for hare dropping densities, only the combined index of abundance of *Plantago maritima* or *T. maritima* was selected as a significant variable at the transect level. We did not find a correlation between dropping densities of hare and geese, neither at the transect-, nor at the community level.

**Discussion**

**Livestock grazing and vegetation composition**

Natural vegetation succession and succession after cessation of livestock grazing on salt marshes often leads to the dominance of a few tall growing species (Jensen 1985, Andresen et al. 1990, Westhoff & van Oosten 1991, Aerts et al. 1996, Olff et al. 1997, van Wijnen & Bakker 1997, Bakker et al. 2002). Studies from barrier marshes show that succession will lead towards a vegetation dominated by *A. portulacoides* on the low marsh or *E. athericus* on the high salt marsh, while the latter may even invade the low marsh if sufficient nitrogen is available (van Wijnen & Bakker 1997, Bakker et al. 2002). These changes take place over periods of decades. Based on comparisons of vegetation maps over time in long-term ungrazed mainland marshes, Bakker et al. (2002) conclude that also on mainland marshes *E. athericus* can get dominant, though areas with low sedimentation rates or influence of fresh water are exceptions to that general pattern. Ungrazed transects in the present study, had a higher incidence of communities dominated by *A. portulacoides*, *A. maritima* or *E. athericus* (Figure 7.1) than grazed transects, but were nevertheless not entirely dominated by them. The six long-term ungrazed transects on the mainland were covered with tall communities for 75% on average against 28% on average for the barrier marshes. For some of these transects at barrier marshes (Griend, Rottumeroog, Schiermonnikoog, Terschelling), this may be due to the fact that the age of the marsh was low, and hence the productivity (Westhoff & van Oosten 1991, van der Wal et al. 2000a). The transects on Langli, however, appear to be an exceptional case. Langli has a well established old salt marsh that has not been cattle grazed for several decades, but which is nonetheless covered for 75% with communities dominated by short grasses. Langli is characterised by high densities of hare (Madsen pers. comm.) and is also inhabited by below-ground grazing water voles *Arvicola terrestris* (pers. obs., not mentioned by van Laar (1981)). The combined impact of these species of small herbivores in this case may be strong enough to halt the vegetation succession.

The effects of livestock grazing regime were also detectable in terms of significant differences in average canopy height, cover of palatable grasses and cover of tall plants on the transects. Even within the communities of *Puccinellia maritima* and *F. rubra*, we observed differences between grazing regimes (Figure 7.3A), with stands of the same community having a taller canopy at ungrazed marshes. The short-term ungrazed
marshes in our study are already different from their grazed counterparts in most of the vegetation parameters we studied (e.g. Figure 7.3A), although the plant communities were still the same. This is in agreement with data for the *Puccinellia maritima* community at the mainland marsh of the Hamburger Hallig (Kiehl et al. 2000b).

Kiehl et al. (1997, 2000a) argue that heterogeneity in abiotic conditions in space and time will prevent absolute dominance of a single community in the absence of livestock grazing. Waterlogging in undrained mainland marshes, for example, may render parts of the marsh unsuitable for *E. athericus* and *A. portulacoides*, and may be a reason why the results of studies on well-drained sandy barrier marshes only have limited value for mainland marshes. Results of Esselink (2000) indeed indicate that a lack of drainage, although in interaction with goose and cattle grazing, affects vegetation composition substantially at the brackish marshes of the Dollard. Some of the short-term livestock-ungrazed marshes along the coast of Schleswig-Holstein are subject to neglect of the drainage system since about ten years and have high goose grazing pressure. For the present, it remains an open question to what extent the geese may be able to maintain suitable habitat within these areas, in the absence of livestock.

**Goose grazing pressure**

Goose grazing pressure was found to be closely correlated to canopy height. This is consistent with observations by several authors (Summers & Critchley 1990, van de Koppel et al. 1996, van der Wal et al. 1998). Canopy height is a good indicator of forage quality, because short canopies refer to homogeneous swards with shortly grazed tillers and a favourable leaf/stem ratio. In spring, shortly grazed tillers are of high food quality. Low canopy height coincides with the plant communities characterised by the forage species of geese. We found a positive relation between the cover of communities with a short canopy and the dropping density at the transect level (Figure 7.5). Decreased intensity of livestock grazing leads to a decrease in the cover of communities with a short canopy (Figure 7.1) and lower grazing pressure by geese (Figure 7.4, Figure 7.5). The magnitude of this effect is considerable, as long-term ungrazed marshes have only 12% of the dropping density found at intensively grazed marshes. However, the effect of livestock grazing is not absolute, as the ungrazed marshes at Griend, Rottumeroog, Schiermonnikoog and Terschelling stand out with high goose dropping densities. The results for these barrier marshes are consistent with the course of vegetation succession at these young marshes with low productivity (van de Koppel et al. 1996). Van der Wal et al. (2000a) in fact showed that the ungrazed barrier marsh of Schiermonnikoog had an optimal vegetation composition, for small vertebrate herbivores, at an age between 20 and 50 years, and a decrease in goose numbers became apparent after succession had proceeded for longer periods of time. Goose dropping densities at the short-term ungrazed marshes on the mainland are intermediate to those on intensively grazed and ungrazed marshes in our study.

Besides canopy height, goose grazing pressure was also related to our index of combined abundance of *Plantago maritima* or *T. maritima*. This relationship may be
interpreted as a direct causal link, as Prop & Deerenberg (1991) have shown that the rate of accumulation of fat in spring staging Brent Geese is contingent upon the amount of these plant species in the diet. It might, however, also be interpreted as a pseudo-correlation, since *Plantago maritima* and *T. maritima* were found to be associated with barrier marshes. It is a general result, that the sandy soils of barrier marshes are a suitable habitat for *Plantago maritima* and *T. maritima* (Schaminée et al. 1998) and barrier marshes may have more benefits to Brent Geese such as lower experienced levels of predation and disturbance. Barnacle Geese do not occur in reasonable numbers on the barrier marshes that were included in this study, except for Schiermonnikoog.

In April, the differences in goose dropping densities between livestock grazing regimes were not statistically significant, while differences were apparent in the combined dataset and the data for May. Similarly, we found that in April three out of eleven of the short-term ungrazed transects had higher droppings than their grazed counterpart, while in May all short-term ungrazed transects had lower dropping densities than the grazed transect at the same site. This may be related to a difference in the presence of the two goose species, as in April the Barnacle Geese are still present together with the Brent Geese, and the two species differ in the selection of habitat to some extent (chapter 3). In May, the majority (> 75%) of the Barnacle Geese had departed to the breeding grounds. Other reasons might be that the differences between salt marshes with different livestock grazing regimes become more pronounced during the growing season, or that higher primary production in combination with lower numbers of geese allows the geese to be more selective in their choice of habitat.

We are aware of only a few published studies that have explicitly considered the effects of livestock grazing at salt marshes on feeding conditions of waterfowl. Detailed studies at the Hamburger Hallig and Westerhever so far give results that are not directly in line with our data. No, or only very small effects of cessation of grazing on goose dropping densities were detected here in spring, not even after 9 years without grazing. Over this period, the prevailing *Puccinellia maritima* community did not transform into another community, but only the canopy became taller. In autumn, the differences in goose dropping densities between grazed and short-term ungrazed parts of the marsh were, however, very pronounced (Stock & Hofeditz 2000). Work at the mainland marshes of the Leybucht and the Dollard, revealed a quick change in the vegetation composition after cessation of grazing, followed by an almost immediate strong reduction in grazing pressure by geese in autumn and spring (Aerts et al. 1996, Bergmann & Borbach-Jaene 2001). Cadwalladr (1972) demonstrated that grazing pressure by Wigeon *Anas penelope* was higher in sheep grazed swards, compared to swards that were left ungrazed. Results presented by Boudewijn & Ebbinge (1994) indicate that the ungrazed barrier marsh at Terschelling, in spite of a relatively young age (less than 50 years), had somewhat lower goose grazing pressure at the end of the 1970s than the grazed marsh. The positive effects of livestock on goose grazing conditions are a result of their long-term effect on the vegetation composition, as livestock is not yet present on the marshes in spring. Within a season, grazing by livestock may also affect goose feeding conditions positively by maintaining a short sward, thus preventing
a decrease in forage quality due to ageing of leaves (Holmes 1989, Riddington et al. 1997). Vickery et al. (1997) found a positive correlation between livestock grazing intensity and Brent Goose grazing pressure within a series of coastal swards that were all livestock grazed, but had very similar vegetation composition.

About 20% of the sites sampled did not show signs of goose grazing. These sites differed from those that were visited by geese in taller canopy height (by 3 cm) and in higher tiller density (35% on average). The small difference in canopy height is likely a result of the geese grazing themselves. The same may apply for the observed differences in tiller density (Bazely & Jefferies 1989), but the differences can also be an inherent to the sites themselves. The importance of this finding remains obscure, but within the selection of transects that were visited by geese tiller density was not found to be related to dropping density. Madsen et al. (1990) mention that the narrow Danish mainland marshes are less suitable for the Brent Geese than the wide mainland marshes along the coast of Schleswig-Holstein due to their dimensions (depth), but we did not find evidence for such a relationship in our sample. So, apart from the unexplained difference in tiller density between sites that were visited by geese and sites that were not, it appears that there was no shortage of available habitat for spring staging geese in the Wadden Sea, during our study period, as was also suggested by Madsen et al. (1990) and Rösner & Stock (1994).

**Hare grazing**

Presence and absence of hare on the barrier marshes is contingent upon the chances for colonisation, and can often directly be traced back to introduction by man. In total, twenty-three of the 42 islands in the chain of barrier-islands bordering the Wadden Sea, were reported to harbour hares (van Laar 1981). Hare dropping densities were not significantly related to livestock grazing regimes at the transect level, but marsh type significantly explained variation as there were a few barrier marshes with high densities of hare. Hare droppings correlated to the index of combined abundance of *Plantago maritima* or *T. maritima*. These plant species do occur in the diet of hare, though in low quantities (van der Wal et al. 2000b) and had higher abundance at barrier marshes. We hypothesise however, that barrier marshes are better suitable habitat for hare compared to mainland marshes for other reasons. Maybe flooding of the marsh has a disproportionate effect on hare mortality at mainland marshes in comparison to barrier marshes, due to difference in geomorphology. Elevated areas such as dunes, that provide refuge during flooding, may be reached directly on barrier marshes without a need to cross gullies or ditches. The seawall bordering mainland marshes can, however, often only be reached over land, via small dams. Above that, foxes are absent from the large majority (39) of Wadden Sea islands (van Laar 1981). There are no large differences in hare dropping densities between the mainland marshes of the Netherlands and Denmark, where hunting for hare is practised, and marshes along the German coast, where there is no hunting. Hunting of hare is prohibited in the barrier marshes we sampled.
At the community level, within the communities dominated by *Puccinellia maritima* and *F. rubra*, we observed higher hare dropping densities under ungrazed conditions at the mainland (Figure 7.3C). Hare live in the marsh year-round and have a different digestive strategy than geese. The diet of hare mainly consists of *F. rubra* (70%) in spring and summer, but in winter half of it is *A. portulacoide* (van der Wal *et al.* 2000b). Hare can digest food more effectively than geese and may thus accept forage of lower quality, which is often associated with higher biomass. We also suggest that the rate of intake for hare at low canopy heights is constrained more than the rate of intake for geese, due to a difference in morphology of the mouth. In a field experiment where a choice between patches with high and low biomass was offered, hare consistently selected the swards with higher canopy (Stahl 2001). Hare furthermore require cover for themselves and their young (Lange 1994) and such cover is more readily available under extensive or ungrazed conditions.

There is no correlation between dropping densities of geese and hare at the scales that we sampled. This suggests that the facilitative effect of hare grazing on geese, which was observed at the barrier marsh of Schiermonnikoog (van der Wal *et al.* 2000b), is not of overriding importance in the Wadden Sea as a whole, under current conditions.

**Consequences for management**

Arctic breeding geese are dependent on the Wadden Sea for fattening up during spring staging (Madsen *et al.* 1999). Natural succession on salt marshes leads to a declining suitability of the marsh as a feeding habitat for geese. To a certain extent the geese may be able to feed in alternative habitat, such as agricultural grassland, but this has financial and maybe ecological disadvantages. Salt-marsh habitat appears to be preferred by the geese over agricultural grassland (Ebbing 1992, Vickery *et al.* 1995), and a comparative study by Prop & Black (1997) suggests that staging in agricultural habitat may have negative consequences for the reproductive performance of the birds. Long-term data on individual reproductive success of Brent Geese presented by Spaans & Postma (2001) do not support the latter suggestion. Seagrass *Zostera* spp. is not an important food source in spring for Brent Geese (Ebbing *et al.* 1999), as its occurrence in the Wadden Sea is low since the 1930s (den Hartog 1987, Reise *et al.* 1989, Landesamt für den Nationalpark Schleswig Holsteinisches Wattenmeer 1998).

Coastal protection works along the Wadden Sea shore, reduce the natural dynamics within the marshes and prevent a landward expansion of the marsh area. However, as a result of enhanced sedimentation within brushwood groynes, the coastal protection measures also contribute to the creation of new and young salt marsh that is not dominated by unpalatable plants. New and young salt marsh also arises on barrier islands as part of the natural build-up and breakdown (de Jong *et al.* 1999). Since the cessation of grazing in large areas leads to an ageing of the vegetation, Esselink (2000) proposed to maintain sufficient area under livestock grazing, as the grazing by large herbivores maintains the marsh vegetation at a younger successional stage. So far we do not have indications that the species of livestock used for this purpose is of crucial importance.
Livestock grazing on salt marshes has been demonstrated to affect more than just the vegetation and the feeding conditions of waterfowl, but also the relative abundance of entomofauna (Andresen et al. 1990, Meyer et al. 1995) and breeding birds (Norris et al. 1997, Esselink 2000, Eskildsen et al. 2000). We support the view that nature management of salt marshes should not be guided by the needs of a single species, but rather aim at maintaining the characteristic communities of salt marshes. Establishing variation in the grazing intensity over large areas will lead to this objective. It is recommended to specify the ecological targets, to consider to what extent livestock grazing is a suitable tool for reaching these targets, and to monitor the developments in the field.

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Maarten Loonen maintains an overall view (photo J. Stahl).
### Appendix 7.1 An overview of the selected sites.

<table>
<thead>
<tr>
<th>No.</th>
<th>Location</th>
<th>Marsh-type</th>
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<th>Species of livestock</th>
<th>Goose dropping density (no. m⁻²)</th>
<th>Cover of communities with short canopy(%)</th>
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Appendix 7.2  Key to the classification of plant communities on saltmarshes. A globalisation of the classification by de Jong et al, 1998. Follow the key from above to below:

There are four salt-marsh zones: The pioneer zone, the low marsh, and the middle to high marsh. First decide on the zone, based on the underlined decision rules. Then choose the first option that fits the plot.

If total cover > 1% and pioneer species > species of low marsh:
Sa - Spartina  
Q - Salicornia  

If Pioneer species < species of low marsh > species of high and middle marsh:
Ap - Atriplex  
Pm - Puccinellia  

If (Pioneer species + species of low marsh) < species of high and middle marsh:
Am - Artemisia  
Ap - Atriplex  
Lv - Limonium  
Jg - Juncus gerardi  
Jm - Juncus maritimus  
Gm - Glaux  
EA - Elymus  
As - Agrostis  
Fr - Festuca  
D - Dune  
0 - No vegetation / Other

Pioneer species:
Spartina anglica, Salicornia sp. and Suaeda maritima

Species of the low marsh:

Species of the middle marsh:
Artemisia maritima, Armernia maritima, Juncus gerardi, Glaux maritima, Festuca rubra

Species of the high marsh:
Potentilla anserina, Trifolium spp., Poa spp., Lolium spp., Elymus spp., Lotus corniculatus, Plantago coronopus
Limonium vulgare on a young livestock-ungrazed salt marsh (photo J. Stahl).