Habitat use of Brent Geese on Ameland:

habitat switching from the polder to the saltmarsh

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1. Introduction

Many animals show one or more distinct habitat shifts in the course of each annual cycle (Baker 1978). The basic theory to explain such movements is that animal's shift from one area to another to capitalise on better or more resources, usually taken to be food. This improved food intake is assumed to enhance fitness (Prins and Ydenberg 1985).

The theoretical expectation of depletion models that predict the distribution of individuals in relation to resources, is that, the predators (including herbivores) will accumulate in patches of the highest density of prey (including plants) and then spread over a range of sites of lower prey density as depletion proceeds (Royama 1971; Comins and Hassell 1979; Bernstein et al. 1988, 1991). Although the theory has been developed for predators moving between sites within a habitat it is also possible to use the same framework to determine the movements between habitats. In such a case it is necessary to determine the pattern of depletion, the habitat preferences of the predators and the patterns of prey mortality caused by other factors (Vickery et al. 1995).

The protein concentration of food plants is an extremely important consideration for geese (Prins et al. 1980; Ydenberg and Prins 1981). Small homeotherms, like geese, require a disproportionately higher concentration of nutrients in their diets than larger homeotherms (Bell 1970; Jarman 1974), and, most herbivores are limited by the rate at which food can be processed (Sibly 1981; Westoby 1974). The protein reserves built up during the winter or on staging areas are critical to the breeding success of Arctic-nesting geese (evidence summarised in Ydenberg and Prins 1981). Changes in the quality of the habitat may cause a habitat switch. Other considerations are the changes in biomass (depletion), production and the extent of disturbance. If the grazing of geese depletes the biomass of the vegetation, the intake rate of the geese (as measured by the defaecation rates) will decline. A lower level of disturbance allows the geese to slow the rate at which they graze which in turn leads to an improved digestion of carbohydrates (Prins and Ydenberg 1985).

In this research the habitat switching in a population of dark-bellied Brent Geese *Branta b. bernicla (L.)* is considered. Prins and Ydenberg (1985) have explained habitat switching by Barnacle geese *B. leucopsis* on their spring staging grounds on the basis of the seasonal increase in the productivity and protein content of saltmarsh plants. Similarly, dietary preferences, in terms of the selection both of different parts of the same plant (e.g. Prop 1991; Summers and Atkins 1991) and of different individual plants or plant species (e.g. Owen 1971, 1975; Drent et al. 1979; Ydenberg and Prins 1981) have traditionally been considered in relation to plant quality or profitability.

On Schiermonnikoog, the Barnacle Geese abruptly switch their foraging activities from the polder to the saltmarsh towards the end of the winter (Prins and Ydenberg 1985). Brent Geese are also supposed to switch from the polder to the saltmarsh (the course of the grazing pressure on the grazed saltmarsh will show a relative strong increase later in the season, while the grazing pressure in the polder will remain relatively at the same level). The grass in the polder mainly consists of *Poa pratensis* and *Lolium perenne*. Because of the dewatering (regulation of soil water level) in the polder the growth of these plants start earlier than those growing on the saltmarsh. The sooner the growth of the plants will start, the earlier the growth stage and the digestibility of the plants deteriorates. As a result, the digestibility of the agricultural grasses decreases strongly in April due to early growth (Deinum 1968; Boudewijn 1984).

The growth of the saltmarsh vegetation, namely *Puccinellia maritima* starts at the end of April/ begin of May and is strongly influenced by the weather conditions. *Plantago maritima* starts to grow strongly in June, but can also be present in considerable amounts in May.

Festuca rubra can be found up the higher parts of the saltmarsh, and can already be in bloom in the beginning of May. In May *Puccinellia maritima* and *Plantago maritima* are in a young growth process, by which the digestibility is high for the Brent Geese as a result of the low raw-cellmaterial content (Spedding 1971; Weijand 1976; Ebbinge and Boudewijn 1984). Because of this high digestibility, the net-energy uptake can be increased strongly (Drent et al. 1979). In the case of regular grazing, these plants stay in a young growth process for a long time and the regrowth and digestibility will be maximal (Prins et al. 1980).
The saltmarsh can be divided in the grazed and the ungrazed area. The composition and structure of saltmarsh vegetation is strongly influenced by the intensity of grazing. On the grazed saltmarsh, the vegetation is dominated by *Puccinellia maritima* (Kiehl et al. 1996). Kiehl et al. concluded that when grazing was stopped, *Puccinellia maritima* had decreased its cover and was successively replaced by *Festuca rubra*, *Atriplex portulacoides* and *Aster tripolium* (Kiehl et al. 1996). As the grazed saltmarsh is dominated by *Puccinellia maritima* it is assumed be more attractive (Owen unpublished and Leisler 1969 in Owen 1971).

On Ameland, despite better quality of food plants on the saltmarsh later in the season, the geese also forage in the polder (Versluys et al. 1997). This may be a result of the maximal carrying capacity reached on the saltmarsh (Versluys et al. 1997).

The better quality on the grazed saltmarsh, compared to the polder, may result in a higher percentage of juveniles within a group. Within Barnacle Goose flocks dominance rank was ordered according to the number of individuals within social units. Large families (many juveniles) are on top of the social hierarchy (Black and Owen 1989). These families are expected to feed on the most preferred areas.

On Ameland there is an "absence" of Barnacle Geese grazing on the saltmarsh. On the saltmarsh of Schiermonnikoog these Barnacle Geese are present and a competitive exclusion between Barnacle Geese and Brent Geese exists. Brent Geese are smaller than Barnacle Geese and will be chased away by the Barnacle Geese, so they are not able to graze on the saltmarsh early in the season. Barnacle Geese start to graze on the saltmarsh early in the season before the Brent Geese arrive. As a result of this regular grazing by Barnacle Geese the food plants stay long in a young growth process (Prins et al. 1980) and Brent Geese will be able to feed on the saltmarsh later in the season, when the Barnacle Geese have left. Without the grazing of the Barnacle Geese the food plants would already be in bloom at this time. In the absence of Barnacle Geese the Brent Geese have to feed on the saltmarsh early in the season to get high quality food during the whole period. Because of the 'absence' of the Barnacle Geese, the habitat switch from the polder to the saltmarsh by Brent Geese may happen sooner compared to Schiermonnikoog.

Hypotheses:

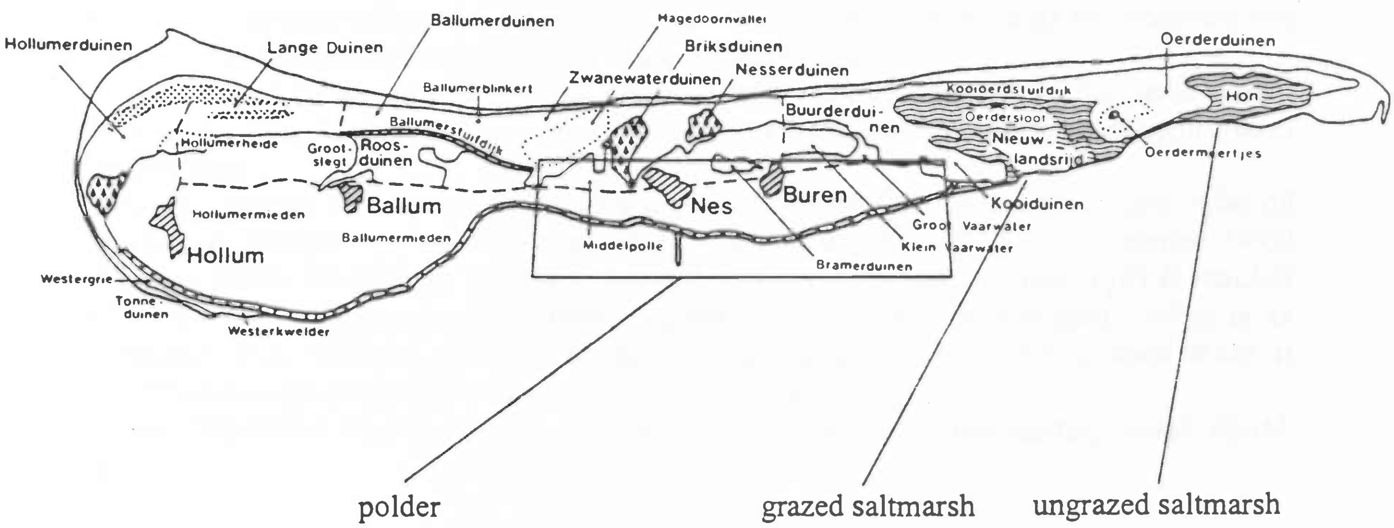
1) The Brent Geese will switch from the polder to the grazed saltmarsh later in the season.
2) On the grazed saltmarsh the biomass of living food plants is higher later in the season than earlier in the season.
3) On the grazed saltmarsh the quality of food plants later in the season is higher than earlier in the season.
4) In the polder the quality (N_2-content) and digestibility of food plants decreases later in the season.
5) In the polder the disturbance increases later in the season (no optimal foraging can take place)
6) Later in the season the juvenile percentage is higher on the saltmarsh than in the polder.
7) Because of the 'absence' of Barnacle Geese the switch on Ameland will happen sooner than the switch on Schiermonnikoog.

2.The study site

The study was carried out from week 10 until the period of departure of the Brent Geese, the end of May. Data was collected on Ameland, one of the Friesian islands in The Netherlands. The total area of Ameland amounts to 5.500 ha.

The Brent geese used two habitat types during this period: grass pastures (polder) and saltmarsh. The polders lie at the south side of the island and are a connected whole from the West of the island to the Kooiduinen (study area: 240 ha). The vegetation type mainly consists of *Lolium perenne* and *Poa pratensis*.

Two types of management can be found for the saltmarsh: grazed and ungrazed. The saltmarshes are located in the east of Ameland. The Hon (50 ha) is the ungrazed saltmarsh and the vegetation type mainly consists of *Festua rubra*. The Nieuwlandsreid (100 ha) is the grazed saltmarsh and is located west of the Hon. On the grazed saltmarsh *Puccinellia maritima* is the most abundant vegetation type.



3.Methods

3.1 Dropping counts

In order to compare grazing pressures on different types of vegetation, dropping densities were recorded. In the polder five circular plots with an area of 4 square meters were marked in twelve different sections. On the grazed saltmarsh five equal circular plots were marked at twelve different places. On the ungrazed saltmarsh also five circular plots were marked at six places. Every week droppings in each plot were counted and removed.

3.2 Island counts

Almost every week the Brent Geese were counted on the whole island. A distinction was made between the study area and the rest of the island. Within the study area, a distinction was made between the polder and the saltmarsh. These counts of the polder and the grazed saltmarsh were converted separately to droppings/m2/day considering the different areas. Droppings/m2/day: number of geese / area (m^2) * (600 minutes / 3.5). The geese foraged for approximately 10 hours a day and every 3.5 minutes a dropping is produced. These results will be used to determine if the dropping counts in the plots were representative for the number of geese and to determine how many geese have been on Ameland.

3.3 Biomass and production of plants

Every two weeks six sods were taken in each habitat type: polder, grazed saltmarsh and

ungrazed saltmarsh. The sods were taken in the neighbourhood of the dropping plots. Another six sods were taken from small exclosures (∅: 50 cm) erected in each habitat type. The exclosures were moved to a new location afterwards. The biomass of each sod was cut off and live (food- and non-food plants) and dead material were separated from each other, dried and weighed (one sample is 10 square centimetres). The live biomass consists of all the live material on the sod, the live food biomass is the live biomass of *Puccinellia maritima, Festuca rubra, Plantago maritima, Triglochin maritima and Spergularia maritima.*
For the production the differences between the biomass on the sods taken outside the exclosures and the sods taken inside the exclosures two weeks later were used. Production (for two weeks) is the biomass of the sod taken outside the exclosure minus the biomass of the sod taken in the exclosure two weeks before (Net Accumulated Primar Production).

3.4 Quality

Every two weeks, six samples (1.5 g) of the food plants were taken in each habitat type in the neighbourhood of the dropping plots (polder: grass at random, grazed saltmarsh: *Puccinellia maritima*, ungrazed saltmarsh: *Festuca rubra*). These samples were used to determine the percentage of nitrogen in the food plants using a CNS-auto-analyser.
Larger samples (3 g) were also taken once in each habitat type, all in the same period (saltmarsh: week 8, polder: week 9). These were used for an ADF (Acid Detergent Fibre) determination:
Filter and residue are put in a destruction tube and 100-ml Adf-substance is added. After 60 minutes of destruction the content of the tube is filtered through a new, weighed (WG) glassfibre filter. The filtering residue is washed with hot water until a neutral pH is reached and then rinsed with acetone. The sample is dried at 105 °C and weighed after cooling in an exsiccator (W2). Filtercup, filter and residue are put in a stove. The content is dried to ash at 550 °C and weighed after cooling in an exsiccator (W4).
*ADF= ((W2-W4) / WM) * 10^4 / % dried material, where WM is the starting weigh (Stahl, 1997).*

3.5 Height

The height was measured with an altimeter consisting of a pvc-pipe and a dropping disk (∅: 20cm, weight: 24 g). Every two weeks the height of the vegetation was measured ten times in the neighbourhood of the sod being taken. The different vegetation types will be characterised by its height. These heights serve as a calibration line for the biomass. The different calibration lines for each habitat type will be compared.
A comparison between the three different vegetation types will be made for the correlation of the height and the percentage nitrogen. This comparison will also be made between the polder and the saltmarsh (ungrazed and grazed saltmarsh put together).

3.6 Behavioural observations

Behavioural observations were made of Brent Geese feeding in the polder and on the **grazed** saltmarsh. In March and April the observations took place from approximately 9.00 to 12.00. In May the observations were made between half an hour past sunrise and 12.00.
These behavioural observations comprise for each observed goose flock the determination of:

- The group size at the start and the end of the observation
- The percentage foraging geese (2x)
- The percentage of juveniles (1x)
- Step rate, time needed for 10 steps during foraging (50x)
- Defecation rate; number of droppings per 10 minutes, 3 bouts of 10 minutes, and the time until the first dropping (Bédard & Gauthier).

3.7 Disturbance
Every potential disturbance was noted during the behavioural observations. The cause of the disturbance and the reaction of the geese were noted. The disturbances were distinguished by disturbances without movement (no reaction, look up) and disturbances with movement (walk away, fly up and fly away) for each area (polder and grazed saltmarsh).

3.8 Composition of the vegetation
A visual cover estimate of the vegetation is made once in the beginning of May. These compositions of the vegetation on the grazed saltmarsh were used to find out which food plants make the grazed saltmarsh attractive. If a particular food plant is attractive to the geese than the squares with the highest percentage of this food plant will be grazed most intensively.

4. Results

4.1 Dropping counts
Figure 1a shows the grazing pressures for each different type of vegetation. The grazing pressure in the polder gradually increased from the beginning of the research (week 10) until week 21, after which time the grazing pressure declined. The grazing pressure on the grazing saltmarsh increased until week 19, and started declining. A drop in the grazing pressure occurred around the period of week 16, but reached its normal level in the following week (week 17). During week 18 a drop in the grazing pressure is shown, although a smaller drop than previously. This small drop is also shown for the ungrazed saltmarsh. The ungrazed saltmarsh showed an increase of the grazing pressure until week 17, and after this the grazing pressure declined. Figure 1b shows the number of geese counted on the island. The number of geese counted in the study area of the polder shows a different pattern, compared to the course of the grazing pressure found in the polder. The grazing pressure shows a considerably higher pattern in week 20 and 21, because the Brent Geese shifted to the east of the polder later in the season, where relatively many plots were situated. As a result, a lot of droppings were counted in these plots leading to a high average grazing pressure.

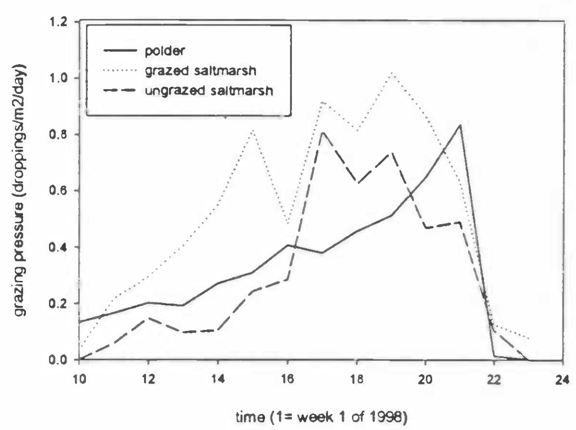


Figure 1a. The grazing pressure (droppings/m2/day) in the polder, the grazed saltmarsh and the ungrazed saltmarsh during the whole period (February-May).

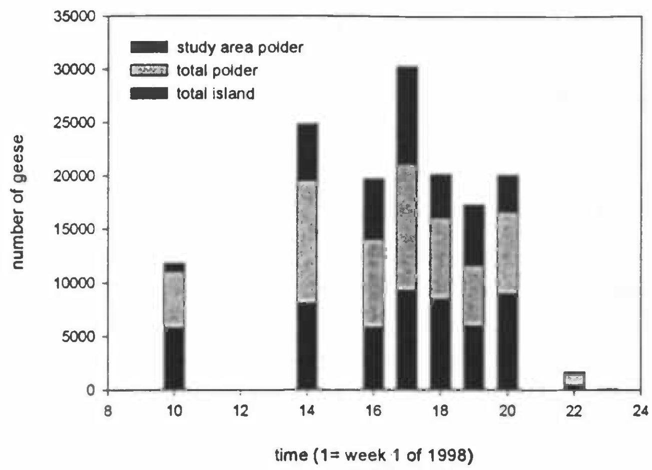


Figure 1b. The number of Brent Geese counted in the polder (study area and total polder) and the total island during the whole period (February-May).

4.2 Island counts

The relationship between the number of geese and the droppings for the polder and the grazed saltmarsh did not show significantly different regression lines. The date acquired in the polder and the grazed saltmarsh can be put together (Fig. 2). The relationship between the number of geese and the droppings counts for the whole area.

Although the regression line is significant, it is not justified to use the dropping counts as a replacement of the island counts ($R^2 = 0.521$, $F_{1,16} = 7.431$, $p = 0.001$). The data show too much distribution.

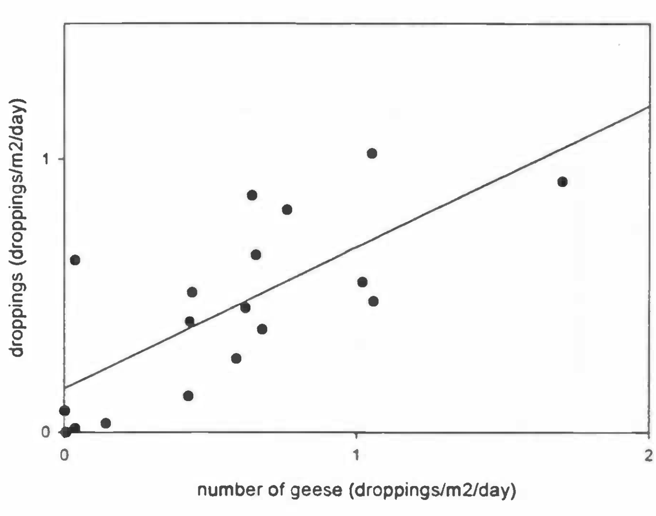


Figure 2. The relationship between the number of geese (droppings/m2/day) and the droppings (droppings/m2/day). Each point reflects a point in time in the study area (polder and grazed saltmarsh).

4.3 Biomass and production of plants

The live biomass increased the whole period for each different vegetation type (Fig. 3a). The

live biomass in the polder showed a tremendous increase since week 17. The live biomass on the grazed saltmarsh showed an increase from week 17 with a peak in week 21.
The live food biomass showed the same course as the live biomass, except for the peak on the grazed saltmarsh (week 21) (Fig. 3b). This peak in live biomass translates itself in the biomass of *Juncus*.
The percentages live biomass increased generally for each different vegetation type (Fig. 3c). The percentage live biomass of the ungrazed saltmarsh is twice as low as the percentage live biomass of the polder and the grazed saltmarsh. The percentage live biomass on the grazed saltmarsh is on a higher level than the polder, but the polder reached the same level in week 21, as a result of the fertilisation of the polder in this period.
The production of the live biomass increased the whole period for the polder. The production of the live food biomass on the grazed saltmars increased from week 15 until week 19 (Fig. 3d). This shows that *Puccinellia maritima* started to grow in the end of April. The production of the live biomass on the ungrazed saltmarsh showed a similar pattern as the grazed saltmarsh.

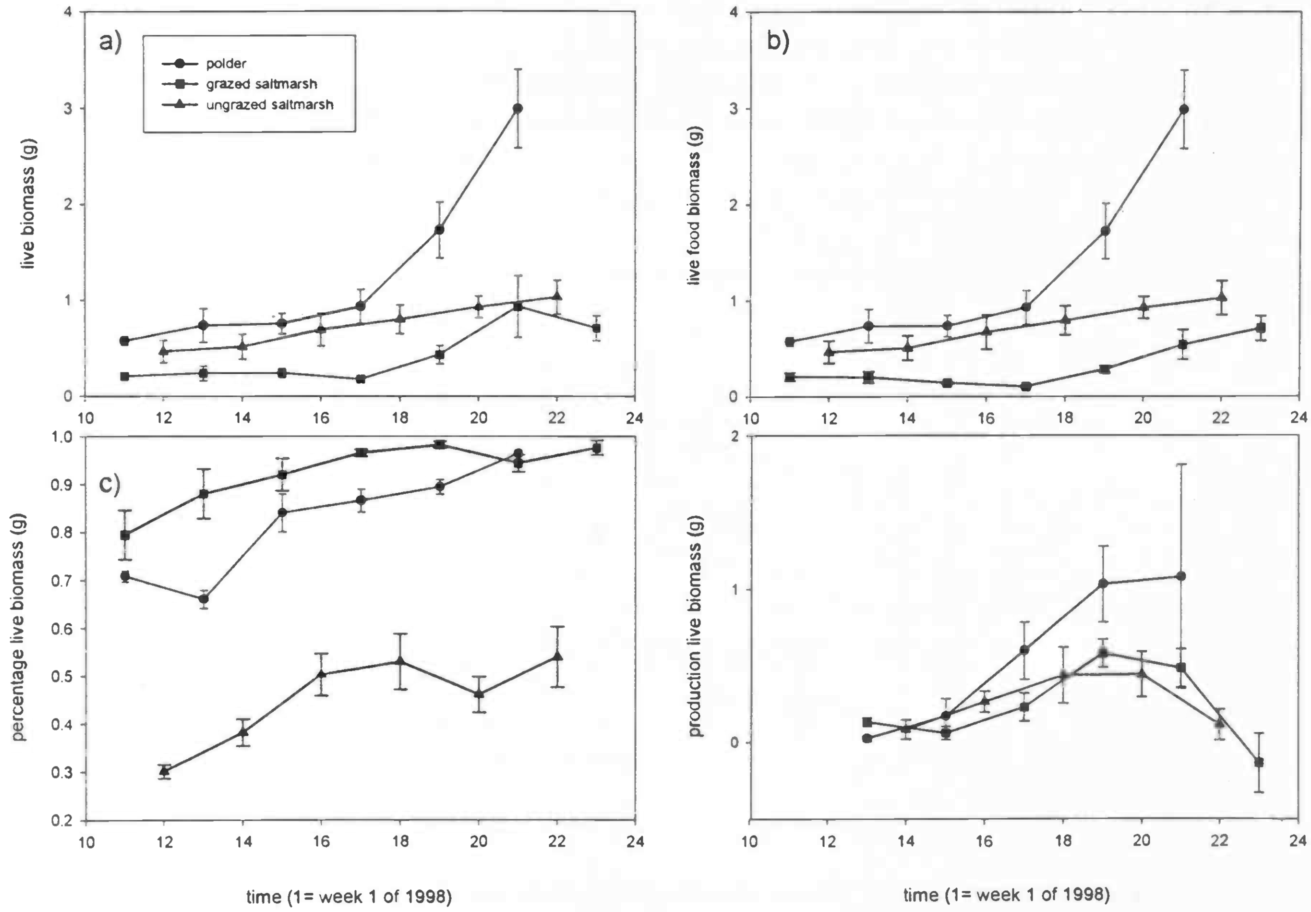


Figure 3. A) The live biomass (g) for the polder grazed saltmarsh and ungrazed saltmarsh in time. B) The live food biomass (g) for the polder grazed saltmarsh and ungrazed saltmarsh in time. C) The percentage live biomass (g) for the polder grazed saltmarsh and ungrazed saltmarsh in time. D) The production live biomass (g) for the polder grazed saltmarsh and ungrazed saltmarsh in time.

4.4 Quality

The percentage of nitrogen for the polder decreased in time (Fig. 4). A negative correlation was found ($y= -0.1253x + 6.5869$, $R^2 = 0.5987$, $p= 0.0027$). The grazed saltmarsh showed a polynomial correlation in time and reached the highest percentage nitrogen in week 16 ($y= 0.016x^2 + 0.5194x + 0.7768$, $R^2 = 0.4366$, linear regression, $p= 0.3664$). The ungrazed salt marsh showed a strong negative correlation in time ($y= -0.2636x + 7.3671$, $R^2 = 0.9671$, $p= 0.0000$). The different habitat types showed a significant interaction effect (Table 1).

Source of variation	DF	MS	F	Sig. Of F
Within + residual	65	0.46		
Group by time	2	3.3	7.09	0.002
Group	2	1.36	2.92	0.061
Time	1	14.03	30.19	0.000

Table 1. Effect of area and time on the nitrogen percentage.
Final model of analysis of variance.
Anova on the nitrogen percentage using group (polder, saltmarsh and ungrazed saltmarsh) and time (every two weeks) as factors.

No positive correlation was found between the percentage nitrogen and the grazing pressure (Fig. 5a,b,c). The different vegetation types shows no correlation (polder: $y= -0.3896x + 2.2838$, $R^2 = 0.144$, $p= 0.0674$, $F_{1,22} = 3.70198$; grazed saltmarsh: $y= -0.0106x + 1.5696$, $R^2 = 0.0005$, $p= 0.9394$, $F_{1,12} = 0.00602$; ungrazed saltmarsh: $y= -0.0305x + 0.3962$, $R^2 = 0.01556$, $p= 0.6993$, $F_{1,10} = 0.15806$). The correlation's are more likely negative than positive, and is contradictory to the expectations.

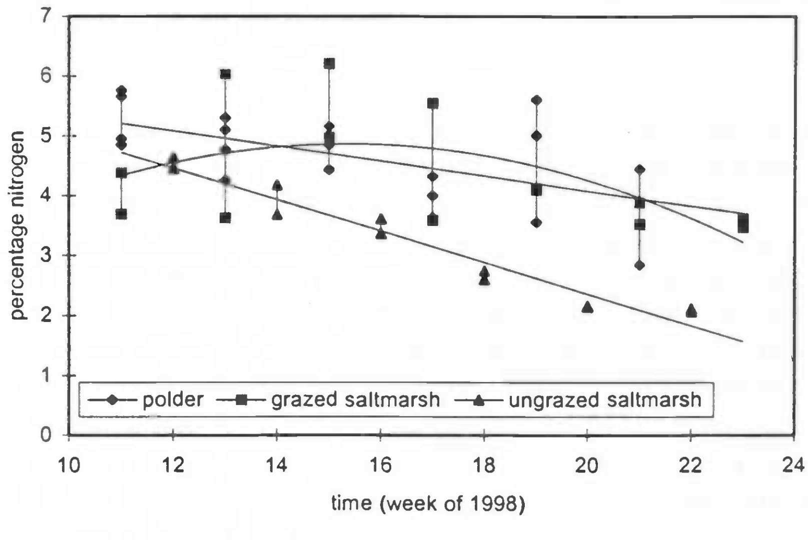


Figure 4. The percentage nitrogen for the polder grazed saltmarsh and the ungrazed saltmarsh in time.

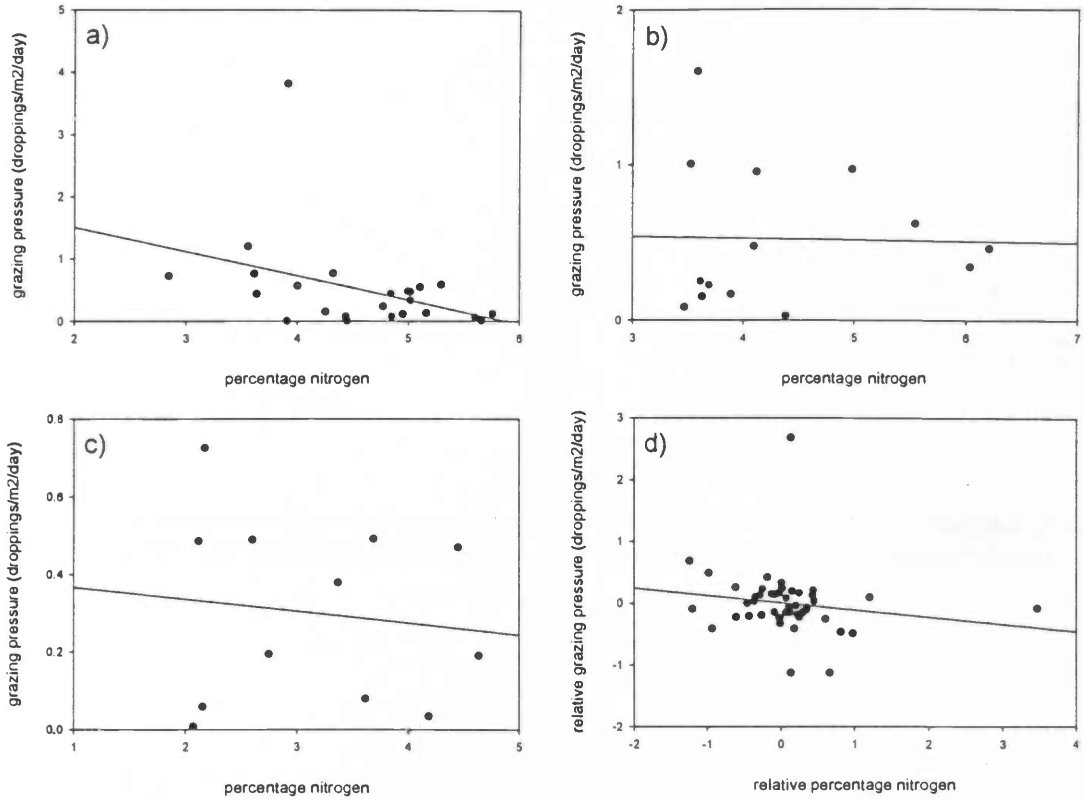


Figure 5. A) The correlation between the percentage nitrogen and the grazing pressure (droppings/m2/day) in the polder. B) The correlation between the percentage nitrogen and the grazing pressure (droppings/m2/day) on the grazed saltmarsh. C) The correlation between the percentage nitrogen and the grazing pressure (droppings/m2/day) on the ungrazed saltmarsh. D) The correlation between the relative percentage nitrogen and the relative grazing pressure (droppings/m2/day).

The relative data for all areas, every value minus the average value of all the data, were also plotted in a graph. These relative data were used because the absolute levels of goose pressure and the nitrogen content change in time. It is important to look at the relative deviation of the present geese at that moment. The choice is at one point of time and depends on the nitrogen content and the amount of geese. In this way the effect of time will be excluded and the relative data will give an idea why the geese made their choice at that point of time. Using these relative data, the nitrogen percentage still did not effect the grazing pressure, no correlation was found (Fig. 5d), implying that the percentage nitrogen was of no importance to the grazing pressure.
As expected, a negative correlation was found between the percentage nitrogen and the ADF (Fig. 6). The higher the percentage nitrogen, the less fibres were found for the ADF-analysis ($y= -3.0004x + 36.829$, $R^2 = 0.5588$, $p= 0.0330$).
As a result, a positive correlation (Fig. 7) was found between the ADF and the grazing pressure ($y= 0.0529x - 0.8676$, $R^2 = 0.1095$, $p= 0.0854$). This relationship is contradictory to the expectation, as found in the relationship between the percentage nitrogen and the grazing pressure. It seems like the percentage nitrogen and the ADF did not effect the grazing pressure in the polder or on the saltmarsh.

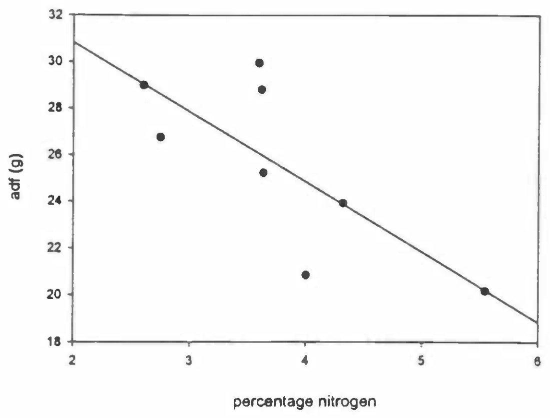


Figure 6: The correlation between the percentage nitrogen and the ADF for all vegetation types.

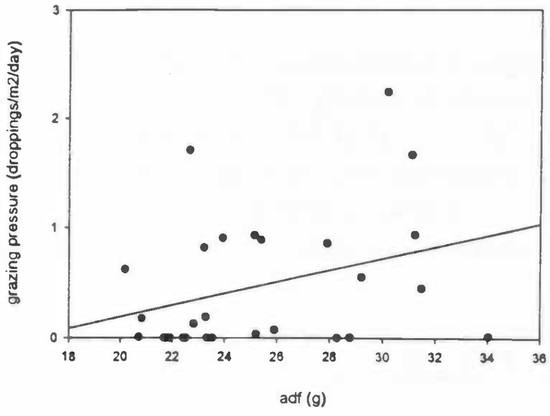


Figure 7. The correlation between the adf and the grazing pressure (droppings/m2/day)

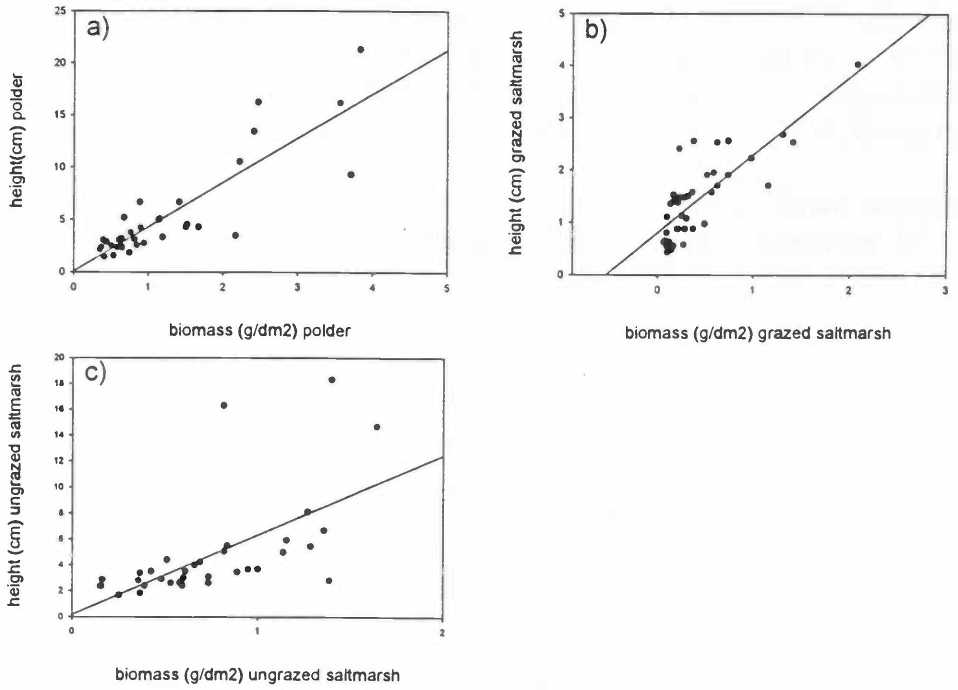


Figure 8. The correlation between the biomass (g/dm2) and the height (cm) for the polder (a), grazed saltmarsh (b) and the ungrazed saltmarsh (c). Each point reflects the biomass and the height of a plot measured at the same time.

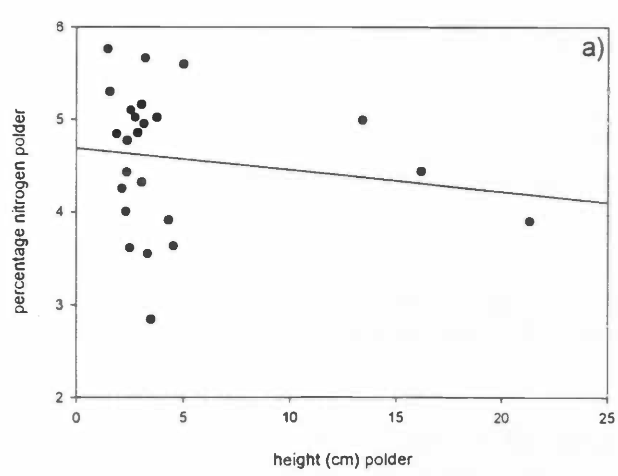
4.5 Height

The height is significantly positive correlated with the biomass for each different vegetation type (Fig. 8) (polder: $y = 4.2354x + 0.0796$, $R^2 = 0.751$, $p<0.0001$; grazed saltmarsh: $y = 1.4884x + 0.8075$, $R^2 = 0.644$, $p<0.0001$; ungrazed saltmarsh: $y = 6.1315x + 0.1767$, $R^2 = 0.380$, $p<0.0001$). Each habitat type is plotted separately, while an Anova on the height, using habitat type and biomass as factors, showed a significant interaction effect (Table 2).
Now the height of the plants can be used as a replacement for the biomass, each habitat type having its own regression line.

Source of variation	DF	MS	F	Sig. Of F
Within + residual	106	4.95		
Group by biomass	2	35.85	7.25	0.001
Group	2	2.49	0.5	0.606
Biomass	1	393.24	79.49	0.000

Table 2. Effect of area and biomass on height.
Final model of analysis of variance.
Anova on the height using group (polder, saltmarsh and ungrazed saltmarsh) and biomass as factors.

The different vegetation types all showed a negative correlation between the height and the percentage nitrogen of the food plants (Fig. 9a, b, c). The polder showed the weakest relationship between the height and the percentage nitrogen, and the ungrazed saltmarsh the strongest (polder: $y = -0.0232x + 4.6884$, $R^2 = 0.0234$, linear regression: $p= 0.4750$, $F_{1,22} = 5.2828$; grazed saltmarsh: $y = -0.4137x + 5.0069$, $R^2 = 0.2049$, linear regression: $p= 0.1041$, $F_{1,12}= 3.09213$; ungrazed saltmarsh: $y = -0.1233x + 3.9487$, $R^2 = 0.4719$, linear regression: $p= 0.0136$, $F_{1,10} = 8.93410$).
The saltmarsh put together (grazed and ungrazed) showed a significant negative correlation (Fig. 9d) between the height and the percentage nitrogen (linear regression: $R^2 = 0.44911$, $p= 0.0002$, $F_{1,24}= 19.566$).



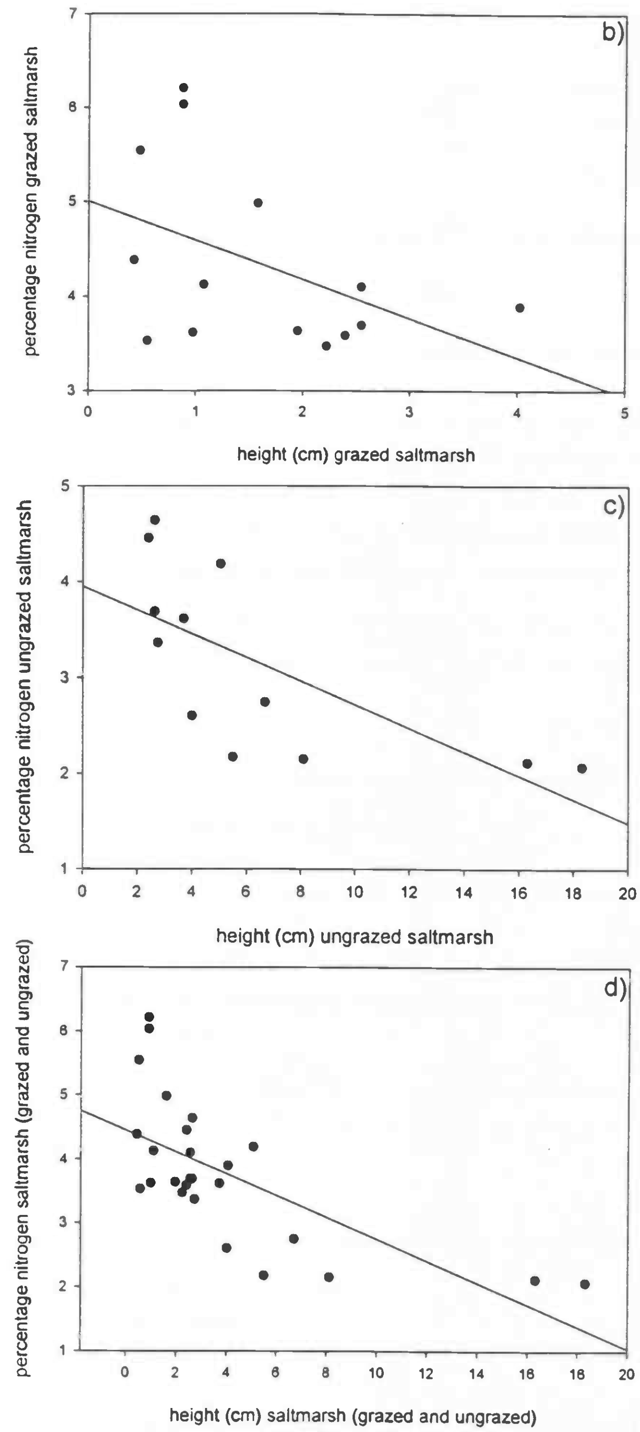


Figure 9. The correlation between the hieght (cm) and the percentage nitrogen of the plants: a) in the polder, b) on the grazed saltmarsh, c) the ungrazed saltmarsh and d) the saltmarsh (grazed and ungrazed put together).

4.6 Behavioural observations

Figure 10a shows the juvenile percentage for the areas polder and saltmarsh. The period is distinguished by months (March, April and May). In the polder the juvenile percentage increased in April and remained at this level until May. On the saltmarsh the juvenile percentage remained at the same level in the months March and April and increased in May. During the whole period the juvenile percentage in the polder was higher than on the saltmarsh, implying that the dominant groups foraged in the polder. No significant differences were found (Table 3).

Source of variation	DF	MS	F	Sig. of F
Within + residual	64	0.00		
Group	1	0.01	2.86	0.096
Time	2	0.01	2.45	0.095

Table 3. Effect of area and time on juvenile percentage.
Final model of analysis of variance.
Anova on juvenile percentage using group (polder, saltmarsh) and time (March, April, May) as factors.

The percentage of birds foraging within a group on the saltmarsh was higher than the percentage in the polder. There was a significant increase in the percentage of birds foraging in both areas (Fig. 10b and Table 4). In the polder the percentage of birds foraging within a group later in the season is lower. But no significant difference was found. The percentage of birds foraging within a group on the saltmarsh remained at the same level.

Source of variation	DF	MS	F	Sig. of F
Within + residual	64	0.00		
Group	1	0.02	5.14	0.027
Time	1	0.00	0.78	0.381

Table 4. Effect of area and time on forage percentage.
Final model of analysis of variance.
Anova on forage percentage using group (polder, saltmarsh) and time (early and late) as factors.

Figure 10c shows the steprate for the polder and the saltmarsh and is distinguished in months. For both areas the steprate increased significantly over time (Table 5). There is no significant difference between the areas.

Source of variation	DF	MS	F	Sig. of F
Within + residual	60	10.34		
Group	1	0.05	0.00	0.944
Time	2	40.85	3.95	0.024

Table 5. Effect of area and time on steprate.
Final model of analysis of variance.
Anova on steprate using group (polder, saltmarsh) and time (March, April, May) as factors.

The defaecation rates did not show a difference between the areas, polder and grazed saltmarsh (Fig. 10d and Table 6). A small increase has been found in time for the polder and the grazed saltmarsh, but no significant difference was found between the periods.

Source of variation	DF	MS	F	Sig. of F
Within + residual	34	0.34		
Group	1	0.00	0.00	0.962
Time	1	0.19	0.56	0.461

Table 6. Effect of area and time on the daefecation rate.
Final model of analysis of variance.
Anova on the defaecation rate using group (polder, saltmarsh) and time (early and late) as factors.

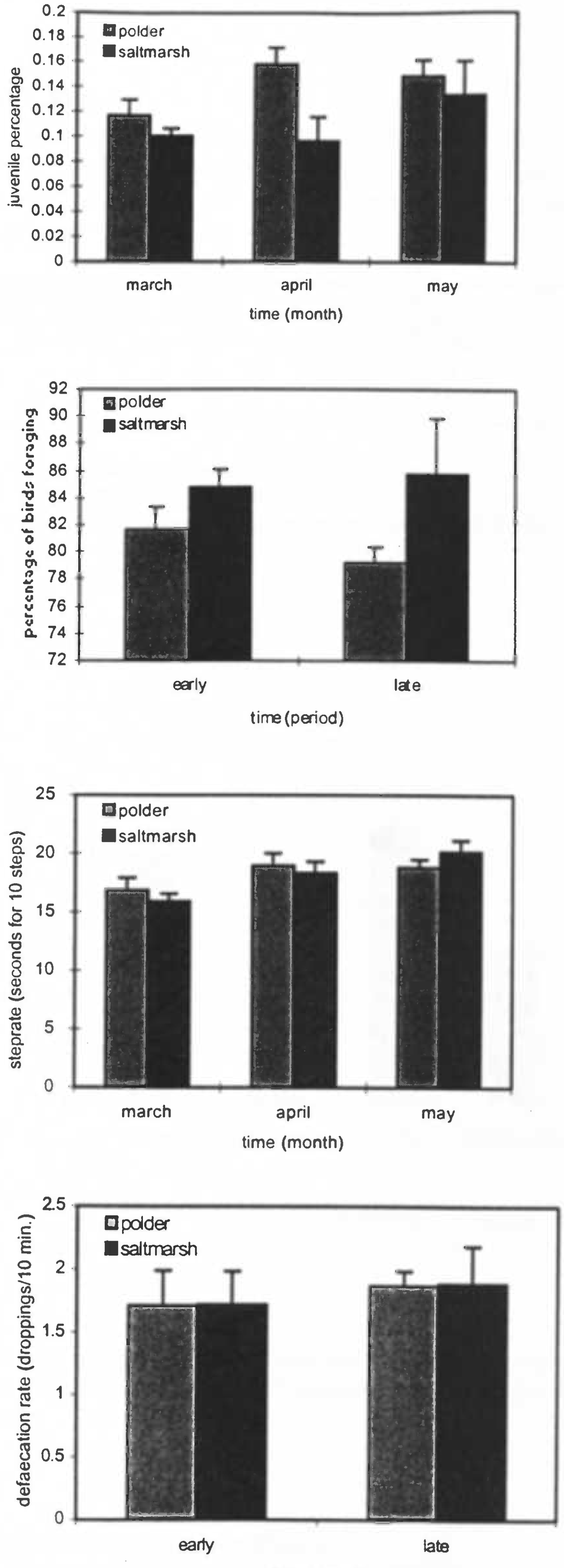


Figure 10. The behavioural observations in the polder and the grazed saltmarsh. A) The juvenile percentage in the months March, April and May. B) The percentage of birds foraging within a group in the early and the late period. C) The steprate (seconds needed for ten steps while foraging) in the months March, April and May. D) The defaecation rate (number of droppings/ten minutes) in the early and the late period.

4.7 Disturbance

Figure 11 shows the disturbance in the polder and on the saltmarsh in the months March, April and May. Each month the saltmarsh showed significantly less disturbance, compared to the polder (Table 7). Over the whole period the degree of disturbance decreased significantly for both areas.

Source of variation	DF	MS	F	Sig. of F
Within + residual	66	23.33		
Group	1	230.88	9.90	0.002
Time	2	144.34	6.19	0.003

Table 7. Effect of area and time on disturbance.
Final model of analysis of variance.
Anova on disturbance using group (polder, saltmarsh) and time (March, April, May) as factors.

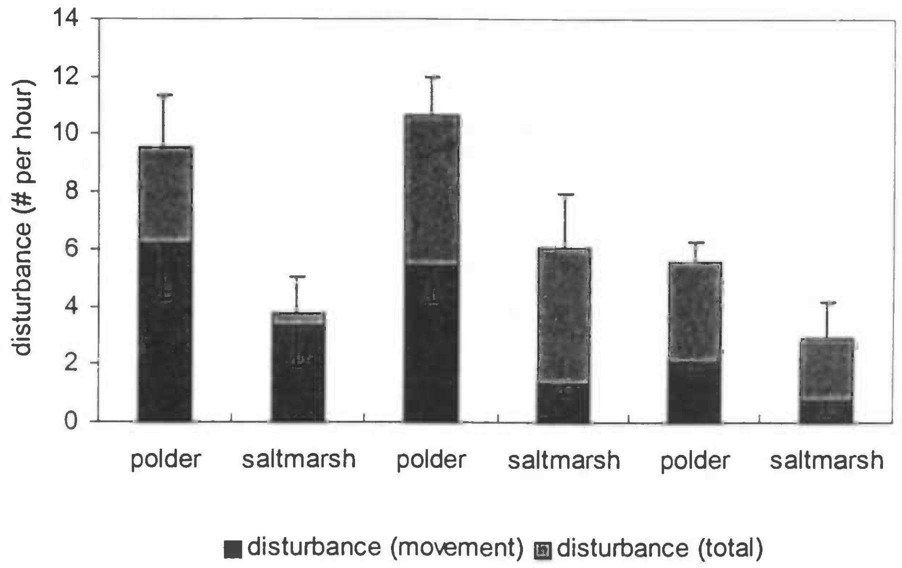


Figure 11. The disturbances in the polder and the grazed saltmarsh in the months March, April and May. The disturbances which resulted in a movement (walk away, fly up and fly away) are distinguished from the total disturbances.

4.8 Composition of the vegetation

Figure 12a shows almost weekly the correlation between the percentage *Puccinellia maritima* and the grazing pressure on the grazed saltmarsh. This correlation is shown to give an idea of the course during the whole period. A positive correlation is shown between the percentage *Puccinellia* and the grazing pressure, except for half April (week 16). The opposite is shown for the percentage *Festuca* and the grazing pressure, here a negative correlation existed during the whole period and half April showed a positive correlation (Fig. 12b).

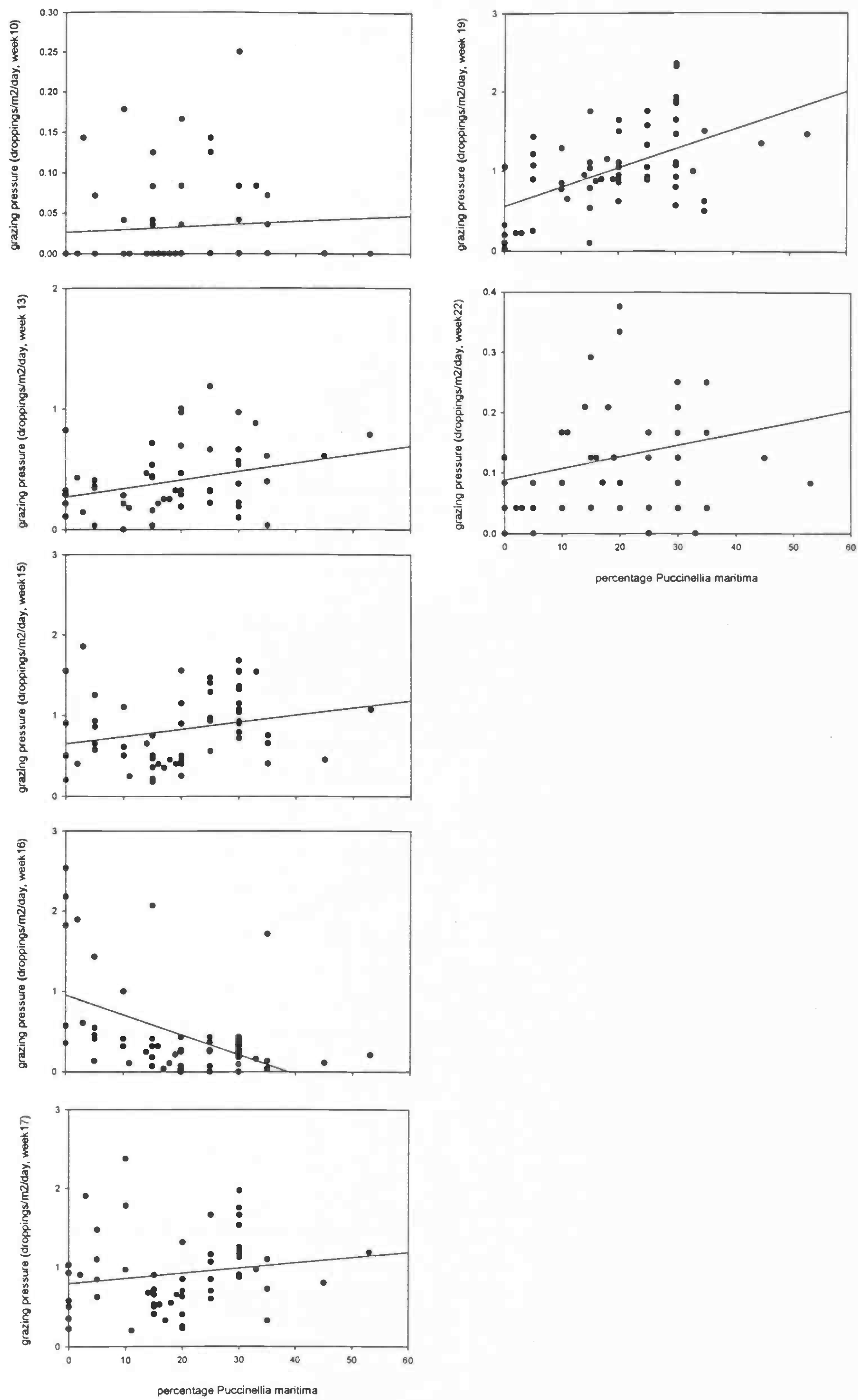


Figure 12a. The correlation between *Puccinellia maritima* and the grazing pressure (droppings/m2/day)

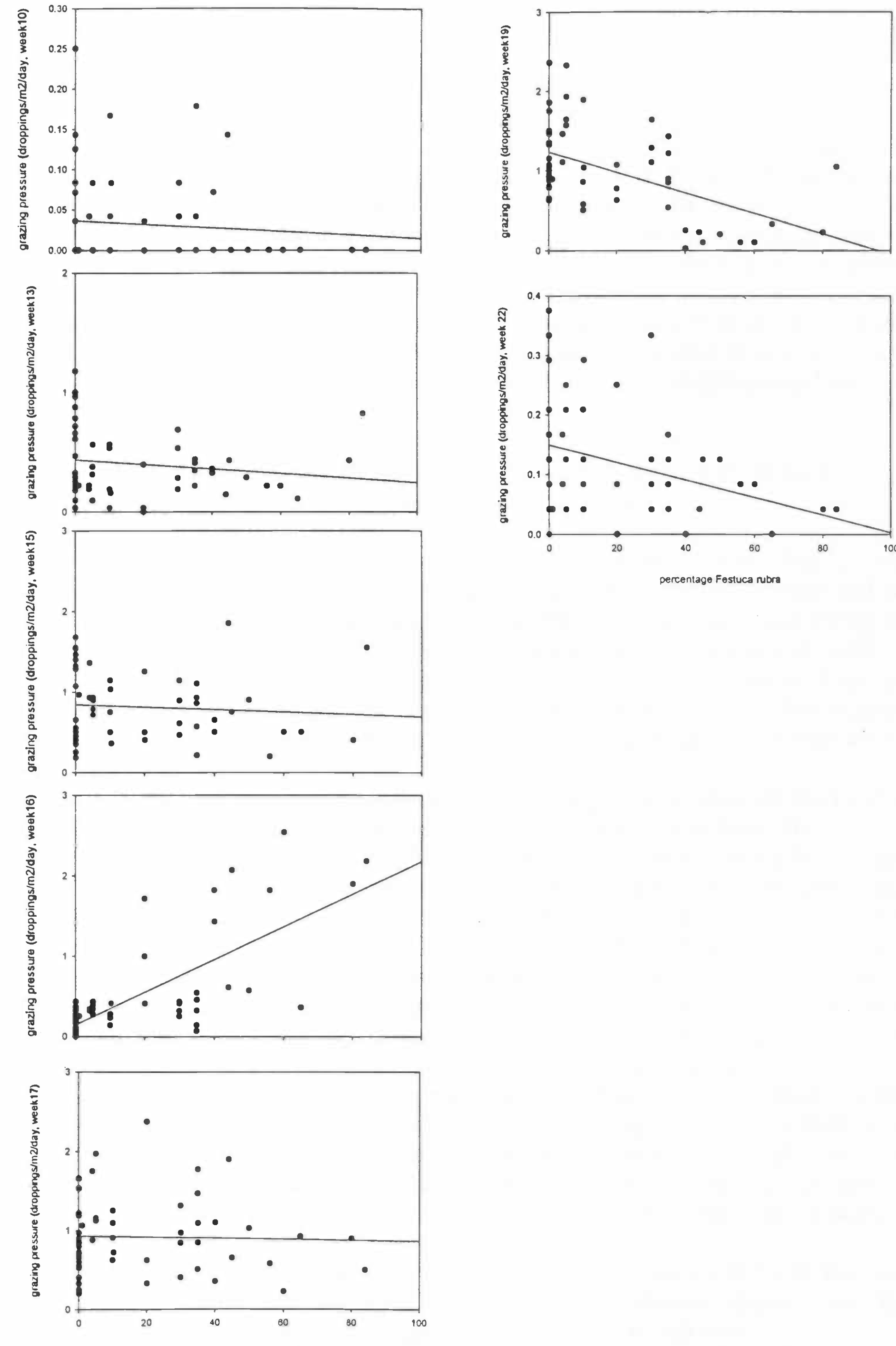


Figure 12b. The correlation between the percentage *Festuca rubra* and the grazing pressure (droppings/m2/day).

5. Discussion

The habitat use of Brent Geese in time

At the beginning of the research (week 10) the grazing pressure in the polder is higher than the grazing pressure on the grazed saltmarsh (Fig. 1). After week 10 the grazing pressure on the grazed saltmarsh is higher than the grazing pressure in the polder, however, a habitat switch from the polder to the saltmarsh did not occur. The course of the grazing pressure on the grazed saltmarsh does not show a relatively strong increase later in the season. The polder and the grazed saltmarsh both show a gradually increase in grazing pressure until the first flocks of geese start to leave the island (week 19). Despite the lower production of live biomass on the grazed saltmarsh, the Brent Geese still forage on the grazed saltmarsh more intensively. Thus, the Brent Geese prefer to feed on the grazed saltmarsh (Prins and Ydenberg 1985).

The preference of the Brent Geese for the grazed saltmarsh in relation to the biomass, productivity and quality of the food plants

The preference for the grazed saltmarsh can not be explained by the biomass (Fig. 3). The grazed saltmarsh had the lowest live (food) biomass in time compared with the polder and the ungrazed saltmarsh. Plant production was also better for the polder and increased during the whole period. The plant production on the grazed saltmarsh started to increase in week 15 until week 19. Considering these facts the polder seems to be more attractive. Only the percentage live biomass was found best for the grazed saltmarsh. But the amount live biomass of the grazed saltmarsh, taking in account the area as well, is insufficient to provide all the Brent Geese with food.

The percentage nitrogen on the grazed saltmarsh reached a higher level than the polder (Fig. 4). No significant difference was found and no positive correlation was found between the percentage nitrogen and the grazing pressure (Fig. 5). This implies that the choice of the geese was not based on the quality of the vegetation type (polder, saltmarsh). An explanation may be the high level of the percentage nitrogen in each vegetation type. The geese do not have to consider a certain quality, while the quality is sufficient at every place. In time the percentage nitrogen decreased in the polder and on the ungrazed saltmarsh. This may have been a result of the mild winter. The high temperature during the first months of 1998 resulted in an early growth of the vegetation and hence, a high percentage nitrogen early in the season. Possibly the peak of the percentage nitrogen already occurred before the Brent Geese arrived.

Since week 11 the Brent Geese have foraged on the grazed saltmarsh more intensively, while the productivity was at a rather low level and the nitrogen percentage reached its highest level in week 16. Until week 13 the nitrogen percentage in the polder was even at a higher level. At this time the preference for the grazed saltmarsh can not be explained on the basis of seasonal increase in the productivity and protein content of saltmarsh plants (Prins and Ydenberg 1985).

May be the period after week 15 until week 19 can be explained on the basis of seasonal increase in the productivity and the nitrogen percentage of saltmarsh plants. Here the productivity strongly increased and the nitrogen percentage is still at high level.

The juvenile percentage did not reflect a difference in quality for the polder and the grazed saltmarsh. The grazed saltmarsh did not show a higher quality by means of the juvenile percentage. Actually the polder showed a little higher juvenile percentage than the grazed saltmarsh. No explanation has been found for this result, while the quality of the vegetation in the polder was not better than on the grazed saltmarsh and thus did not play a role.

The preference of the Brent Geese within the grazed saltmarsh explained by quality

Besides a preference between the habitat types, the Brent Geese have a preference within the habitat type. Figure 12 shows the connection between the percentage *Puccinellia maritima* & the grazing pressure (Fig. 12a) and the percentage *Festuca rubra* & the grazing pressure (Fig. 12b) on the grazed saltmarsh. The geese preferred to feed on *Puccinellia*, while there is a positive correlation between the percentage of this food plant and the grazing pressure. This correlation can not be found for the food plant *Festuca*. There is an exception half April (week 16), which shows a negative correlation between the percentage *Puccinellia* and the grazing pressure and a positive correlation for *Festuca*. The geese stopped feeding on *Puccinellia* and started feeding on *Festuca*, moving between sites within a habitat (Vickery 1995). These results agree with those of Prop & Deerenberg (1991). They found a significant negative relationship between the proportion of *Festuca rubra* in the diet and the growth rate of *Puccinellia maritima*. *Festuca* becomes an important food source as soon as the *Puccinellia* production drops ($R = -0.73$, $p<0.001$). This negative correlation between the percentage *Puccinellia* and the grazing pressure is shown as the decrease in grazing pressure on the grazed saltmarsh at this point of time (Fig. 1) meaning that *Puccinellia* is the most important food plant and is preferred within the habitat (saltmarsh) by the Brent Geese.
Figure 4 shows that during week 16 the percentage nitrogen has reached its highest level on the grazed saltmarsh and the grazing pressure declined at this point of time. The food biomass on the grazed saltmarsh reached its lowest level half April (Fig. 3b). Altogether this means that the geese depleted their food source on the grazed saltmarsh, namely *Puccinellia maritima*, at its best quality. Despite the decreasing nitrogen percentage, the geese again started feeding on *Puccinellia* as soon as it recovered from depletion (Fig. 1,4, 12). Probably *Puccinellia maritima* was still of better quality than *Festuca rubra*.
The percentage nitrogen on the grazed saltmarsh appeared to be of importance until half April within the habitat type. At this time both nitrogen percentage and grazing pressure increased.

The preference of Brent Geese for the grazed saltmarsh explained by disturbance

Figure 11 shows the disturbances in the polder and the grazed saltmarsh in March, April and May. During the whole period the disturbances in the polder were higher than on the grazed saltmarsh. In May the disturbance significantly declined for both areas. It is logical to observe more disturbances in the polder than on the grazed saltmarsh, while there were more tourists in the polder. The decline of the disturbance in May appears to be the result of habituation. In this month still a lot of tourists were visiting the island, actually May is one of the lively months of the year. This month is also the most active month of the farmers. The farmers were busy fertilising their land, mowing their grass and putting the cows outside.
A significant difference is shown for the percentage of birds foraging within a group between the polder and the grazed saltmarsh. Both in the early and the late period the grazed saltmarsh showed a higher percentage of birds foraging within a group than the polder. An explanation may be the higher quality of the grazed saltmarsh or the fewer disturbances on the grazed saltmarsh (Fig. 11). The nitrogen percentage did not show a significant difference between the two areas, so it seems reasonable to explain the higher percentage of birds foraging within a group by the fewer disturbances on the grazed saltmarsh.

A comparison: island counts (number of geese) and grazing pressure (droppings/m2/day)

From the beginning of March until the beginning of May the grazing pressure (droppings/m2/day) is in general increasing for each vegetation type (Fig. 1). The total

number of Brent Geese decreased since the end of April (week 17), while the grazing pressure still increased. The remaining geese seemed to have increased their intake rate (as measured by the defaecation rate). Figure 10d shows a small increase of the defaecation rate in the late period, but it is not significant and can not be the only explanation of the increasing grazing pressure.
The increasing daylength may be another explanation. These longer days gave the geese the possibility to spend more time on foraging, without increasing the intake rate. So, it could be possible the Brent Geese just spent more time on foraging. From week 13 until week 19 the daylength increased with factor 1.25 and the grazing pressure (droppings/m2/day) with factor 3.3. The increased grazing pressure is not only the result of the longer days.
The percentage of birds foraging within a group increased on the grazed saltmarsh in the late season, but decreased in the polder. May be the grazed saltmarsh played a larger role, while the grazing pressure is more intensively here.
The steprate increased significantly in time for both vegetation types (polder and grazed saltmarsh), which could be the result of an increased peck rate, a declining quality/biomass of the vegetation or an increase of the intake rate. Figure 2 shows that the biomass increased for the whole period, so the biomass is not the case. The quality showed a small decline in time for the polder and the grazed saltmarsh (Fig. 4). The declining quality and the increasing intake rate may have resulted in an increasing step rate. This possibly increasing intake rate agrees with the small increased defaecation rate.
During this period the live (food) biomass for both vegetation types increased. Geese appear to obtain more food per peck as a result of the higher biomass of the vegetation (Black et al. 1992). The intake rate may be the result of all these little changes. There is not one obvious change that caused the increase of the intake rate.

Correlation between the percentage nitrogen and the height

All different vegetation types showed a negative correlation between the percentage nitrogen and the height. The polder showed a weak correlation, which does not compare with observations by Hassall and Riddington (1996). The nitrogen content was inversely proportional to their height. They found a strong correlation between the percentage nitrogen and the height ($p<0.001$) for unfertilised swards. The issue here is the fertilisation of the pastures. Application of fertiliser not only increased the nitrogen content of grass laminae, but also completely eliminated the relationship between nitrogen content and sward height ($p= 0.679$). The polder on Ameland had been fertilised (ca. 500 kg/ha), when the quality samples were taken. This explains the weak correlation between the nitrogen percentage and the height in the polder. According to the results found by Hassall and Riddington (1996) on pastures, one would expect the same for the saltmarsh vegetation. The grazed saltmarsh showed a better correlation between the height and the percentage nitrogen than the polder. The grazed saltmarsh had been fertilised once in April (ca. 50 kg/ha), but less intensively than the polder. This difference in the amount of fertiliser may be an explanation for the difference between the regression lines of the polder and the grazed saltmarsh. The more fertiliser, the weaker the correlation between the height and the percentage nitrogen. The ungrazed saltmarsh had not been fertilised, and hence, showed the strongest correlation. If the vegetation types, grazed saltmarsh and ungrazed saltmarsh, were put together the correlation was even stronger ($p= 0.0002$) as shown in figure 9d.

A comparison: Ameland and Schiermonnikoog

The Brent Geese did not switch from the polder to the saltmarsh on Ameland. It is not possible to compare the moment of switches on Ameland and Schiermonnikoog. It is clear that the Brent Geese on Ameland prefer to graze on the grazed saltmarsh and there are more Brent Geese foraging on Ameland (ca. 20.000) than on Schiermonnikoog (ca. 2.000). Ameland appears to be more attractive than Schiermonnikoog.

6. Conclusion

No habitat switch occurred on Ameland. During the whole research period the Brent Geese showed the same course of grazing pressure for the polder and the grazed saltmarsh. However, it is obviously that the Brent Geese prefer to feed on the grazed saltmarsh.
Within this habitat type (grazed saltmarsh), the Brent Geese prefer to feed on *Puccinellia maritima.* If they deplete *Puccinellia maritima* they start feeding on *Festuca rubra* more intensively.
No prove has been found, only suggestions can be made about the cause of the preference for the grazed saltmarsh. The first suggestion is the higher quality of the grazed saltmarsh, in particular *Puccinellia maritima*. Secondly, the fewer disturbances on the grazed saltmarsh, compared to the polder.

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Appendix 1

Number of disturbances per hour in the polder and on the saltmarsh until the 15th of April. (1=unknown, 2=car,tractor, 3=people, 4=bird of prey, other birds, 5=airplane)

	source	polder	saltmarsh	polder	saltmarsh	polder	saltmarsh
Reaction		<50%	<50%	=,>50%	=,>50%	100%	100%
no reaction	1						
	2					0.43	
	3					0.21	
	4						0.14
	5					0.36	0.43
look up	1	0.29	0.14	0.36	0.14	0.36	1.14
	2	0.29		0.36	0.14	0.29	
	3			0.14		0.07	
	4	0.36		0.21		0.36	
	5	0.14		0.29		0.07	0.14
walk away	1	0.14		0.14			
	2	0.14					
	3	0.07					
	4						
	5						
fly up	1	0.21	0.14	0.21	0.14	0.79	0.71
	2	0.07		0.07			
	3						
	4	0.07					
	5			0.07			0.14
fly away	1					0.29	0.29
	2			0.07			
	3	0.07		0.07		0.14	
	4					0.14	
	5					0.07	
Location		polder	saltmarsh	polder	saltmarsh	polder	saltmarsh

Appendix 2

Number of disturbances per hour in the polder and on the saltmarsh from the 15th of April until the end of May.
(1=unknown, 2=car,tractor, 3=people, 4=bird of prey, other birds, 5=airplane)

	source	polder	saltmarsh	polder	saltmarsh	polder	saltmarsh
Reaction		<50%	<50%	=,>50%	=,>50%	100%	100%
no reaction	1					0.04	
	2					0.36	
	3					0.24	
	4					0	
	5					0.16	0.72
look up	1	0.032	0	0.51	0	0.28	
	2	0.47	0	0.32	0	0.36	
	3	0.12	0	0	0	0.08	
	4	0.08	0.24	0.16	0.24	0.12	0.48
	5	0.16	0.24	0.24		0.08	
walk away	1	0.17		0		0	
	2	0.04		0.24		0	
	3	0.17		0		0.12	
	4	0.20		0.08		0.04	
	5	0.04				0.04	
fly up	1	0.04		0.04		0	
	2			0		0	
	3			0.04		0	
	4			0.04		0.16	
	5					0.04	
fly away	1	0.16		0.04	0.24	0.20	0
	2			0		0.12	0
	3			0.04		0.04	0
	4			0.08		0.16	0.48
	5					0	
location		polder	saltmarsh	polder	saltmarsh	polder	saltmarsh