

**Experimentally testing foraging preferences
with captive brent and barnacle geese**

Nicol Heuermann

Diplomarbeit Universität Osnabrück

Fachbereich Biologie/Chemie

Supervisor

H.-H. Bergmann, Universität Osnabrück

R.H. Drent, Rijksuniversiteit Groningen

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Rijksuniversiteit Groningen
Bibliotheek Biologisch Centrum
Kerklaan 30 — Postbus 14
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Abstract

In relation to different approaches to explain the diet selection of herbivores, the influence of plant characteristics, functional response and quality of the forage was investigated for geese as a model for small herbivores.

The preference of captive geese for three plant species and a wide range of biomasses was tested during cafeteria style experiments with small patches of natural vegetation. During the same trials the instantaneous intake rate was measured.

The geese showed a preference for fertilized turfs, and the protein content of the chosen plants was a better predictor for the preference than the dry matter intake rate. The preferred turfs had a lower biomass than it would be predicted from the intake rate maximization hypothesis.

Nevertheless fertilization shifted the preferred biomass to a higher level, closer to the optimum of intake rate. The relation between intake rate and biomass showed a large variation and neither the model of a dome-shaped nor that of an asymptotically functional response could be confirmed clearly.

2. Introduction

The optimal foraging theory tries to develop models for the diet selection of animals. There are two different basic assumptions: animals either try to minimize foraging time to avoid predation or they try to maximize their energy and/or nutrient intake.

Short term intake rates (per second, minute or hour) and daily intake have been measured or estimated to investigate whether animals really prefer the food that offers the highest intake rate. Many authors have stressed the necessity to distinguish between herbivores and carnivores (especially in searching and handling time) though there are also integrating models. Unlike most carnivores, herbivores have to deal with the problem that different food sources often contain different nutrients or at least different amounts of certain nutrients. This often results in the necessity for a to some extent mixed diet to meet all nutrient requirements.

BELOVSKI has developed a model to predict the optimal ratio of herbs and water plants in the diet of moose (1978). This model was based on the fact that herbs are rather low in sodium content while water plants are rich in sodium but if they also contain a large amount of water. On a pure water plant diet the moose could not meet its daily energy requirements because the rumen capacity is too small to consume enough plant material. Without consuming any water plants the moose would not be able to take up a sufficient amount of sodium.

Full grown plants are normally quite low in their protein content. Protein concentrations are higher in young plant parts but decrease as the plant grows older, mainly because of investments in structural components which also decrease the digestibility (CRAWLEY, 1983).

Consequently herbivores need relatively large amounts of plant material to derive sufficient energy and nutrients. To achieve this they spend most of the day foraging (and especially in ruminants also ingesting). There are only restricted possibilities to increase foraging time as food contains less energy or nutrients per volume. Therefore an intake maximization strategy would be expected to occur quite frequently in herbivores.

Different experiments have been done to find out which factors determine the intake rate, which is the product of bite size and bite rate. Many of the experimental approaches were done with artificial swards, either small patches of natural vegetation or single plants that were fastened to a large board from which the animal could forage (GROSS et al., 1993a). By this method plant height and density could easily be modified to determine their influence on intake rate. Plant characteristics like plant size and density influenced both bite size and bite rate. As bites became larger bite rates decreased because it took longer to swallow larger bites.

Most authors found that bite size determined intake rate (GROSS et al, 1993a, SPALINGER et al., 1988) and others indicate that bite rate was the main determinant of intake rate. Bite size and intake rate have been shown to increase with vegetation height, density or biomass and reach a plateau at high biomasses, which is defined as type II functional response. But there are also indications that intake rate shows an optimum and decreases when biomass gets very large especially in small herbivores (VAN DER WAL et al., 1998). This can be explained by increasing percentage of dead material which reduced foraging efficiency. Other explanations are the increase in structural components that are not digestible and because of this reduction of the energy and also the protein content (WILMSHURST & FRYXELL, 1995).

In many experiments the intake rates are related to choices made by wild animals or to additional choice experiments. But it is also possible to measure intake rate and test food preferences in one experiment by offering different food patches. ILLIUS et al. (1999) were able to show that although his goats only exhibited partial preferences the preferred patches had higher intake rates than the less preferred patches. DISTEL et al. (1995) could show the same for cattle.

Geese have been shown to be very selective feeders. White-fronted geese selected the largest lamina to maximize their intake rate (KRISTIANSEN et al., 2000) when the quality in terms of protein/nitrogen content is more or less equal. They are also able to respond to quality changes in their food plants. Fertilization has been shown to alter the habitat choice of geese (RIDDINGTON et al., 1997). In unfertilized areas they prefer short swards which are younger and therefore higher in protein content. On fertilized pastures geese prefer higher plants which are still relatively rich in protein.

2. Introduction

Barnacle geese have also been shown to switch from the polder on Schiermonnikoog in the Netherlands to the salt marsh exactly when the protein content of the salt marsh grasses is equal to that of the polder plants (PRINS & YDENBERG, 1985). Other authors (POP & DEERENBERG, 1991) argued that quality does not matter as long as protein content is above a certain threshold and that the geese would then select for the highest energy intake rates.

But as the habitat switch on Schiermonnikoog shows it is not possible to reduce the habitat selection of geese to only one factor as the protein content in the polder is equal or higher compared to the salt marsh throughout the whole season. Other factors concerning the vegetation like different growth rates or non-food related factors like the amount of disturbance might influence the choice of the geese.

In most cases investigations are done with only one factor that varies between treatments. However herbivores normally face a more complex problem because their food plants vary in different factors therefore a trade-off between those is necessary.

There are several measurements of intake rate of geese in relation to biomass. VAN DER WAL et al. (1998) found that barnacle geese had higher intake rates on low biomass compared to high biomass. TOLSMA (1998) found a dome-shaped functional response for brent geese where the intake rate increased with biomass, reached an optimum and decreased again. Also for brent geese GROS (1998) found an increase of intake rate with biomass at the quite low biomass level tested and intake rate as well as bite size were larger on fertilized patches than on unfertilized patches of the same biomass.

These experiments should be supplemented by combining intake rate measurements with tests of preference. Within cafeteria-style choice experiments with small vegetation patches the relationship between the functional response in terms of intake rate and the role of biomass, quality and functional response in diet selection of brent and barnacle geese should be tested for different vegetation types. Unlike in a traditional cafeteria experiment where the availability of all patches offered should be equal and the variation is restricted to only one parameter, the turfs tested here differed in a lot of respects. The patches that should be

compared were taken directly from the natural environment of the geese and part of them were additionally manipulated by fertilization and the exclusion of grazers for a period prior to testing. Therefore a lot of different factors could influence the foraging preferences.

The main questions that should be answered were:

- Which characteristics of the vegetation influence the preference?
- What shape does the functional response have for the different food species?
- Do the geese prefer patches that offer a high dry matter intake rate?
- Which role does the quality of the forage play for the preference?

3. Material and Methods

Study area

Brent and barnacle geese use to spend the winter in the wadden sea area where they feed on salt marshes, pastures and agricultural land. On Schiermonnikoog, one of the Friesian islands in The Netherlands, they spend most of the winter foraging on polder pastures which mainly contain *Lolium perenne* and *Poa annua* but from March onwards they abandon the polder and move to the saltmarsh in the eastern part of the island. There the grasses *Puccinellia maritima* and *Festuca rubra* are their main food species. Additionally the dicotyledons *Plantago maritima* and *Triglochin maritima* are consumed. The barnacle geese leave the island at the end of April to migrate to their breeding grounds while the brent geese stay until the end of May.

With the background of the habitat selection of wild geese on Schiermonnikoog during spring the foraging behavior of captive brents and barnacles should be tested.

For the foraging trials vegetation from the salt marsh and from the polder of Schiermonnikoog was used. In order to get patches that differ in quality and biomass, small exclosures were erected on the salt marsh and part of the chosen area was fertilized. Several data were collected on the vegetation parameters to control the development of the plots. After the different treatments had exhibited an effect on the vegetation, small turfs were harvested and presented to the captive geese in a cafeteria experiment. The foraging trials were used to collect data on the preference and on the mechanistic aspects of the foraging process.

3.1 Vegetation

Manipulation of the vegetation

The salt marsh on Schiermonnikoog can be divided into a western, cattle-grazed part that is between 50 and 200 years old and a younger part in the east which has never been grazed. As the island is growing to the east, the more eastern parts of the saltmarsh are younger than the western parts.

On the saltmarsh plots at eight different sites were established in the begin of April 2000 (table 3.1 and figure 3.1).

Table 3.1: Names and location of the different sites that were established on the salt marsh. Other plants that occurred quite frequently in the plots are listed. *Puccinellia* is distinguished in high and low *Puccinellia* (for further explanation see text).

| code | cattle-grazing | location | main species | other characteristics |
|------|----------------|------------------|--------------------|---------------------------------|
| 1 | yes | NBK | <i>Puccinellia</i> | high, <i>Glaux maritima</i> |
| 2 | yes | NBK | <i>Puccinellia</i> | low, <i>Suaeda maritima</i> |
| 5 | no | near Willemsduin | <i>Puccinellia</i> | high, <i>Artemisia maritima</i> |
| 6 | no | near Willemsduin | <i>Puccinellia</i> | low, <i>Salicornia europaea</i> |
| 3 | yes | NBK | <i>Festuca</i> | <i>Armeria maritima</i> |
| 9 | yes | OBK | <i>Festuca</i> | <i>Potentilla anserina</i> |
| 7 | no | near Kobbeduin | <i>Festuca</i> | - |
| 10 | no | near Willemsduin | <i>Festuca</i> | <i>Artemisia maritima</i> |

In total there were four *Festuca*- and four *Puccinellia*-sites, half of each on the cattle-grazed part and the others on the ungrazed part. The *Festuca*-sites differed in age, the biggest difference between the *Puccinellia*-sites was the distance to the mudflats or a gully and therefore the frequency of inundation. The *Puccinellia* (low *Puccinellia*) close to the sea was sparse and the plants were quite small during spring while the patches further away from the sea were much denser.

3. Material and Methods

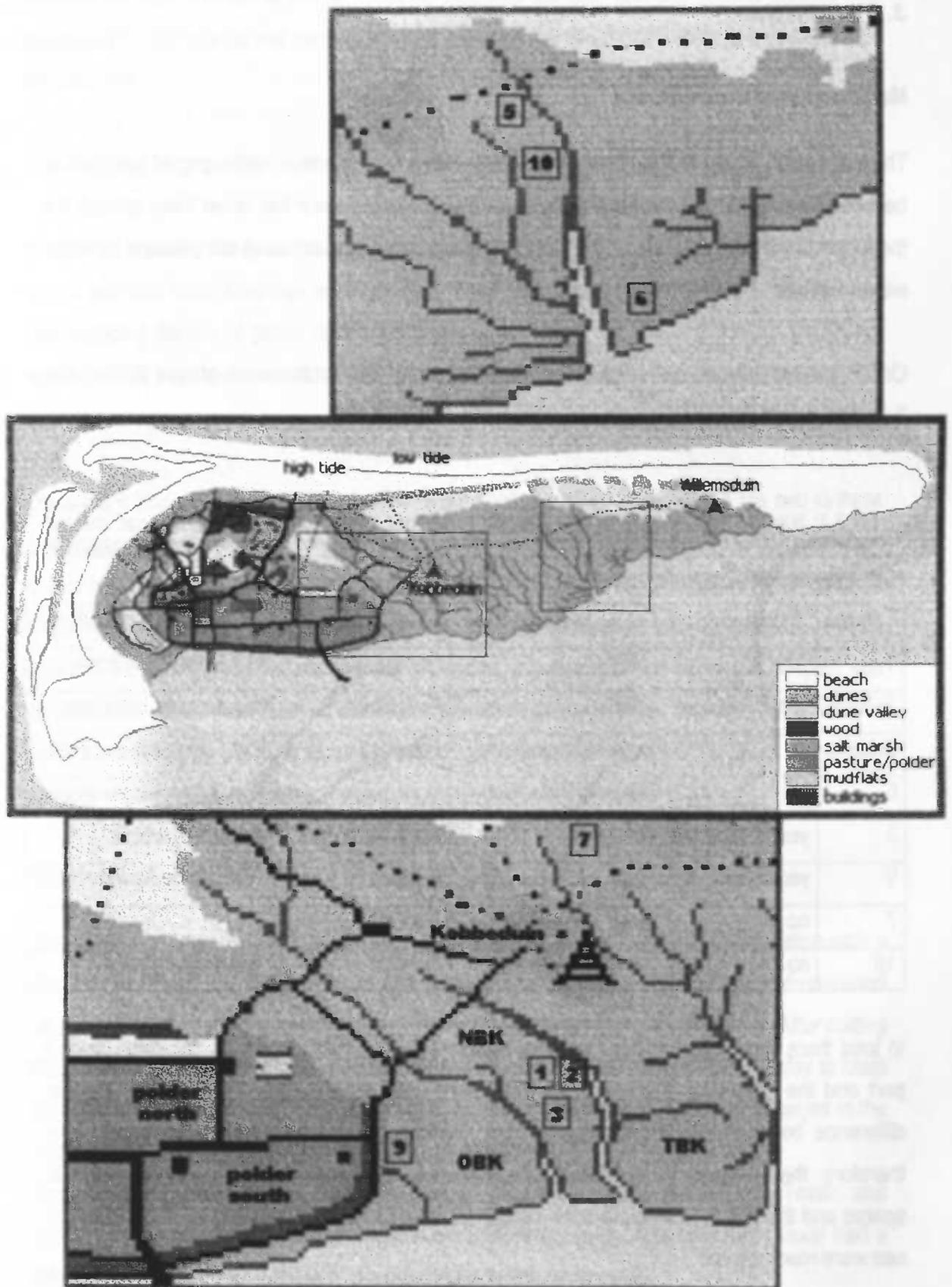


Figure 3.1: Map of Schiermonnikoog with all sites at the salt marsh and at the polder with enlargements of the Kobbeduin- and Willemsduin-area.

Each of the sites contained four different treatments in plots of 1 times 2 metres: fertilized and excluded, fertilized and not excluded, not fertilized and excluded, not fertilized and not excluded (figure 3.2). Fertilized plots were fertilized twice with a ten day interval in between. An amount of 25g of customary nitrogen fertilizer / m² solved in 5l of water was used for each plot at both days.

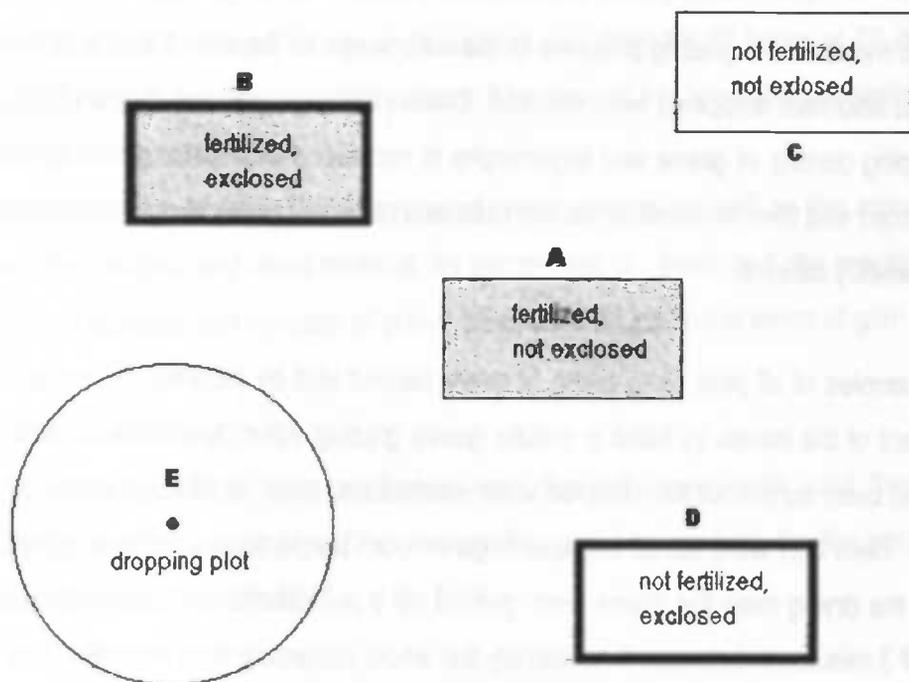


Figure 3.2: Structure of each salt marsh site. The arrangement of the plots was random. Fertilized plots are indicated by a grey background, excluded plots by a thick rim.

The exclusions consisted of a 50 centimetres high chicken wire fence to keep geese and hare out of the plot. The not excluded plots were marked by small (10 cm above the ground) bamboo sticks at the corners. Each site contained an additional circular dropping plot, marked by a plastic or bamboo stick.

Vegetation parameters

The plots were visited on average once a week to measure several vegetation parameters: Vegetation height was measured five times per plot with a polystyrene disc, which slid along a graduated stick and came to rest on top of the canopy while the end of this stick was pushed

through the sward to the soil. The distance between the disc and the ground surface was measured to the nearest half centimetre. The mean of the five measurements was calculated for each plot.

The coverage of green and dead material at each plot was estimated in per cent.

In order to measure the grazing pressure of the wild geese on the island on the different plots, goose and also hare droppings were counted. OWEN (1971) respectively WOOD (1988) showed that dropping density of geese and lagomorphs is correlated with grazing density. Droppings were counted and then removed at the not exclosed plots and at the 4m² circular dropping plot at about weekly intervals.

Quality samples of all plots were taken at every second visit by plucking the top two to three centimeters of the leaves by hand to imitate goose grazing. After dead material and non-food plants had been sorted out the samples were washed and dried at 70 degrees for 48 hours in the oven. Then they were stored in paper bags at room temperature prior to analysis. After 24 hours in the drying oven the plants were ground by a pulverisette for 3 times 3 minutes with breaks of 3 minutes in between. If necessary the whole procedure was repeated. The samples were then analyzed CNHS analysator for nitrogen and carbon content. To attain the protein content of the sample the nitrogen content was multiplied by the factor 6.25.

The turfs

The vegetation was offered to the geese as turfs, small, round patches of vegetation with a diameter of 16 cm. The turfs were cut with a metal cylinder with a serrated rim and contained all aboveground vegetation and an approximately three-centimeter thick soil layer. After cutting they were kept at the field station protected by a small fence and watered twice a day to keep them fresh. They were used in the experiment as soon as possible to avoid any changes in the vegetation. However many of the turfs were reused later.

The turfs originated from different places: different polder areas on Texel and Schiermonnikoog, and from the salt marsh on Schiermonnikoog. The turfs from Texel had a different shape and size, they were squares of ten by ten centimetres.

Biomass samples

The biomass of turf was determined by clipping all aboveground biomass. This was done for one turf per treatment while the remaining turfs were used during the experiments at the same time.

The biomass was divided into dead material, dicotyledons and grasses. Each section was weighed separately to the nearest 10 mg, then washed and dried for 48 hours at 70 degrees and weighed again to determine the dry biomass. The ratio of fresh weight/ dry weight was determined for the monocotyledons.

For the analysis the total biomass, the biomass of green grasses as well as the amounts of green grass, dicotyledons and dead material (in percentage of fresh and dry weight) were determined. Total biomass and biomass of green grass were expressed in terms of g/m².

The salt marsh experiments

The turfs from the salt marsh trials originated from the salt marsh plots and they were harvested during the first half of May. The *Puccinellia*- and *Festuca*-turfs for the polder-salt marsh comparison came from the NBK and the OBK.

The polder experiments

Schiermonnikoog: Turfs from two different pastures were taken, one in the northern part of the polder and the other situated in the southern part of the polder, only separated by a road. The first was not visited by geese any more at the beginning of April, the later was still heavily used by geese during March and April.

The turfs from Texel originated from an experiment done by Daan Bos and Lutz von der Heyde (VON DER HEYDE, 2001). They had built up exclosures on two different pastures at the Zeeburg polder. These exclosures were opened at the same date for the wild geese (at May, 7th) and they had been established one, two, four or six weeks prior to the opening date. Some of the plots have been excluded from fertilization by putting plastic foils on the ground when the farmer fertilized the pasture. The fertilizer was then removed together with the plastic foils. In total there were 8 different treatments with seven replicates each (further referred to as plots) (table 3.2). From each plot four turfs (10 x 10 cm) were taken.

Table 3.2: The different treatments of the Texel-experiment.

| treatment | fertilization | exclosure established ... weeks prior to May, 7th |
|-----------|---------------|---|
| 2l | no | no exclosure |
| 4l | no | 1 |
| 8l | no | 2 |
| 2n | yes | no exclosure |
| 4n | yes | 1 |
| 8n | yes | 2 |
| 12n | yes | 4 |
| 20n | yes | 6 |

3.2 Animals and experimental procedure

The geese

The experiments were done with three male dark-bellied brent geese *Branta bernicla bernicla* (NYJ, "red" and "white") and three barnacle geese *Branta leucopsis*. Two of the barnacles (NSX and NZN) were males, the only female in the group (DFA) was replaced by a third male (NNS) in the middle of May. Thus seven different individuals have been used during the trials altogether. One of the brents ("white") and one of the barnacles (NSX) were juveniles born in the previous year. All the barnacle geese were born in captivity in the goose colony kept at the University of Groningen in Haren while the brent geese were captured from the wild. The adult males have been caught on Texel in 1996, the juvenile male has been caught on Schiermonnikoog on April 6th, 2000 with a mistnet.

The geese were kept in an approximately 250m² large enclosure built of netting next to the field station "De Herdershut" on Schiermonnikoog. Part of the enclosure was also covered with netting. The pen was separated into three bigger and four smaller compartments (figure 3.3). The geese were able to use all the small compartments and two of the bigger (either I and II or II and III) while the sward third large one was able to regrow. All compartments contained a grass sward which enabled the geese to feed continuously and water buckets for drinking and bathing (water was missing in one of the small compartments).

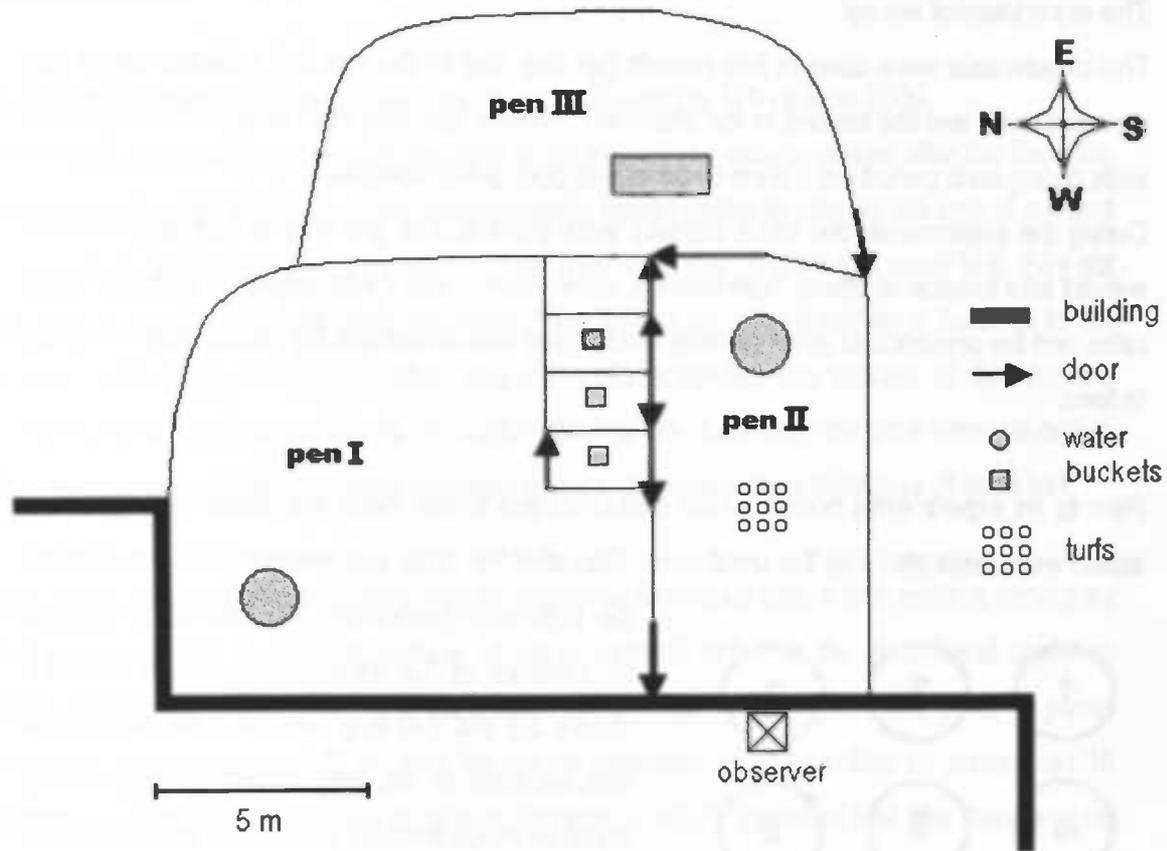


Figure 3.3: Schematic set-up of the goose enclosure

The geese arrived on Schiermonnikoog at April 4th, 2000. They were weighed every second week to monitor their condition (the weight data are given in the appendix). They were touched only at these occasions.

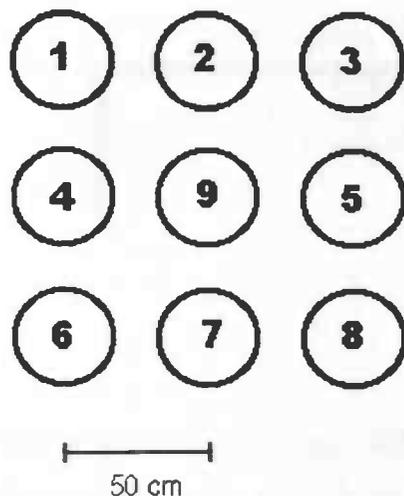
The first feeding trial with turfs started at 5th of April, first including the whole group later two or three geese at once. From April 17th on, the geese were separated and then released for individual foraging trials. The experiments that were taken into account for the analysis started at April 20th. Some turfs were placed in the pen during the rest of the day to maintain the feeding motivation especially during periods in which not that many trials were conducted.

The experimental set-up

The experiments were done in two periods per day, one in the morning between seven and eleven o'clock and the second in the afternoon between four and eight o'clock. If possible the trials during each period were done by turns with both goose species.

During the experiments the focus animals were separated to get data of individual animals without interference of others. Interference would have made it impossible to estimate intake rates and the presence of other animals would have also influenced the choice from which turf to feed.

Prior to an experimental period, which contained one to five trials, the geese that should be tested were separated into the small pens. One after the other was released into pen II where



the turfs were presented. The turfs were arranged in a square of 1.2 meter in the middle of pen II (figure 3.3 and 3.4) in a random order. As the pen was adjacent to the field station all observations could be made through the window to minimize the disturbance by the observer. Big parts of the window were additionally covered with paper. Because of the construction of the pen by nets the geese were able to see and hear each other even when they were separated.

Figure 3.4: Arrangement of the turfs in the experiment. The numbers indicate the position.

After a trial the geese were able to feed from additional waterfowl food pellets for one to two hours. As the dominant individuals in the group tried to monopolize the food, the low ranking animals were allowed to feed on the pellets after a feeding trial for about ten minutes before they were released to the group. This was done to ensure that all geese were able to obtain sufficient additional food.

The experiments

The experiments were done between the 20th of April and the 17th of June 2000.

All the turfs that were supposed to be used in an experiment were prepared after the previous experimental period was over. They were placed in plastic dishes to prevent the loss of soil and to be able to clean them prior to weighing. Then they were kept in a barn to avoid that they got wet by rain or dew. All turfs were weighted twice before an experiment on a balance to the nearest tenth gram. Additionally other vegetation characteristics like species of dicotyledons present and the number of plants of certain species like *Artemisia maritima* were recorded. After the experiment the turfs were weighted again to determine the weight loss of each turf.

One of the goals of the experiments was to determine the intake rate, which made it necessary that the goose took a sufficient number of pecks from all turfs. On the other hand depletion effects should be avoided. So the experiment was stopped after approximately 30 to 50 pecks had been taken from all turfs or after the goose obviously stopped eating for more than 10 minutes or after 30 to 40 minutes in total dependent on which happened first. But there was no identical stopping rule for all trials. In some trials only part of the turfs were presented, especially those that had been rejected by the geese in earlier trials to get intake rate data from these turfs, too. In other trials the most preferred turfs were removed after a while for the same reason and to avoid the depletion of the favorite turfs.

Per trial between four and nine turfs were offered simultaneously to the goose as a cafeteria style experiment. (Table 3.3) gives an overview over the different types of experiments with the various turfs involved.

Table 3.3: The different types of experiments

| type of experiment | geese | turf 1 | turf 2 | turf 3 | turf 4 | turf 5 | turf 6 | turf 7 | turf 8 | turf 9 |
|-----------------------------|--------|----------------------------|--------|-----------------------|-----------------------|-------------|------------------------|-----------------------|-----------|--------|
| | | south with fresh water | high | south with salt water | north with salt water | medium | north with fresh water | north with salt water | short | - |
| polder: salt, height | all | 2l | 4l | 8l | 2n | 4n | 8n | 12n | 20n | - |
| polder: height | all | polder | | Festuca | | Puccinellia | | | | |
| Texel | brents | polder | | Festuca | | Puccinellia | | | | |
| polder-Festuca-Puccinellia | all | 3A | 3B | 3C | 3D | 9A | 9B | 9C | 9D | |
| grazed Festuca | all | 7A | 7B | 7C | 7D | 10A | 10B | 10C | 10D | |
| ungrazed Festuca | all | 3C | 3D | 9C | 9D | 7C | 7D | 10C | 10D | |
| grazed/ungrazed Festuca | all | 1A | 1B | 1C | 1D | 2A | 2B | 2C | 2D | |
| grazed Puccinellia | all | 5A | 5B | 5C | 5D | 6A | 6B | 6C | 6D | |
| ungrazed Puccinellia | all | 1C | 1D | 2C | 2D | 5C | 5D | 6C | 6D | |
| grazed/ungrazed Puccinellia | all | with Artemisia | | without Artemisia | | | | | | |
| Artemisia removed | all | with Artemisia | | without Artemisia | | | | | | |
| clipped | all | A old | B old | C old | D old | A clipped | B clipped | C clipped | D clipped | |
| control | all | 8 turfs from the same plot | | | | | | | | |

The evaporation

Each turf was weighted three times (w_1 , w_2 , w_3), twice before the experiment and once afterwards. The times at which the weighing took place (t_1 , t_2 , t_3) were noted. The evaporation was estimated by the weight loss before the experiment divided by the time between the weighing:

$$\text{evap (gram/minute)} = w_1 - w_2 / (t_2 - t_1)$$

This evaporation value had to be corrected due to the fact that evaporation was changing during the day (figure 3.5) and therefore also during the experiment. The percentage of change was calculated from soil evaporation data measured at the weather station on Schiermonnikoog.

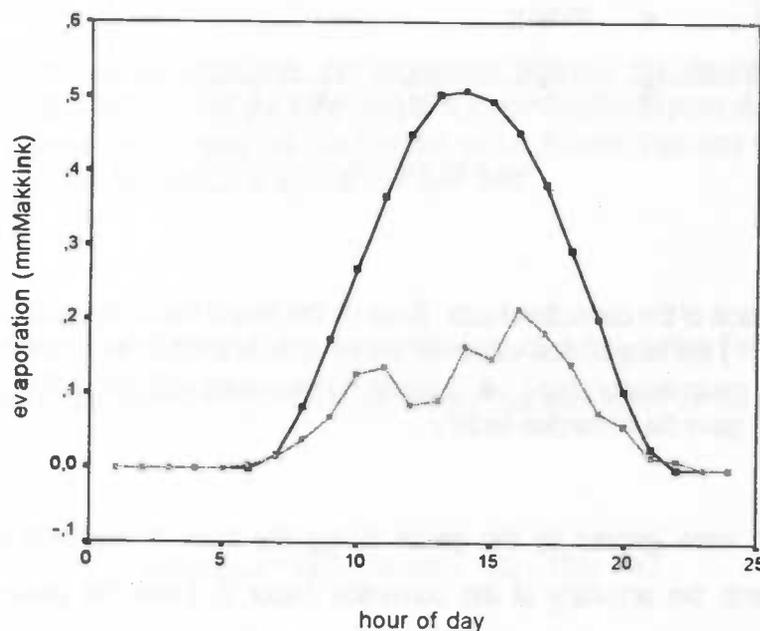


Figure 3.5: The daily pattern of the evaporation at the example of May 6th (black line) and June 13th, 2000 (grey line)

The soil evaporation was determined for the exact times t_1 , t_2 and t_3 . Then the correction factor was calculated as:

$$c = ((\text{evap}_{t_2} + \text{evap}_{t_3}) / 2) / ((\text{evap}_{t_1} + \text{evap}_{t_2}) / 2)$$

The measured evaporation was corrected by c:

$$\text{evaporation}_{\text{corrected}} = \text{evaporation}_{\text{measured}} * c$$

An example for this calculation is given in figure 3.6.

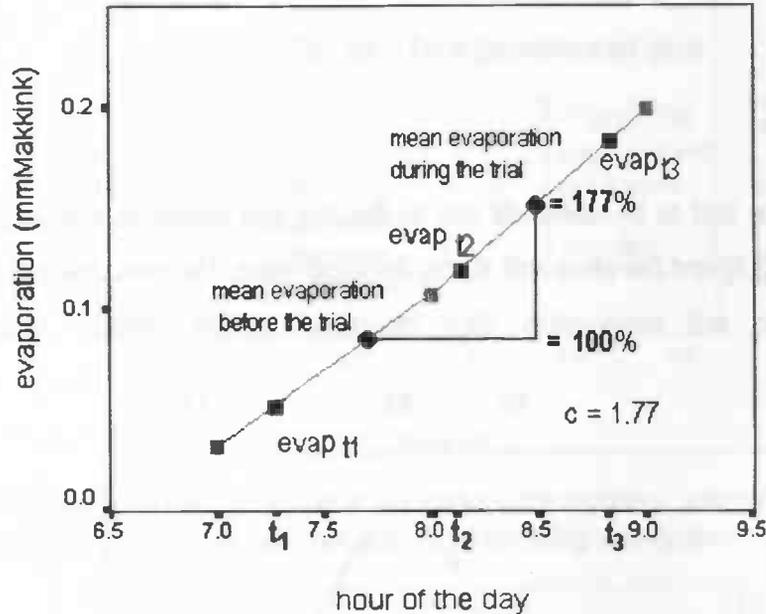


Figure 3.6: Calculation of the correction factor. Base on the hourly measurements from the weather station (■) the evaporation values for the times t_1 , t_2 and t_3 (■) were calculated. The quotient of the mean evaporation (●) during $((\text{evap}_{t_2} + \text{evap}_{t_3})/2)$ and before the trial $((\text{evap}_{t_1} + \text{evap}_{t_2})/2)$ gave the correction factor c .

Some of the turfs were ignored by the geese during the trials. These turfs provided an opportunity to check the accuracy of the correction factor c . From the unused turfs the evaporation during the trial was determined and a new, directly measured correction factor c_m was calculated. c_m was compared with the calculated correction factor c trials were only used in the intake rate analysis if the relationship of the two factors was within the 95% confidence interval for the regression (figure 3.7).

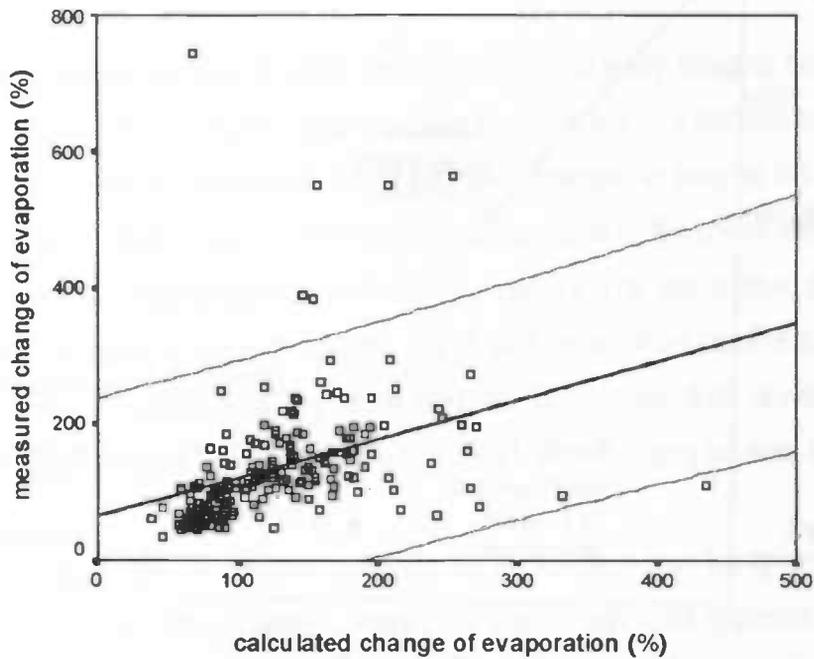


Figure 3.7: Check of the correction: the regression between the measured c_m and the calculated correction factor c with the 95% confidence intervals. Each point represents one trial during which at least one turf was not used by the goose. If more than one turf had not been used, the mean of the derived correction factors was used.

With help of the corrected evaporation the weight loss of a turf during the experiment was divided into water loss due to evaporation and weight that was eaten by the goose (figure 3.8 and 3.9):

$$\text{intake}_{\text{goose}} = (w_2 - (\text{evap}_{\text{corr}} * (t_2 - t_3))) - w_3$$

In some cases the weight loss of a turf was negative even after correction of the evaporation.

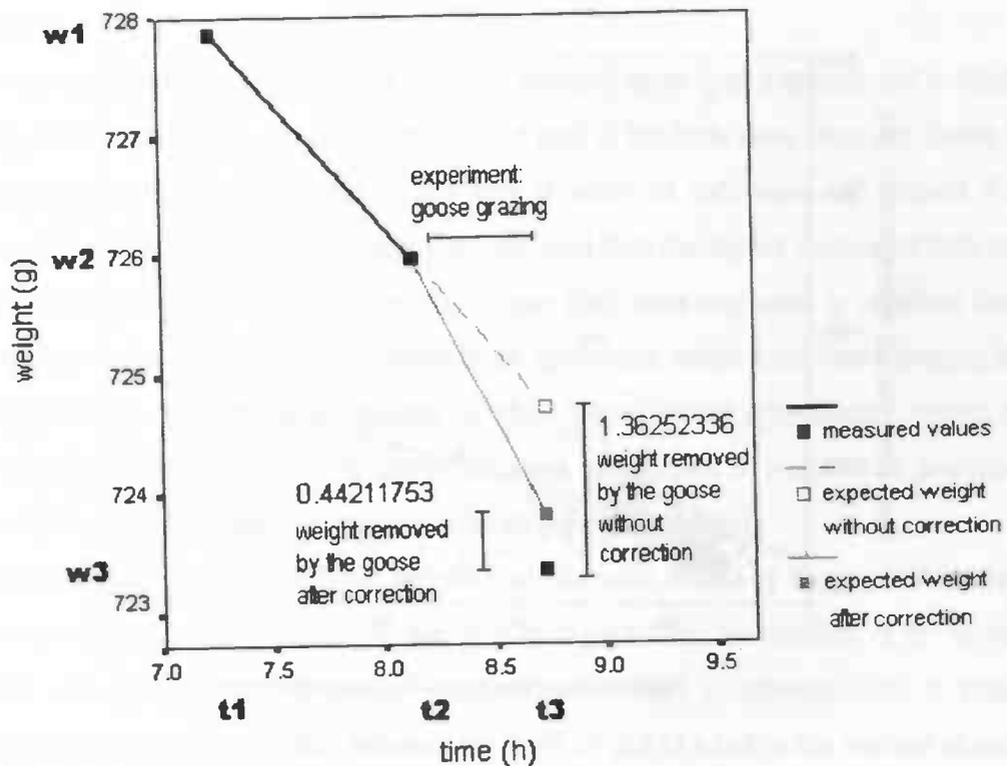


Figure 3.8: Example for the calculation of the intake in the morning, without the correction the weight loss would be overestimated because of a increasing evaporation.

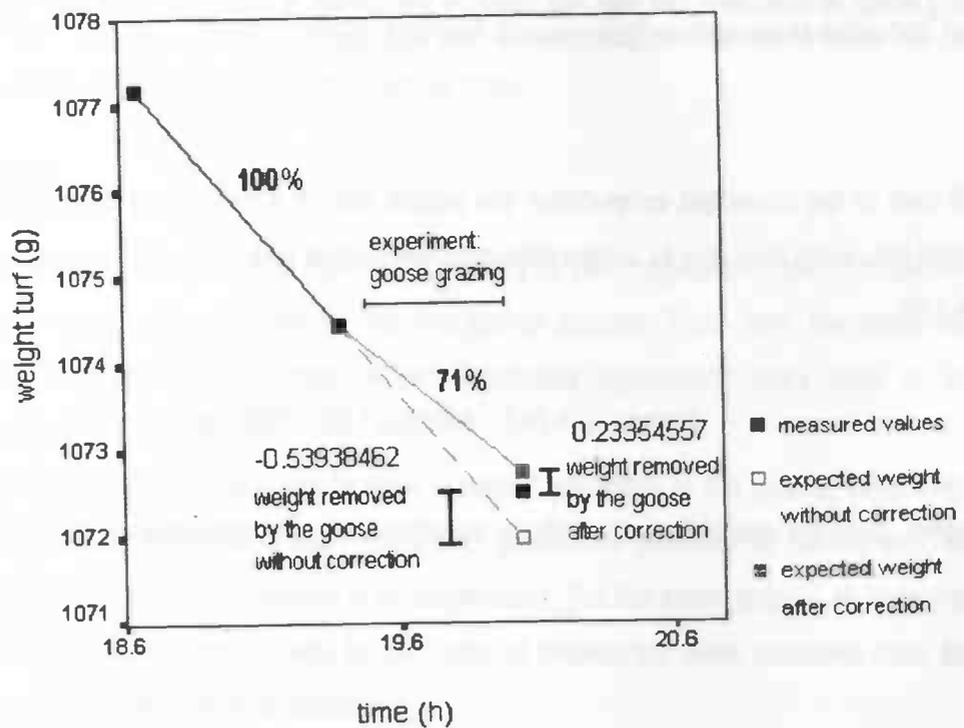


Figure 3.9: Example for the calculation of the intake in the afternoon. Without correction the weight loss would have been negative due to a decrease of the evaporation during the trial.

Intake rate

During the experiment the number of pecks and the duration of every foraging bout at a turf was recorded together with the number of pecks taken from that turf on a portable computer. A foraging bout began when an animal took a first bite and continued as long as the animal did not raise its head above the horizontal. Time was stopped as soon as the goose lifted the head from the turf but after swallowing the bite that it had taken before. The goose could then start to feed at the same turf again or move to another one. A visit ended when there was a break in the feeding behavior, if the goose left the turf to feed somewhere else, drink or rest. The total foraging time for each turf was calculated as the sum of all single foraging bouts at that specific turf.

Additional to the pecks from the different turfs also the pecks taken from the grass of the pen surrounding the turfs were counted and the occurrence of other behaviors recorded.

Instantaneous intake rates of dry matter (further just called intake rates) were calculated as weight loss minus estimated evaporation (which could result in negative values for weight loss and therefore also intake rates) divided by foraging time.

$$\text{intake rate (mg dry weight)} = \frac{\text{(weight removed by the goose * dry weight/fresh weight)} / \text{foraging time (s)}}{\text{foraging time (s)}}$$

The ratio fresh weight/dry weight was determined for each type of turf by dividing the amount fresh biomass of grasses by the dry weight of grasses.

Bite size was calculated as weight loss of the turf minus evaporation divided by number of pecks taken.

$$\text{bite size (mg dry weight/peck)} = \frac{\text{(weight removed * dry/fresh)} / \text{number of pecks}}{\text{number of pecks}}$$

Peck rate was calculated as number of pecks divided by foraging time.

$$\text{peck rate (pecks/s)} = \frac{\text{number of pecks}}{\text{foraging time (s)}}$$

Calculated bite sizes and the corresponding intake rates were used in the analysis only if they were within the five times standard error of the mean bite size.

Preference

Preference was defined as proportion of pecks (in percent) taken from a specific turf in relation to pecks taken from all turfs present in that trial. If part of the turfs were removed during the trial, preference was only calculated for the time at which all turfs were still present if not indicated differently. In the same way also trials with less than the regular number of turfs were ignored for preference data. Data derived from those trials were only used to calculate intake rates and bite sizes. Alternative measurements for preference would have been foraging time and intake (weight removed by the goose). All three measurements were closely related and would have given similar results. The number of pecks was chosen as indicator for preference because it was the parameter that could be determined most accurately.

Additionally to that, in each experiment all turfs that had been visited by the geese have been assigned to ranks of preference for both the number of pecks and the duration of the foraging time. This was done in order to enable a comparison of trials of different types to look at general patterns like the correlation between the order of visit of a turf or the number of pecks per visit and the preference.

The motivation of the geese was calculated as number of pecks taken from all turfs together or as sum of pecks from the turfs and from the grass of the pen. Both values were related to the duration of a trial to be able to compare the various trials.

3.3 Analysis

All experiments have been analyzed together according to their vegetation type to determine the functional response but separate for the two goose species. Turfs from the trials with mixed-species turfs (id est the polder-*Festuca-Puccinellia* experiment) were used in the corresponding vegetation types.

For the preference data the different turfs were analyzed according to the type of experiment they have been tested in because the measure of preference (number of pecks) was not independent from the other turfs present in an experiment. For the same reason all trials that did not contain the full number of turfs for this type of experiment were excluded from the preference analysis unless indicated otherwise.

The statistics

Values are given as means \pm standard error if not specified otherwise.

The analysis was done with SPSS, version 8.0. Only significant regression lines were shown, first a linear regression was done and if that was significant a quadratic regression was calculated and only used if the derived term gave a significant improvement of the regression. For the regression the degree of freedom is given for the analysis of variance of the residuals. The influence of different factors and covariates on variables were tested with the univariate anova (general linear model, GLM, in SPSS). For the regression lines significant p-values were indicated by "***". For the GLM analysis only significant effects were given

For analysis intake rates as well as preference data were compared in pairs as the natural logarithm (ln) of the ratio of intake rates from turf A and B. The method was described by ILLIUS et al. (1999) and ELSTON et al. (1996). This was done to overcome the problem of correlation between the number of pecks taken from the different turfs in one trial. Two turfs (of the same trial) were compared directly by the ratio of different parameters measured on the turfs to explain differences in preference, which means in the proportion of pecks taken from each turf.

$$\ln pA/pB = \ln (\text{number of pecks taken from turf A} / \text{number of pecks taken from turf B})$$

In a trial with eight different turfs there are 28 different pairs of turfs. The two turfs of each combination were randomly attributed to be either A or B. If no pecks have been taken at all from a turf the ln ratio could not be calculated. Therefore zero values are treated as if they were 0.5 while 0.5 was subtracted from the number of pecks from the corresponding turf. This means:

If the number of pecks was 0, the ln ratio was calculated as: $\ln (0.5/(n - 0.5))$

A regression analysis was done for the natural logarithm of the ratio of pecks against the natural logarithm of the ratio of either protein content, intake rate, protein intake rate or complete biomass. The ratio of intake rate and protein intake rate was derived from the regression between intake rate and biomass.

3. Material and Methods

The derived regression line was back-transformed and the results shown as proportion of pecks taken from turf A ($pA/(pA + pB)$) against the ratio of intake rates, biomasses and so on. The sensitivity to the difference in the characteristics (c) of the turfs is indicated by b, which is the slope of the regression between $\ln(pA/pB)$ and $\ln(cA/cB)$,

$$\ln(pA/pB) = b * \ln(cA/cB)$$

or the exponent in the formula

$$pA/pB = (cA/cB)^b.$$

For a given \ln ratio of characteristics $x = \ln(cA/cB)$, the proportion of pecks taken from turf A can be calculated as:

$$y = e^{x*b} / (e^{x*b} + 1)$$

This method is quite effective in detecting simple positive or negative relations between the two ratios but fails to detect quadratic, dome-shaped relations.

In order to investigate the switching between the turfs during the trials the grazing pattern of the captive geese was analyzed for all trials that contained eight turfs. A matrix was formed that contained the frequency of switching between the different positions of turfs (table 3.4 gives a part of this matrix).

Table 3.5 : Frequency of switches from turf at position A to the turf at position B (part of the matrix)

| from turf A | to turf B | | | |
|-------------|-----------|-----|-----|----|
| | 1 | 2 | 3 | 4 |
| 1 | 34 | 140 | 26 | 95 |
| 2 | 88 | 21 | 133 | 67 |
| 3 | 26 | 84 | 10 | 20 |
| 4 | 112 | 64 | 16 | 8 |

To take account of the fact that some turfs were visited less often the expected frequencies were computed from the matrix as:

$$f_{\text{expected}} = (\text{sum of rows} * \text{sum of column}) / \text{total sum}$$

3. Material and Methods

The observed pattern was compared to the expected values by the Chi-square test for the goodness of fit (in SsS). The strength of the relation between two factors (id est the fact that a switch from turf A to turf B occurred significantly more frequently than expected) was derived from the c-values which were calculated as:

$$c_2 = \text{observed frequency} / (\text{expected frequency} + \sqrt{\text{expected frequency}})$$

$$c_3 = \text{observed frequency} / (\text{expected frequency} + 10 \cdot \sqrt{\text{expected frequency}})$$

If c_2 was larger than 1 a relation between the two factors was indicated and if c_3 was also larger than 1, this relation was considered as strong.

4. Results

4.1 Vegetation

The different treatments started to effect the vegetation development after about two weeks after the establishment of the exclosures and the first fertilization. The vegetation was higher inside the fertilized exclosure than inside the unfertilized and in most cases it was higher at the exclosed plots compared to the plots that were open for the wild herbivores. An example of the vegetation development is given in figure 4.1 for the high *Puccinellia* on the NBK (site 1). The turfs were harvested at day 40. The decrease in vegetation height after day 40 for the exclosures is due to the start of cattle grazing on the NBK which was not prevented by the small exclosures.

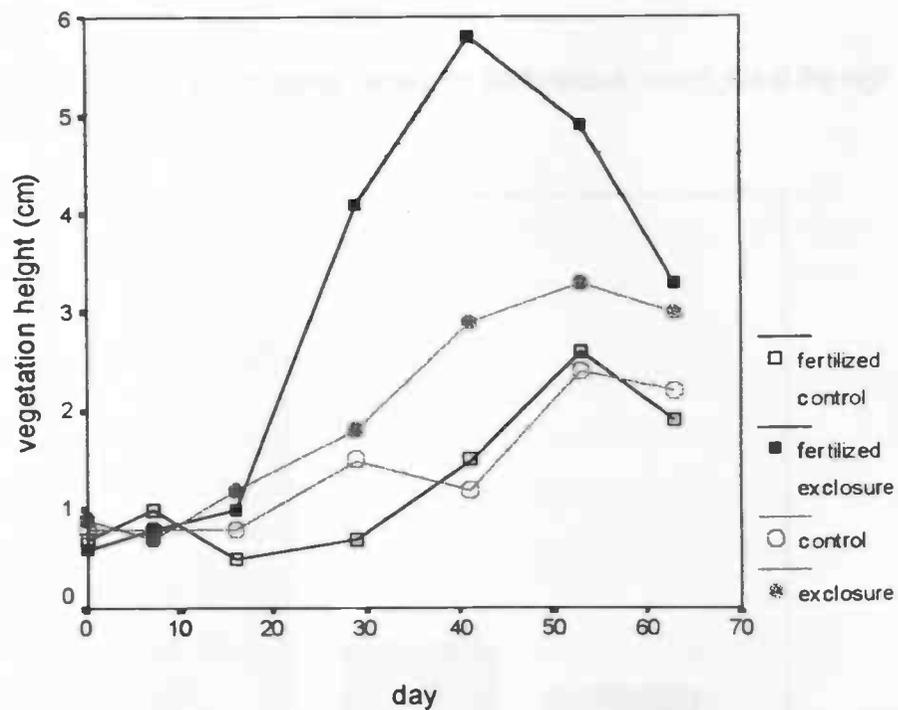


Figure 4.1 : Development of the vegetation height for the for different treatments at site 1, the high *Puccinellia* on the NBK. Day 1 is the 7 th of April.

The development of the control (goose and hare grazed) plots depended on the grazing pressure. If hardly any grazing took place like at the not fertilized control plot at Kobbeduin the vegetation height increased as much as inside the exclosure and the actual height was even higher due to the greater height at the beginning. The same was true for the high *Puccinellia*

4. Results

site at Willemsduin where both control plots have been abandoned from grazing and developed similar to the exclosures (figure 4.2).

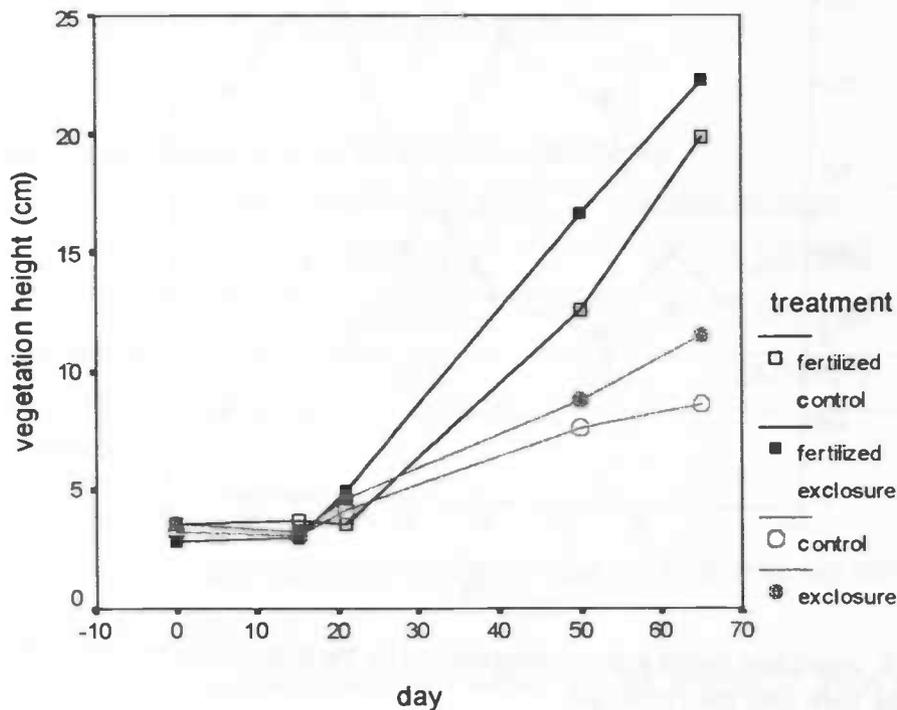


Figure 4.2: Development of the vegetation height at site 5, the high *Puccinellia* near Willemsduin after the establishment of the different treatments on April 9th. The turfs were harvested at day 30.

The relationship between the grazing pressure in terms of dropping density and the vegetation height is shown in figure 4.3 for the fertilized control plot of the high *Puccinellia* on the NBK. The vegetation height hardly increased or even decreased during periods with high dropping densities.

The cumulative dropping densities differed for the fertilized and unfertilized plots of a site as shown for the same site, the high *Puccinellia* on the NBK (figure 4.4). The fertilized plots were used more intensely by the wild geese than the other two unfertilized plots.

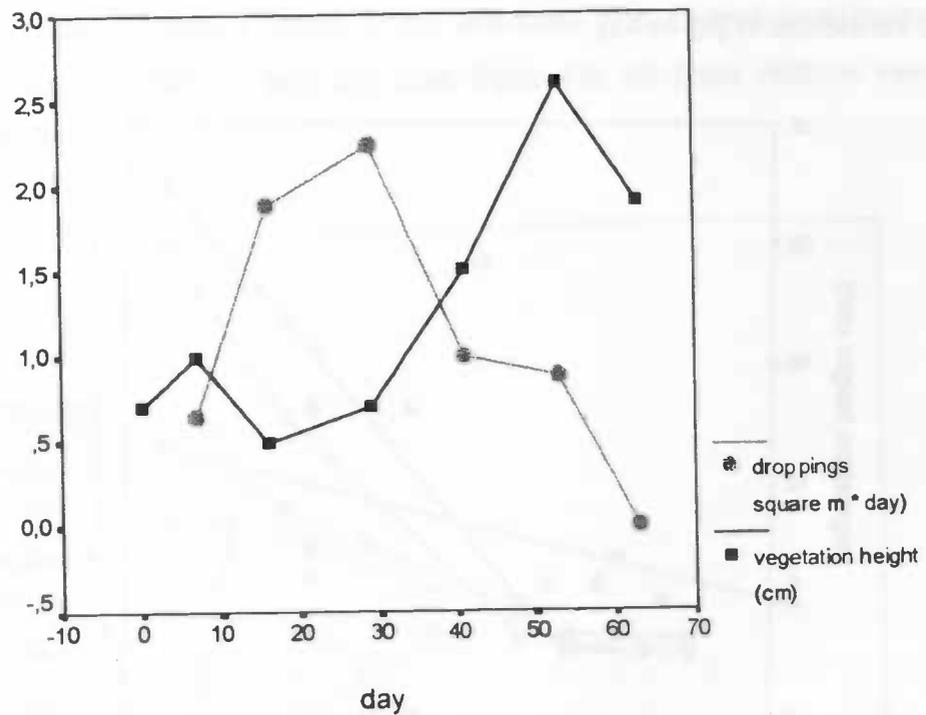


Figure 4.3: Vegetation height and dropping density for the fertilized control plot at the high Puccinellia, NBK after the 7th of April.

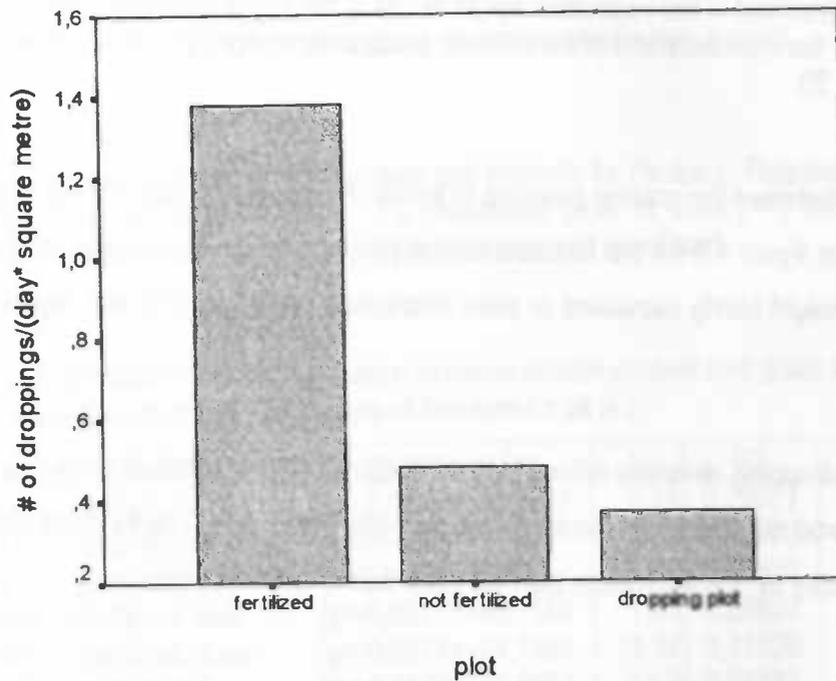


Figure 4.4: Cumulative dropping densities at site 1, high Puccinellia NBK for the interval between 7th of April and 30th of May

Quality

The quality in terms of the protein content was compared for the three vegetation types. The protein content was highest for the polder and lowest for the *Festuca* (table 4.1), but the differences were not significant (Kruskal-Wallis test, $p = 0.067$).

Table 4.1 : Mean protein content (n=2) for the different plants species

| plant species | mean protein content (%) | standard deviation |
|---------------|--------------------------|--------------------|
| Lolium/Poa | 29,234375 | 0,29610096 |
| Puccinellia | 23,89375 | 0,64523494 |
| Festuca | 19,9 | 2,42184073 |

Quality and biomass

For the salt marsh plots the protein content of the different sites and treatments was compared in relation to the biomass of the grass.

The protein content of the *Puccinellia* decreases linearly with the biomass of green grass if lines were fitted separately for fertilized and unfertilized plots. Additionally it was distinguished between the quality of the fertilized plots at begin of May and at the begin of June (figure 4.5).

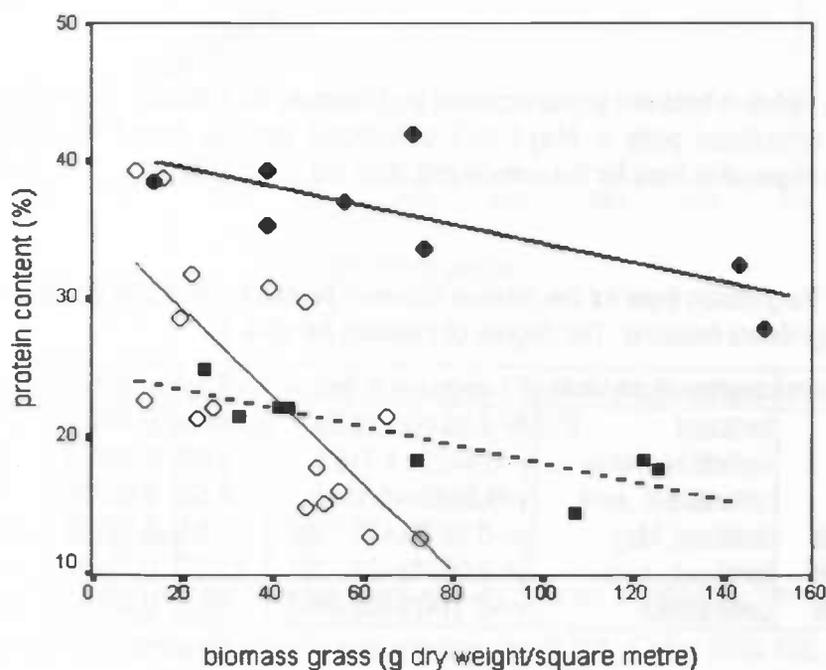


Figure 4. 5: Relation between protein content and biomass for *Puccinellia*. Regression lines are given for unfertilized plots (○), fertilized plots in May (●) and fertilized plots in June (■).

For the *Festuca* there was a significant decrease in protein content with increasing biomass for the fertilized plots. The protein content of the unfertilized plots showed an increase with biomass if fitted separately for May and June (figure 4.6) but these relations were not significant (table 4.2.)

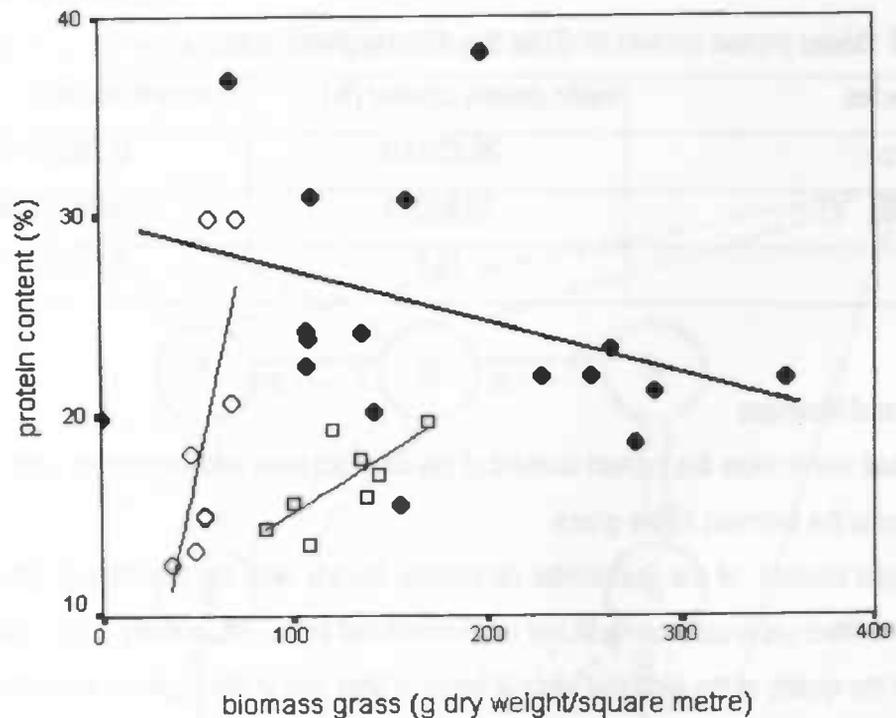


Figure 4.6 : relation between protein content and biomass for *Festuca*. Regression lines are given for unfertilized plots in May (\diamond), unfertilized plots in June (\square) and fertilized plots (\bullet). The regression lines for the unfertilized plots are not significant.

Table 4.2: Regression lines for the relation between protein content and grass biomass. ** indicate significant relations. The degree of freedom for all is 1.

| plant species | treatment and time | regression line | F | R2 | p |
|--------------------|--------------------|--------------------------|-------|---------|----------|
| <i>Festuca</i> | fertilized | $y = -0,0411x + 32,2277$ | 5,74 | 0,29071 | 0,0311** |
| <i>Festuca</i> | unfertilized, May | $y = 0,4401x - 4,7167$ | 5,95 | 0,49772 | 0,0506 |
| <i>Festuca</i> | unfertilized, June | $y = 0,0603x + 9,1515$ | 6,59 | 0,52359 | 0,0603 |
| <i>Puccinellia</i> | fertilized, May | $y = -0,0677x + 40,7359$ | 7,63 | 0,55976 | 0,0328** |
| <i>Puccinellia</i> | fertilized, June | $y = -0,0674x + 24,7361$ | 15,07 | 0,71528 | 0,0081** |
| <i>Puccinellia</i> | unfertilized | $y = -0,3147x + 55,6687$ | 15,9 | 0,53183 | 0,0013** |

4.2 Experiments

Preference: foraging time, number of pecks and amount of weight removed

The three possible indicators for preference gave very similar results because they were correlated with each other.

The number of pecks taken from a turf and the time spent foraging at this turf are highly correlated ($p < 0.001$) (figure 4.7). The same is true for both the relationship between foraging time and weight removed ($p < 0.001$, $F = 39.769$, $d.f. = 996$, $y = 0.097x + 14.924$) and the number of pecks and the amount weight removed ($p < 0.001$, $F = 40.065$, $d.f. = 996$, $y = 6.619x - 165.782$).

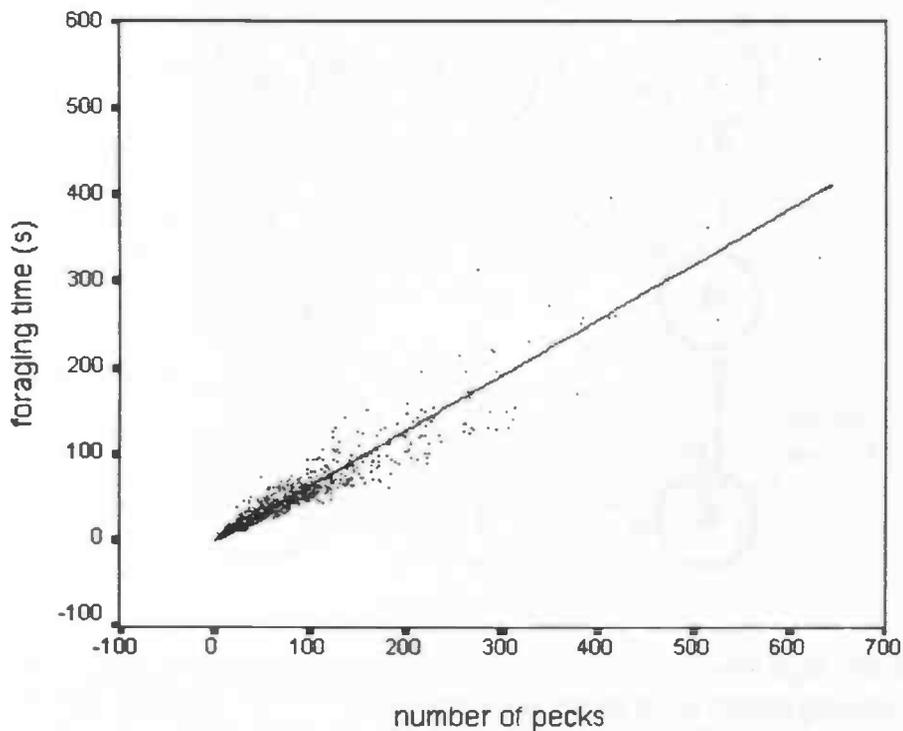


Figure 4.7 : Correlation between the number of pecks and the foraging time (geometric mean regression, $p < 0.001$, $F = 101.249$, $d.f. = 996$): $y = 0.64x - 0.679$

Grazing pattern of the geese

The frequency of switches between certain pairs of turfs differed significantly from a random order. This was true if a normal distribution was expected ($p < 0.001$, $\text{Chi}^2 = 2620.135$, $d.f. = 80$) and if the observed pattern was compared with the expected frequency based on the different number of visits observed for each position ($p < 0.000001$, $\text{Chi}^2 = 2197.421$, $d.f. = 64$, $K(\text{Pearson}) = 0.665$, $C = 0.314$).

The geese moved clockwise or sometimes counterclockwise around the arrangement of turfs (figure 4.8). In some cases they skipped the corners, especially turfs one and eight were left out. More often than expected the geese began to forage at turf one or two, which were closest to their starting point. After one or more rounds they stopped, which often happened after turf one, two or eight.

On average six out of eight turfs were visited during a trial.

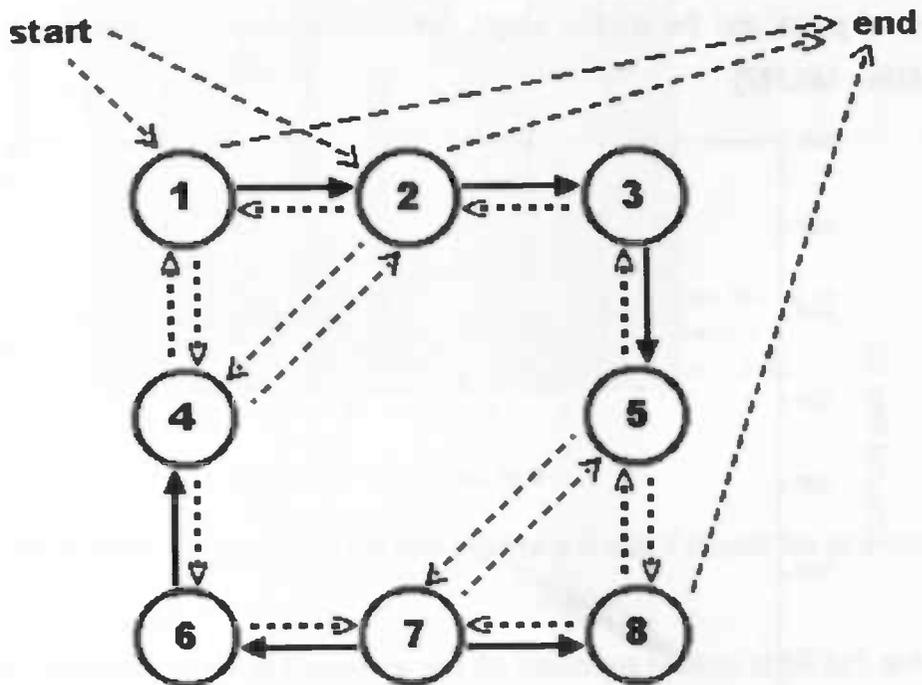


Figure 4.8 : Grazing pattern of the geese. Black arrows (\longrightarrow) indicate most frequently observed switches ($c_3 > 1.0$), dotted arrows ($\cdots\cdots\rightarrow$) indicate switches that also occurred more frequently than expected ($c_2 > 1.0, c_3 < 1.0$).

Preference

For the analysis of the preference in relation to the characteristics of a turf other effect that were independent of these characteristics had to be excluded. As a certain grazing pattern was found, the effect of the order of first approaches on the rank of preference was determined.

Order of visits

The order of first visits was influenced by the starting position of the animal. It normally started at the closest turf and continued with one of the neighboring turfs. In many cases the first turf was either the one at position one or two (figure 4.9). There was a significant relation between the position of a turf ($p < 0.001$, $F = 122.39$, d.f. = 1050, $y = 0.3067x + 2.5147$) and the order of visit as well as between the order of first visit and the preference ($p < 0.001$, $F = 223.73$, d.f. = 1046, $y = 0.4086x + 2.1493$).

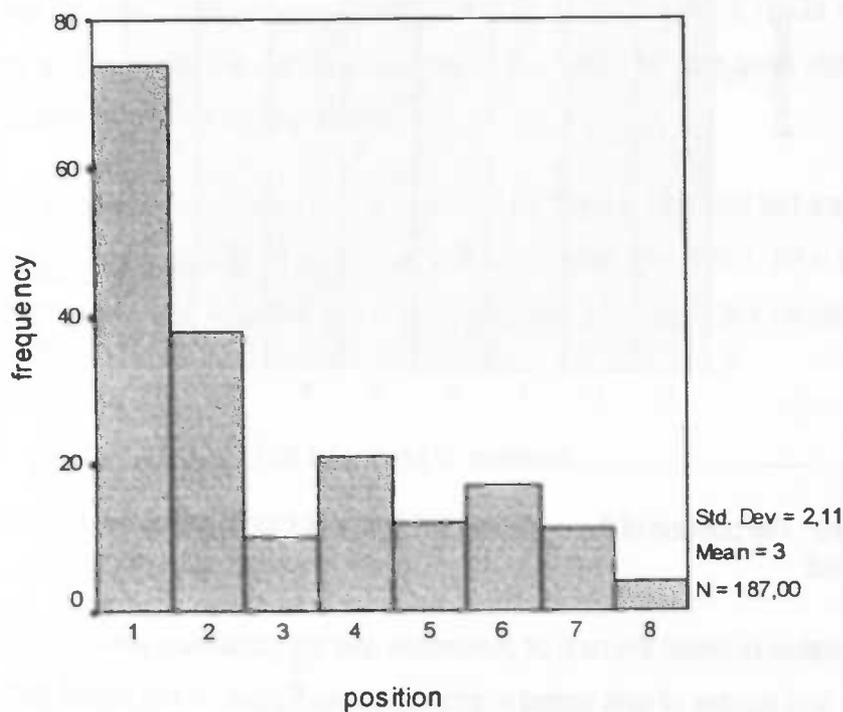


Figure 4.9 : Position of the turf the goose started to feed on for trials with eight turfs in total

Position effects

The position of a turf influences the order in which it is visited by the goose. Furthermore there was a relation between order of visit and preference. However the position of a turf and its rank of preference in a trial were not related if more than half of in total eight turfs present have been visited ($p = 0.082$, figure 4.9. The p-value increased with the number of turfs visited.). If all trials with eight turfs were included, in the analysis the position had a significant effect on the preference ($p < 0.001$, $F = 14.37$ d.f. = 1045, $R^2 = 0.01355$). The relation found was $y = 0.107x + 3.2475$. This means that the means rank of preference for the first turf was 0.749

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higher than the mean rank of preference of the turf at position eight. For trials with four, five, six or nine turfs present no relation between rank of preference and position was found at all.

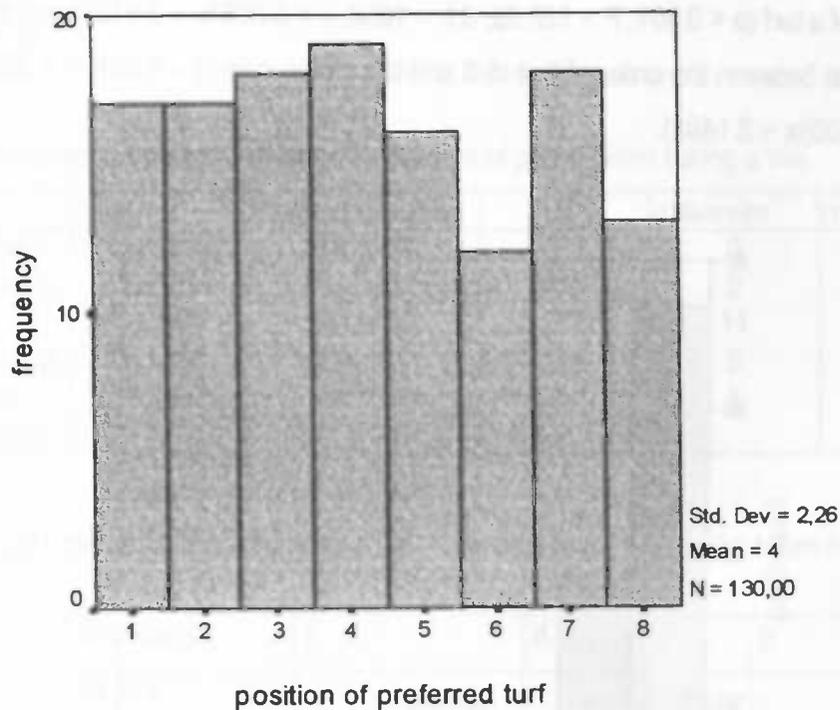


Figure 4.10 : The position of the preferred turf from eight turfs in total if at least five turfs have been visited.

The correlation between the rank of preference and the covariates position of the turf, order of first visits and number of turfs visited in total was investigated. In this model (table 4.3) the rank of preference could be predicted by the order in which the turfs are visited and the number of turfs that have been visited in total for trials with eight . There was no significant influence of the position of the turfs or of the interaction between position and order of visit.

Table 4.3 : GLM-model of the factors that influence the rank of preference in a trial with eight turfs

| variable | coefficient | F | d.f. | p |
|--------------------|-------------|---------|------|---------|
| constant | 0.281 | | | |
| order of visit | 0.350 | 104.854 | 1 | < 0.001 |
| # of turfs visited | 0.242 | 101.67 | 1 | < 0.001 |

4. Results

The rank of preference is determined as sum of pecks taken from a turf in relation to the pecks taken from the other turfs. This could be attributed to the fact that a turf is visited more frequently or that more pecks are taken during a visit.

Number of visits

There was a relation between the number of visits and the rank of preference. The more frequently visited turfs were the preferred ones ($p < 0.001$, $R^2 = 0.06436$, $F = 95.62$, $d.f. = 1390$, $y = -0.3744x + 4.5687$ with number of visits as independent variable). The number of visits was also correlated with the order of approach ($p < 0.001$, $F = 82.35$, $d.f. = 1394$, $y = -0.1562x + 2.9106$ with order of visits as independent variable) which means that turfs that have been visited later have a lower possibility of a second or third visit.

The larger number of pecks was not only caused by the fact that the preferred turf was visited more frequently but also the number of pecks per visit was higher ($p < 0.001$, $R^2 = 0.14997$, $F = 244.71$, $d.f. = 1387$, $y = -0.03x + 4.4354$ for number of pecks as independent variable figure 4.11).

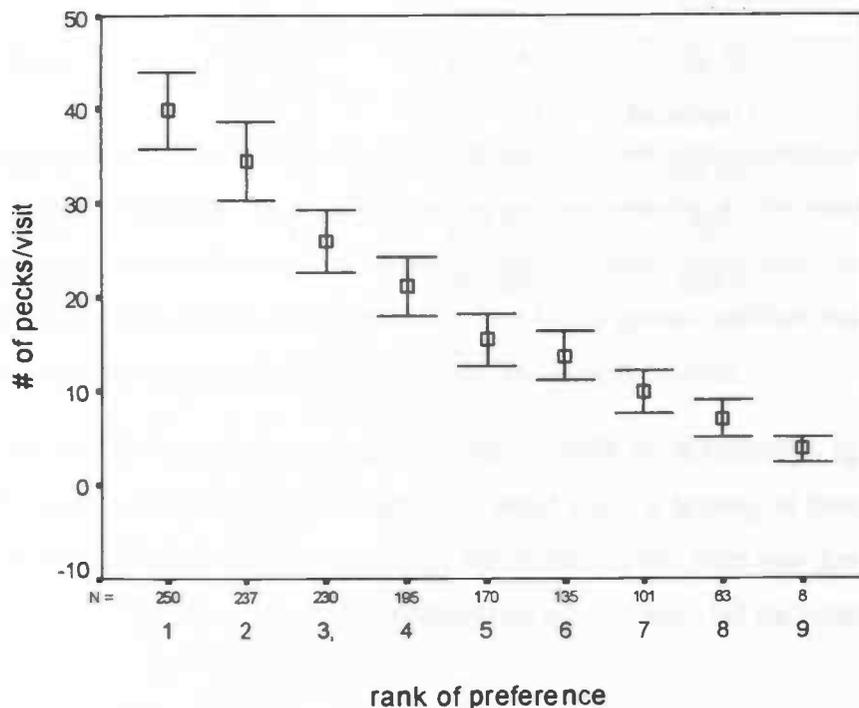


Figure 4.11: The preferred turfs did not only reach a higher number of pecks because they were visited more often but also the mean number of pecks per visit was higher.

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Motivation

The total amount of pecks taken from the turfs and also from the surrounding grass inside the enclosure showed high variation (table 4.4). Significant effects on the number of pecks taken per minute had the date, the type of experiment, the species and the individual goose ($p < 0.001$ for all, table 4.5).

Table 4.4: Means and standard deviations for amount of pecks taken during a trial

| variable | mean | standard deviation | N | maximum | minimum |
|----------------------------------|----------|--------------------|-----|---------|---------|
| pecks from turfs | 309.5992 | 309.7864 | 262 | 0 | 1672 |
| pecks from grass | 577.6484 | 614.4833 | 219 | 0 | 2746 |
| total pecks | 792.4427 | 538.6422 | 262 | 11 | 3024 |
| turf-pecks/minute | 18.1263 | 21.1284 | 262 | 0 | 114 |
| duration of the experiment (min) | 24.2634 | 11.819 | 262 | 5 | 72 |

Table 4.5: GLM - model for the influence on the motivation defined as pecks taken from turfs/minute

| variable | coefficient | F | d.f. | p |
|----------|--------------------------|--------|------|--------|
| constant | 54.473 | | | |
| species | -35.958 (barnacles) | 46.746 | 1 | <0.001 |
| goose | -35.958 | 12.372 | 1 | <0.001 |
| type | 5.294 | 18.516 | 1 | 0.001 |
| day | -0.560 | 39.704 | 1 | <0.001 |

The average motivation of the different individuals is shown in figure 4.12. The two adult brent geese showed in general a much higher motivation than the barnacle geese. "White", the juvenile brent, was more comparable to the barnacles in terms of pecks taken from the turfs while the barnacles fed more from the surrounding grass.

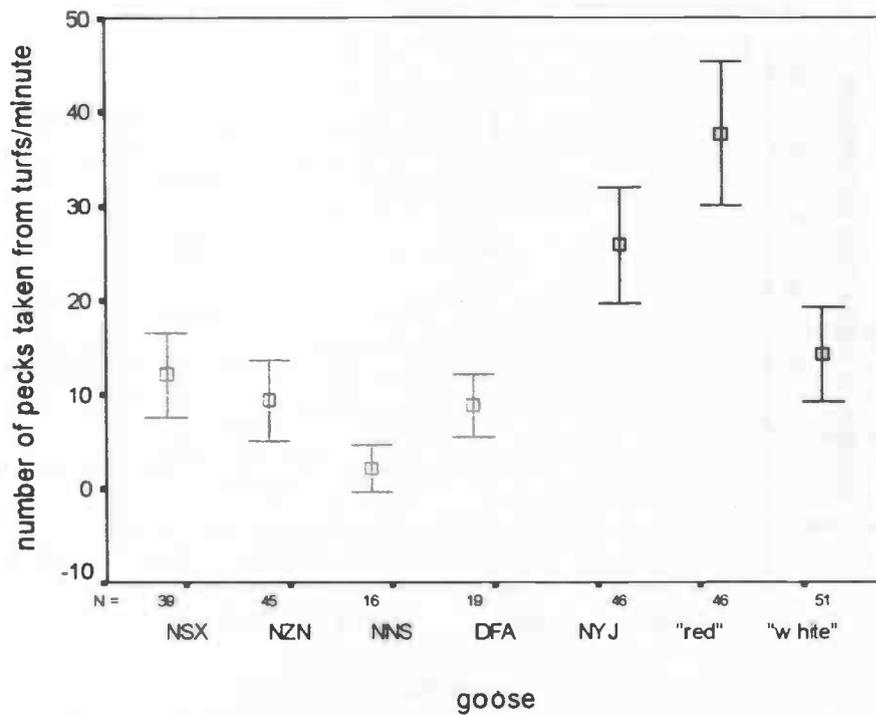


Figure 4.12: Foraging motivation for the different individuals in terms of pecks taken from turfs divided by the duration of the experiment. Barnacle geese are indicated with grey marks, brents with black marks.

There was not only a general difference in the motivation between the individuals but also between the different vegetation types offered which was not included in the model (figure 4.13). The motivation of the barnacles was highest during trials with *Lolium* and *Poa* present and when all three plant species were present. The brent geese exhibited the highest motivation during the mixed-vegetation-trials and during the *Puccinellia*-trials.

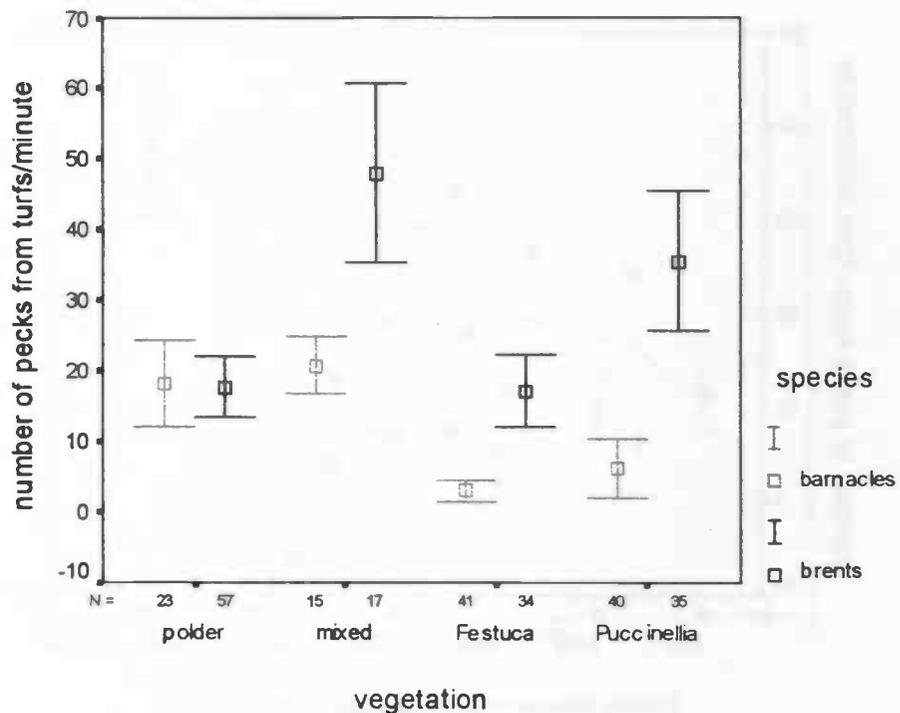


Figure 4.13: Foraging motivation in terms of pecks taken from the turfs per minute for trials that contained turfs of a single plant species and trials where all three plant species were present.

4.3 The different types of experiments

Polder

During polder trials vegetation of a low biomass and a high biomass site were offered, part of the turfs were sprayed with salt water, the others with fresh water. There was no difference for the two species. Both showed a preference for the higher vegetation and within each height those turfs sprayed with fresh water were preferred (figure 4.14). The preference could be predicted by the total biomass and the interaction between total biomass and salt-treatment (table 4.6).

Table 4.6 : GLM-model for the effect on preference for the salt/height comparison at the polder

| variable | coefficient | F | d.f. | p |
|--------------------|-------------|--------|------|--------|
| constant | 3.959 | | | |
| total biomass | 0.143 | 29.108 | 1 | <0.001 |
| total biomass*salt | -0.0423 | 7.692 | 1 | <0.001 |

4. Results

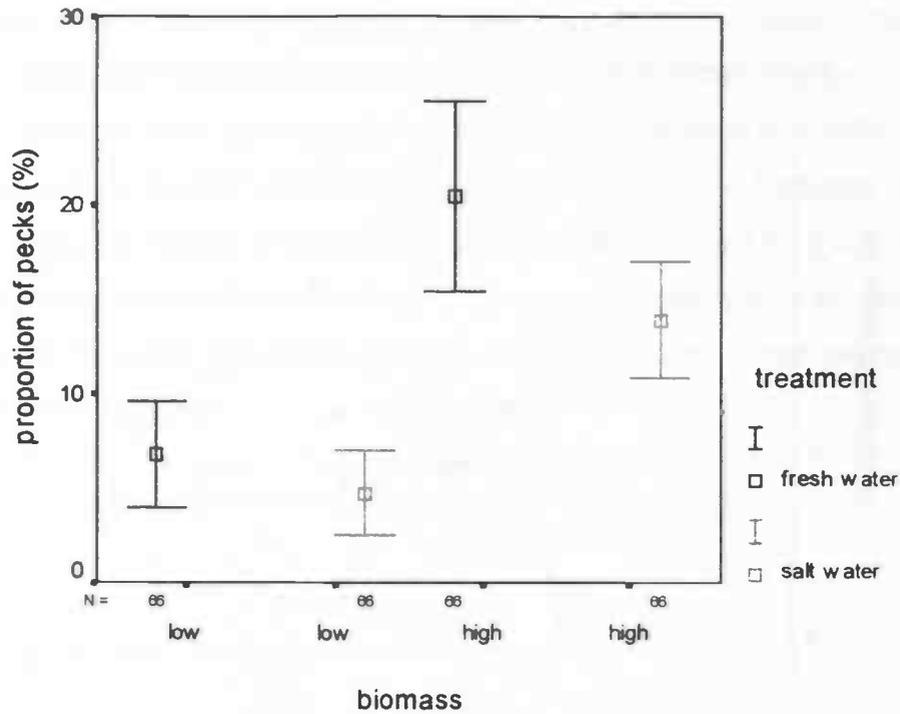


Figure 4.14 : Preference of all individuals for polder grass turfs that differed in biomass and that were either sprayed with salt or with fresh water. Two turfs of each type were present per trial and means were calculated for each turf separately.

During the experiments with the turfs from Texel which were only done with the brents, the geese showed a preference for intermediate biomasses (figure 4.15). The preference could be either explained by the total biomass or the by the fertilization-regime (table 4.7). The regression between preference and biomass is shown in figure 4.16 ($p < 0.001$, $R^2 = 0.53915$, $F = 12.28$, $d.f. = 21$, $y = -0.0011x^2 + 0.4472x - 28.381$).

Table 4.7 : GLM-model (1 and 2) that show the influence of biomass or treatment on the preference for Texel-turfs.

| model | variable | coefficient | F | d.f. | p |
|-------|---------------|-------------|--------|------|--------|
| 1 | constant | 0.104 | | | |
| 1 | total biomass | 0.06808 | 9.964 | 1 | 0.005 |
| 2 | constant | 4.349 | | | |
| 2 | fertilization | 9.021 | 31.518 | 1 | <0.001 |

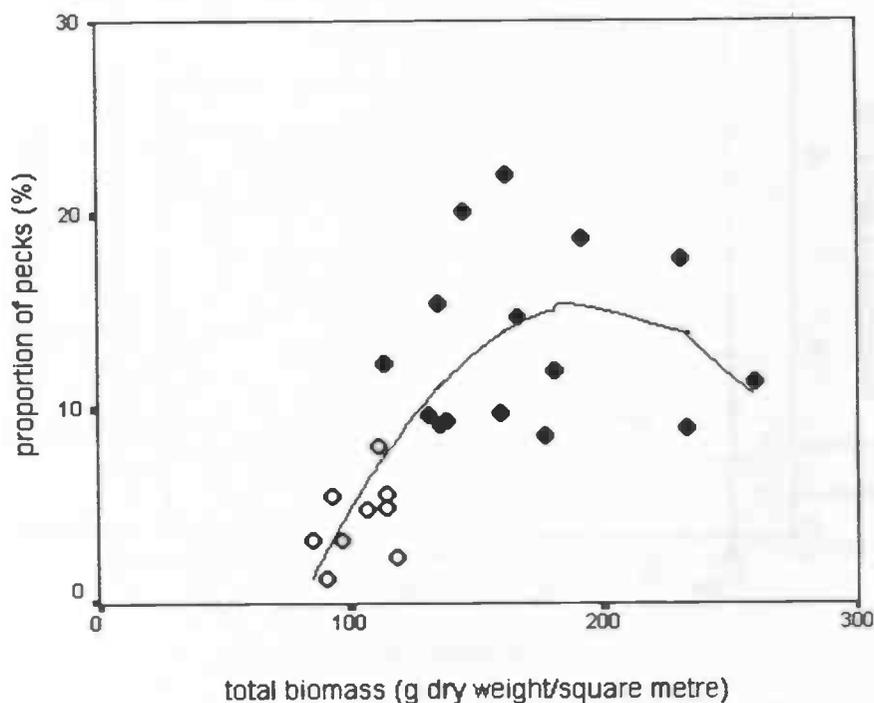


Figure 4.15: Preference in relation to biomass for the Texel-experiment. Values for biomass and preference are given as means per treatment (1-8) and per goose. Open circle indicate unfertilized turfs, filled circles indicate the fertilized turfs.

Polder – Festuca – Puccinellia comparison

The preference of the geese was influenced by the goose and the plant species and by the biomass as well as the interaction between goose and plant species and plant species and biomass. The complete model is given in table 4.8.

Table 4.8: GML-model for the factors influencing the preference during the comparison of polder, Festuca and Puccinellia. The species was a fixed factor, the other variables covariates.

| variable | coefficient | F | d.f. | p |
|-------------------------------|-------------------------|---------|------|---------|
| constant | -18.614 | | | |
| goose species | 29.658 (for barnacles) | 95.350 | 1 | < 0.001 |
| plant species | 0.82 | 26.638 | 1 | 0.002 |
| total biomass | 17.82 | 10.249 | 1 | < 0.001 |
| total biomass * plant species | 0.510 | 48.439 | 1 | < 0.001 |
| plant species * goose species | -14.801 (for barnacles) | 110.823 | 1 | < 0.001 |

The barnacles almost exclusively ate polder grasses (figure 4.16). The choice of the brent geese was not that clear. The preference changed during consecutive trials. The goose "white" reduced the amount of polder and *Festuca* consumed while the amount of *Puccinellia* chosen increased (figure 4.17). For "red" and "NYJ" the preference for polder and *Puccinellia* seemed to change in turns. The amount of *Festuca* consumed was rather constant but it was high for "red" (figure 4.18) and low for "NYJ". For all geese the amount of polder consumed decreased to the benefit of *Puccinellia* between the first row of experiments and a later trial (one per individual) at the begin of June.

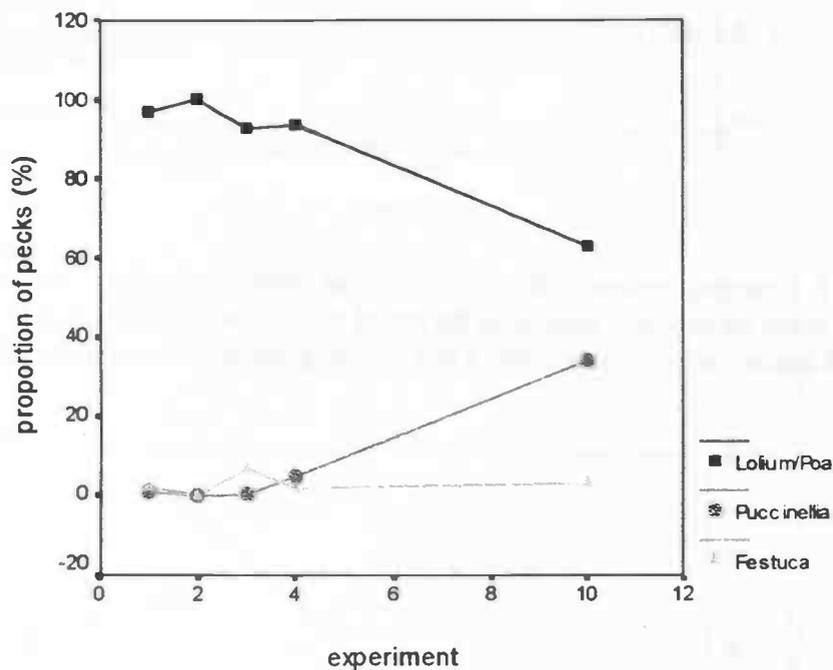


Figure 4.16 : Preference for the different plants species during consecutive trials for the barnacle goose "NSX". The last trial (10) took part more than one month after the first four, the percentage of pecks from all three turfs of each plant species that were present during a trial were added up.

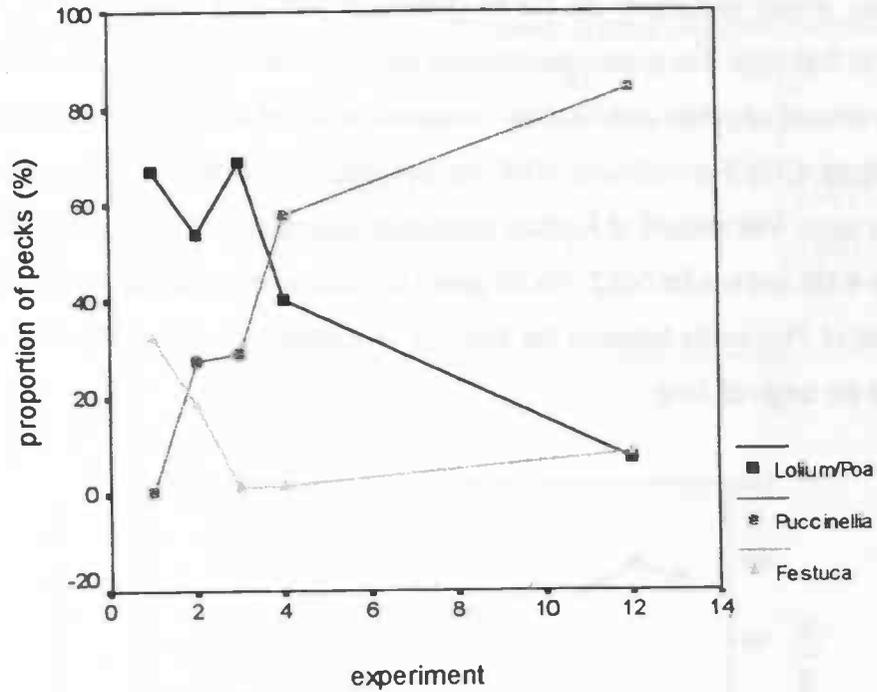


Figure 4.17: Changing preference for the brent goose "white" during time. The last trial (12) was done at the beginning of June while the others took place at the end of April. Three turfs of each plant species were present during a trial and the proportion of pecks were added up.

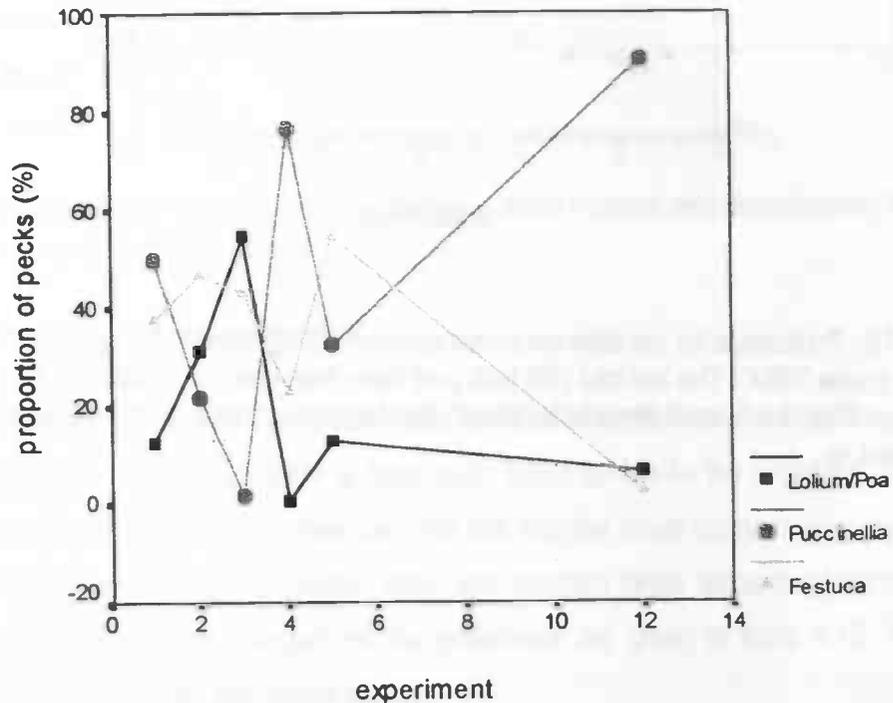


Figure 4.18: Changes in preference for the goose "red". The proportion of pecks is given as sum of the three turfs of each plant species. The last experiment (12) was done about one month later than the first five.

The saltmarsh experiments

There were two general types of salt marsh experiments within both vegetation types (*Festuca* and *Puccinellia*): During the first type unfertilized turfs (control and enclosure) of the cattle grazed part of the salt marsh were compared with turfs from the ungrazed part. In the second type the two different sites on either the cattle grazed or the ungrazed part were compared. For these trials fertilized and unfertilized turfs were used.

Within the grazed/ungrazed comparison the low *Puccinellia* was preferred at both the grazed and the ungrazed salt marsh, with a higher proportion of pecks removed from the grazed part. Within the low *Puccinellia* the turfs from the grazed part were preferred (figure 4.19).

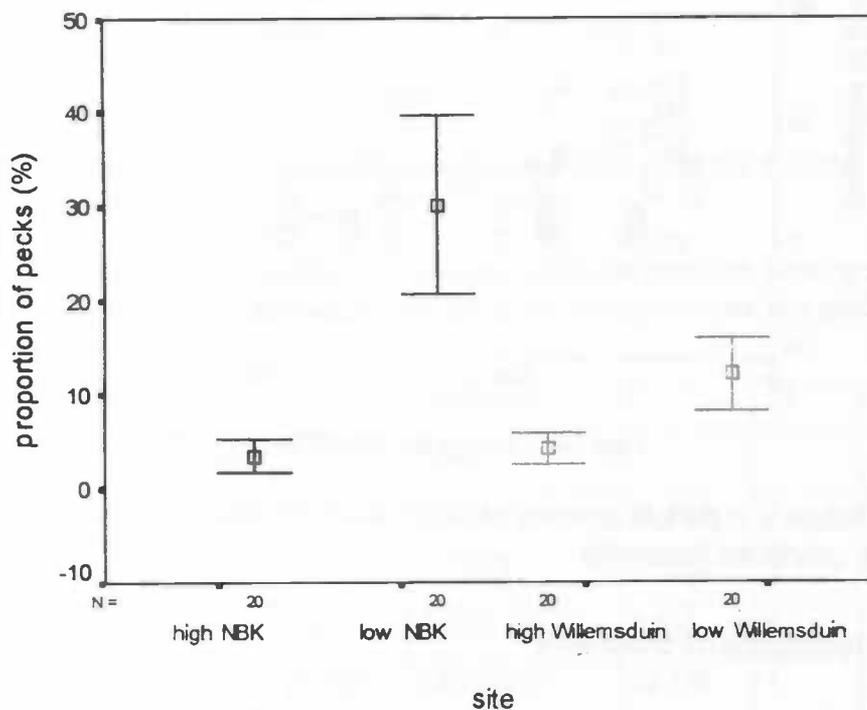
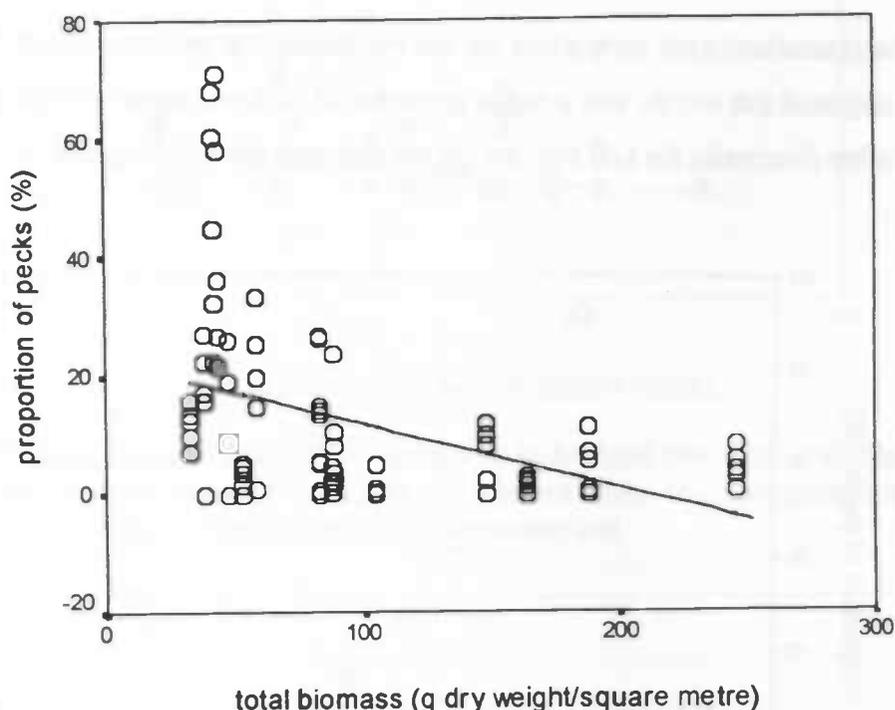


Figure 4.19: Preference for the grazed/ungrazed comparison of *Puccinellia*. Both goose species are included and only those trials used where pecks from more than four turfs have been taken. Grazed sites are indicated in black, ungrazed sites in grey.

This preference did not differ between the two goose species and it can be explained by the total biomass of the of the plots (table 4.9). The protein content of the different turfs had no significant influence in the model. The preference decreased with increasing biomass (figure 4.20, $p = 0.001$, $R^2 = 0.17081$, $F = 16.07$, $d.f. = 78$).

Table 4.9: GLM-model for the preference in the *Puccinellia*-grazed/ungrazed comparison

| variable | coefficient | F | d.f. | p |
|------------------------------|-------------|--------|------|-------|
| constant | 35.560 | | | |
| total biomass | -0.388 | 12.971 | 1 | 0.001 |
| (total biomass) ² | 0.00112 | 7.047 | 1 | 0.010 |

Figure 4.20 : Influence of the total biomass (inclusive dead material and dicotyledons) for the preference for unfertilized *Puccinellia*

Influence of fertilization on preference

During the comparison between unfertilized and fertilized turfs the later were preferred by the geese, although the biomass is higher at these turfs. This is shown for the ungrazed-*Puccinellia* experiment in figure 4.21. On the other hand the site with the lower biomass (low *Puccinellia*) site is preferred over the high *Puccinellia* which also contains larger amounts of biomass. The factors that had a significant impact on the preference are given in table 4.10. Again no difference was found for the two goose species.

For the ungrazed *Puccinellia* the relation between preference and total biomass is shown in figure 4.22. The regression lines were $y = -0.1977x + 41.5368$ ($p < 0.001$, $F = 15.83$, $d.f. = 30$) for fertilized turfs, and $y = -0.0388x + 9.9483$ with $p = 0.002$ ($F = 11.43$, $d.f. = 30$) for the unfertilized turfs.

4. Results

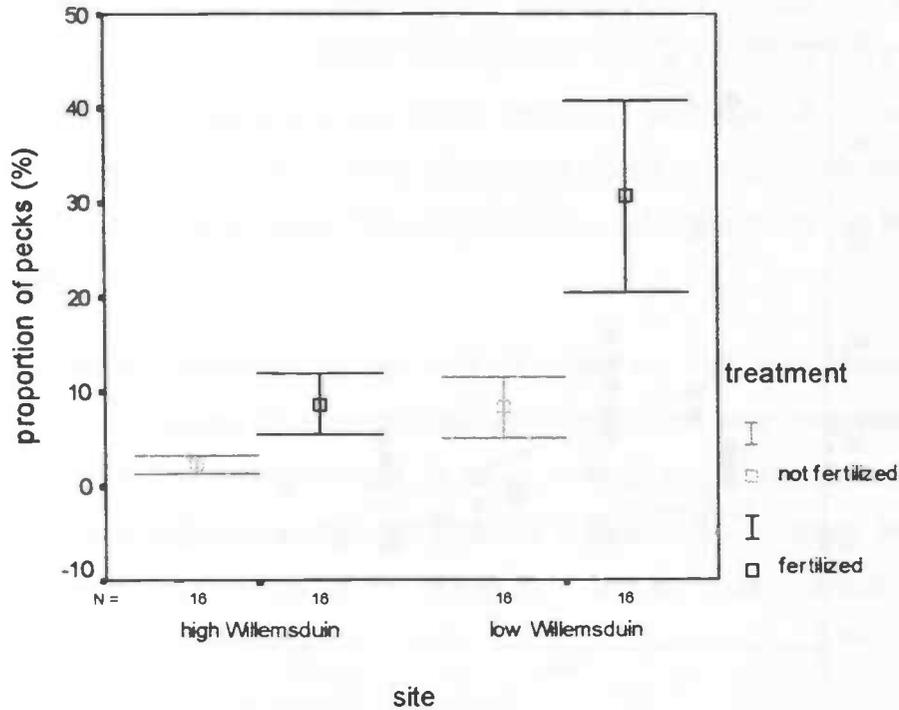


Figure 4.21: Preference at the ungrazed *Puccinellia*. Only trials with more than four turfs visited have been analysed

Table 4. 6: GLM-models for the preference observed during the trials with either grazed or ungrazed *Puccinellia*. For the later two models are given, a more complex one and a simple approach.

| experiment | model | variable | coefficient | F | d.f. | p |
|------------|-------|---------------------------------|-------------|--------|------|--------|
| grazed | 1 | constant | 40.879 | | | |
| grazed | 1 | (total biomass) ² | -0.0014 | 11.868 | 1 | 0.001 |
| grazed | 1 | fertilization | -17.333 | 37.550 | 1 | <0.001 |
| grazed | 1 | protein content | -0.508 | 4.487 | 1 | 0.0038 |
| grazed | 1 | (biomass) ² *protein | 0.0000417 | 10.136 | 1 | 0.002 |
| grazed | 1 | site | -9.414 | 23.290 | 1 | <0.001 |
| ungrazed | 1 | constant | 42.153 | | | |
| ungrazed | 1 | (total biomass) ² | 0.0007327 | 4.984 | 1 | 0.029 |
| ungrazed | 1 | fertilization | -28.075 | 37.475 | 1 | <0.001 |
| ungrazed | 1 | (biomass) ² *protein | -0.0000207 | 5.366 | 1 | 0.024 |
| ungrazed | 1 | biomass grass | -0.449 | 18.414 | 1 | <0.001 |
| ungrazed | 2 | constant | 30.128 | | | |
| ungrazed | 2 | total biomass | -13.550 | 19.281 | 1 | <0.001 |
| ungrazed | 2 | fertilization | -0.0945 | 15.897 | 1 | <0.001 |

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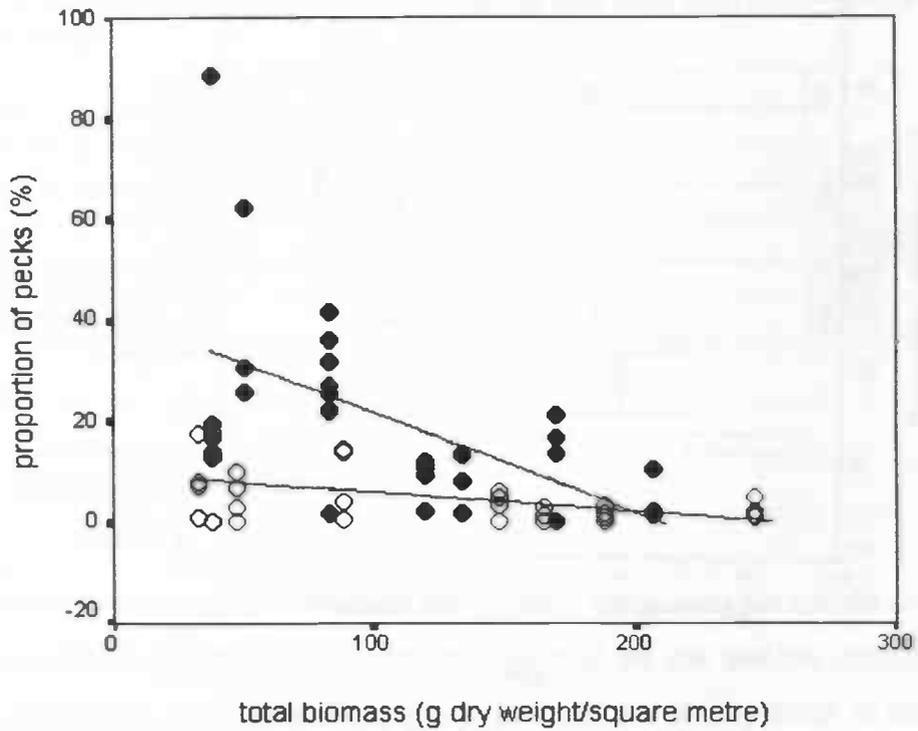


Figure 4.22: Relation between biomass and preference for fertilized (filled dots) and unfertilized turfs (open dots) from the ungrazed *Puccinellia*. Included are values from both goose species if at least five turfs have been visited during the corresponding trial.

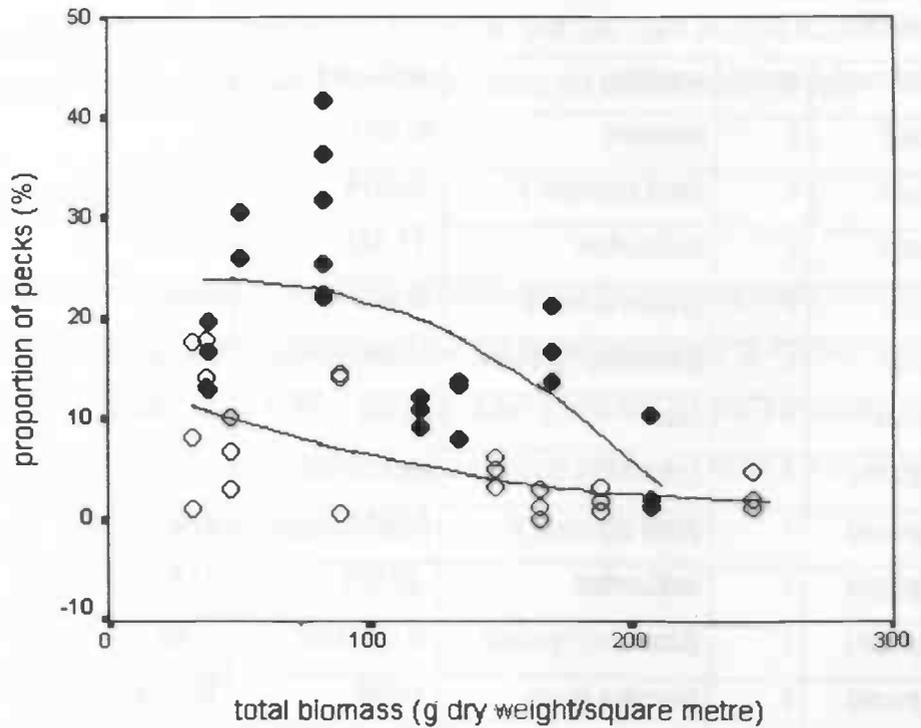


Figure 4.23: Relation between biomass and preference for the brent geese and the ungrazed *Puccinellia*. Fertilized turfs are indicated by filled dots, the unfertilized turfs by open dots.

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The relation between biomass and preference was quadratic if only the data from the brents were analysed (figure 4.23). ($y = -0.0008x^2 + 0.0723x + 22.1971$, $p = 0.003$, $R^2 = 0.41727$, $F = 7.52$, d.f. = 21 for the fertilized turfs and for the unfertilized $y = 0.002x^2 - 0.1007x + 14.4272$, $p = 0.004$, $R^2 = 0.40771$, $F = 7.23$, d.f. = 21). Within the fertilized turfs such with intermediate biomass were preferred by the brents. The preferred biomass of fertilized turfs was higher than that of not fertilized turfs.

During the clipping experiments the four turfs of a site that had been clipped for the determination of the biomass (three respectively two weeks earlier) were compared with four turfs of the same site that were not clipped. All geese preferred the previous clipped turfs with the much shorter vegetation and with much less litter in between young, green, high quality plants (table 4.12). The biomass of the clipped turfs and the protein content were not measured.

Table 4.12 : GML-model for the clipping experiments.

| variable | coefficient | F | d.f. | p |
|----------|-------------|-------|------|-------|
| constant | 9.597 | | | |
| clipping | 7.085 | 6.963 | 1 | 0.009 |

The role of *Artemisia*

In order to test the influence of large dicotyledons present on a turf on the preferences of the geese they were offered four turfs from the same plot (unfertilized plots of the *Festuca Willemsduin* or the high *Puccinellia Willemsduin*). Two of them still contained *Artemisia maritima*, from the other two it had been removed. No significant effect of the treatment on the preference could be found.

Control experiments

These experiments were done to test the reaction of the geese to equal turfs. Therefore eight turfs from the same plot were used. There was a large variance in the number of pecks taken from different turfs, the motivation was generally low, geese stop feeding very soon. The most important factors here were the order of visit, the number of turfs that were visited in total and the position of the turf (table 4.13).

Table 4.13: GLM-model for the control experiments. All trials were used no matter how many turfs were visited.

| variable | coefficient | F | d.f. | p |
|-----------------------|-------------|--------|------|---------|
| constant | 121.035 | | | |
| order | -17.194 | 5.625 | 1 | 0.023 |
| position | -14.209 | 6.641 | 1 | 0.014 |
| turfs visited | -12.378 | 35.663 | 1 | < 0.001 |
| order*turfs visited | 1.968 | 4.414 | 1 | 0.042 |
| position*turfsvisited | 1.701 | 5.402 | 1 | 0.025 |

Intake rates and bite sizes

The determination of the amount of weight that has been removed by the animals was hard to determine precisely. The evaporation changes throughout the day and this change was not regular. As the turfs were exposed to the sun cloud and the shifting shade of the building caused additional changes. And furthermore the plants on the turfs have not always been completely dry. As soon as this water had disappeared from the leaves the evaporation of a turf decreased.

Another source of error was the existence of spilled leaves that had been plucked but not eaten and that were lying on the ground between the turfs but could not be assigned to a certain turf.

Correction of the evaporation

Without correction of the evaporation the bite sizes measured in the morning (mean = 22.5988 ± 2.7596) when the evaporation increased during the trial were significantly ($p < 0.001$) higher than in the afternoon (mean = -9.4540 ± 3.8523). After correction of the evaporation the calculated bite sizes do not differ ($p=0.356$) between morning (mean = 1.3347 ± 2.6228) and afternoon (mean = 5.3023 ± 3.4738) (figure 4.24).

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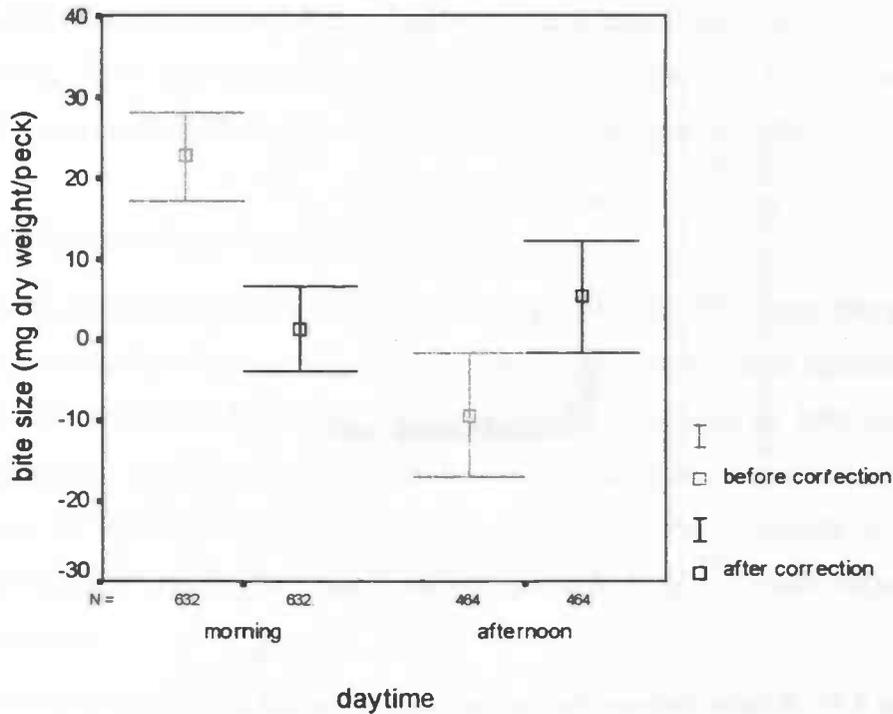


Figure 4.24: Efficiency of the correction of the evaporation in relation to mean bite sizes before (grey) and after correction (black) for the morning and the afternoon trials.

Figure 4.25 shows the relation between the number of pecks the goose has taken and the standard deviation of the measured bite size. The more pecks have been taken the smaller the variation in bite size.

The reason for this is the effect of a mistake in the count of pecks that decreases with the number of pecks. Two pecks more or less with ten pecks counted would cause an error of 20% while a mistake of 10 pecks at a total of 200 would only be an error of 0.5%. Additionally the number/percentage of negative values for bite sizes and intake rates was much higher at low number of pecks when the loss due to evaporation or the assumed loss was much higher than the weight removed by the goose. While 50% of the bite sizes calculated from less than ten pecks were negative, this values decreased to 16% if the number of pecks was between 50 and 75.

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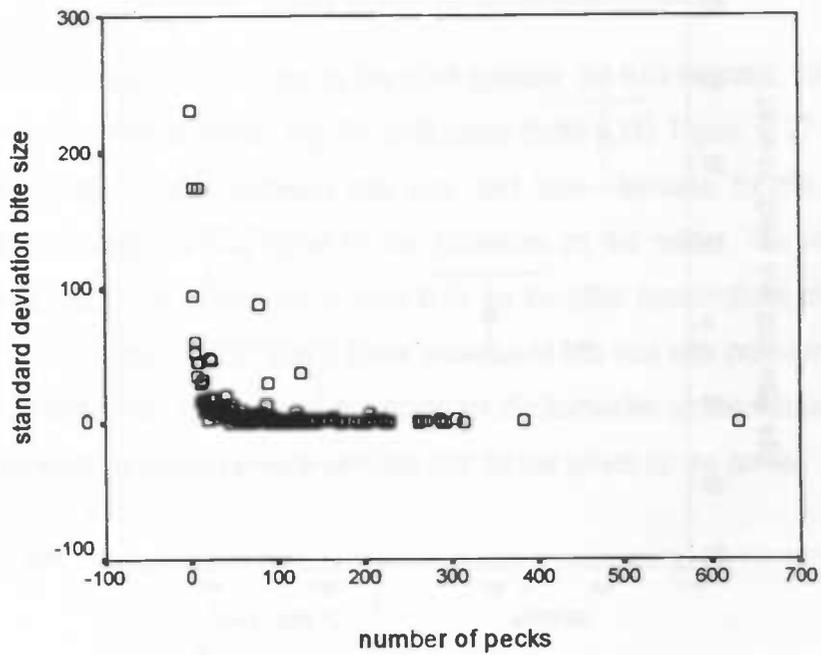


Figure 4.25: Relation between the standard error of the bite size related to the amount of pecks on which the estimation of the bite size was based.

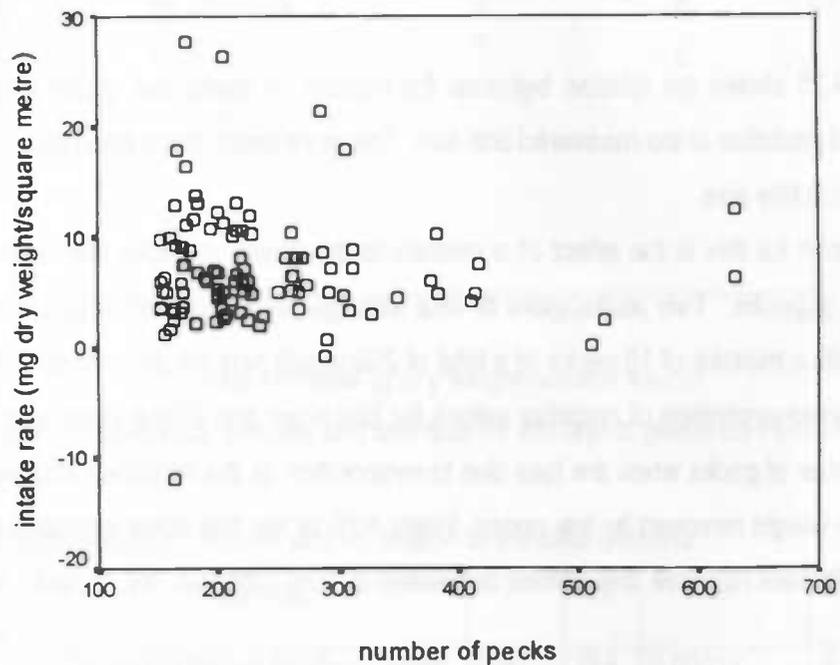


Figure 4.26: The instantaneous intake rate in relation to the pecks that have been taken from a turf in total

Depletion

The turfs were rather small and contained only a limited amount of biomass. Because of this depletion might have occurred and this would have caused a change in the intake rate and in

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preference. As depletion occurs in a patch the instantaneous intake rate decreases and so does the preference. Figure 4.26 shows that the intake rate did not depend on the number of pecks taken from a turf for the plant species with the lowest biomass, the *Puccinellia*.

Mean intake rates for the different vegetation types

Table 4.14 gives the means, standard errors and standard deviations for intake rates, bite size and peck rates for all plant species and the two goose species. There was a large variation in the bite size and the intake rate. Peck rates are highest for the *Puccinellia* for both goose species. The highest bite size with 4.7mg/peck occurred for the barnacles on the polder. the mean intake rates are highest on the polder for the barnacles and on the *Puccinellia* for the brents which corresponds with the preferences of both species during the polder-*Festuca-Puccinellia* experiments.

Table 4.14 : Means, standard errors (S.E.) and standard deviations (Std. Dev.) for intake rates, bite sizes and peck rates

| plant species | polder | | <i>Festuca</i> | | <i>Puccinellia</i> | |
|-----------------------|--------|-----------|----------------|-----------|--------------------|-----------|
| | brents | barnacles | brents | barnacles | brents | barnacles |
| N | 297 | 113 | 112 | 40 | 175 | 62 |
| mean intake rate | 4.6803 | 6.9735 | 5.5389 | 3.8244 | 6.9920 | 4.5493 |
| S.E. intake rate | 0.5039 | 0.5084 | 0.8949 | 1.5912 | 0.6822 | 1.1650 |
| Std. Dev. Intake rate | 8.6847 | 5.4040 | 9.4704 | 10.0638 | 9.0243 | 9.1732 |
| mean bite size | 3.1286 | 4.6724 | 3.6268 | 3.4305 | 3.6512 | 2.6903 |
| S.E. bite size | 0.3207 | 0.3657 | 0.5999 | 1.1272 | 0.3629 | 0.8053 |
| Std.Dev. bite size | 5.5264 | 3.8871 | 6.3484 | 7.1289 | 4.8007 | 6.3406 |
| mean peck rate | 1.5322 | 1.5305 | 1.5517 | 1.3720 | 1.9077 | 1.6543 |
| S.E. peck rate | 0.0198 | 0.02802 | 0.02854 | 0.06142 | 0.0253 | 0.05659 |
| Std. Dev. peck rate | 0.3413 | 0.2979 | 0.3021 | 0.3885 | 0.3333 | 0.4456 |

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Biomass and bite size

The bite size was significantly influenced by the plant species, the total biomass, the square of the total biomass, the grass biomass, and the fertilization (table 4.16). Figure 4.27 shows that there was a quadratic relation between bite size and total biomass for the brents on *Puccinellia*. the same relation was found for the barnacles on the polder. The relationships between biomass and bite size are given in table 4.15 for the other combinations of vegetation and species. For the *Festuca* there was a linear increase of bite size with increasing biomass for both goose species. This relation was also found for the barnacles on the *Festuca* while no relation could be found between biomass and bite size for the brents on the polder.

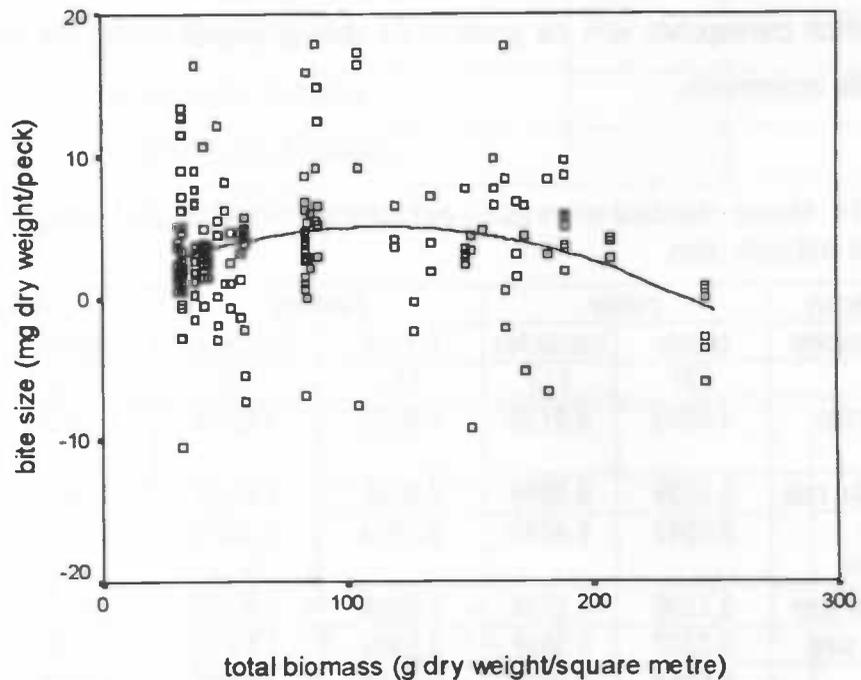


Figure 4.27: Relation between total biomass and bite size for the brents geese on *Puccinellia*

Table 4.15: Regression lines for the bites size in relation to the total biomass

| plant species | goose species | formula | F | d.f. | R ² | p |
|---------------|---------------|--------------------------------------|------|------|----------------|---------|
| polder | brents | $y = -0.00006x^2 + 0.0156x + 2.3056$ | 0.47 | 294 | 0.00317 | 0.627 |
| polder | barnacles | $y = -0.003x^2 + 0.896x - 0.4881$ | 6.64 | 110 | 0.10771 | 0.002** |
| Festuca | brents | $y = 0.0105x + 1.8418$ | 4.20 | 110 | 0.03314 | 0.043** |
| Festuca | barnacles | $y = 0.0291x - 0.9962$ | 5.84 | 38 | 0.13192 | 0.021** |
| Pucc. | brents | $y = -0.0003x^2 + 0.0726x + 0.911$ | 4.80 | 172 | 0.05283 | 0.009** |
| Pucc. | barnacles | $y = 0.0255x + 2.2109$ | 4.74 | 60 | 0.07318 | 0.033** |

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Table 4.16: GLM-model for the relation between bite size and vegetation characteristics

| variable | coefficient | F | d.f. | p |
|------------------------------------|------------------------------------|--------|------|---------|
| constant | -0.309 | | | |
| total biomass | -0.09959 | 14.688 | 1 | < 0.001 |
| (total biomass) ² | -0.000345 | 15.861 | 1 | < 0.001 |
| plant *biomass total | -0.0681 (polder) | 3.125 | 2 | 0.044 |
| | -0.0796 (<i>Festuca</i>) | | | |
| plant*biomass grass | 0.00668 (polder) | 4.469 | 3 | 0.004 |
| | 0.04895(<i>Festuca</i>) | | | |
| | -0.0328(<i>Puccinellia</i>) | | | |
| plant*(biomass total) ² | 0.00022318(polder) | 3.820 | 2 | 0.022 |
| | 0.0002984 (<i>Festuca</i>) | | | |
| plant*fertilization | 1.839 (polder, unfert.) | 4.575 | 5 | < 0.001 |
| | 0.372 (polder fert.) | | | |
| | -0.909 (<i>Festuca</i> , unfert.) | | | |
| | -5.902 (<i>Festuca</i> fert.) | | | |
| | 0.542 (<i>Pucc.</i> unfert.) | | | |

Bite size and peck rate

There was no significant influence of the peck rate on the bite size. There was also no influence of the bite size on the peck rate. The peck rate could be explained better by vegetation characteristics (table 4.17).

Biomass and peck rate

As biomass increased, the peck rate decreased for all three vegetation types (figure 4.28, table 4.18). The peck rate was significantly related with plant species, goose species, total biomass and vegetation height as well as with the interaction between goose and plant species. On the other hand peck rate also depended on the amount of dead and green material. Peck rate decreased as dead material increased and increased with increasing percentage of green grass (figure 4.29). There was also a not significant decrease of the peck rate with increasing amount of dicotyledons.

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Table 4.17: GLM-model of the influence of vegetation characteristics on the peck rate

| variable | coefficient | F | d.f. | p |
|----------------------|----------------------------------|--------|------|---------|
| constant | 2.115 | | | |
| total biomass | -0.00139 | 26.737 | 1 | < 0.001 |
| height | -0.0281 | 31.827 | 1 | <0.001 |
| goose species | -0.204 (barnacles) | 39.099 | 1 | < 0.001 |
| plant species | | 18.876 | 2 | < 0.001 |
| plant*total biomass | -0.000269 (polder) | 11.391 | 2 | <0.001 |
| | 0.001167 (<i>Festuca</i>) | | | |
| plant*gooses species | 0.0736 (barn., polder) | 7.808 | 2 | <0.001 |
| | -0.174 (brents, polder) | | | |
| | -0.323 (barn. <i>Festuca</i>) | | | |
| | -0.363 (brents, <i>Festuca</i>) | | | |

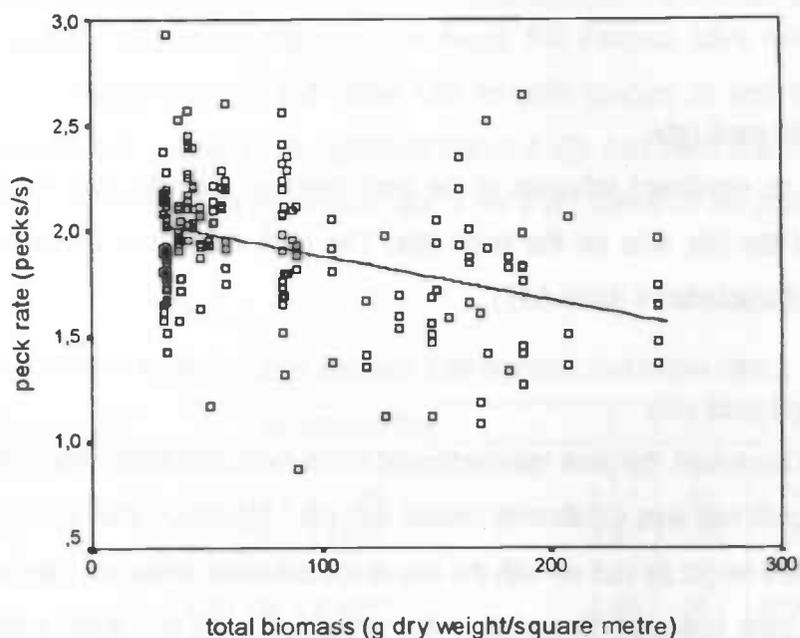


Figure 4.28: Relation between the peck rate and the total biomass for the brents on *Puccinellia*

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Table 4.18 : Regression lines for the relation between total biomass and peck rate

| vegetation | goose species | formula | F | d.f. | R ² | p |
|--------------------|---------------|-------------------------|--------|------|----------------|-----------|
| polder | brents | $y = -0.0026x + 1.8787$ | 96.09 | 295 | 0.24570 | < 0.001** |
| polder | barnacles | $y = -0.0031x + 1.8909$ | 153.62 | 111 | 0.58453 | < 0.001** |
| <i>Festuca</i> | brents | $y = -0.0011x + 1.7394$ | 24.12 | 110 | 0.17299 | < 0.001** |
| <i>Festuca</i> | barnacles | $y = -0.001x + 1.8272$ | 2.22 | 38 | 0.05489 | 0.145 |
| <i>Puccinellia</i> | brents | $y = -0.0021x + 2.0938$ | 30.29 | 173 | 0.14555 | < 0.001** |
| <i>Puccinellia</i> | barnacles | $y = -0.0018x + 1.8255$ | 4.56 | 60 | 0.07059 | 0.037** |

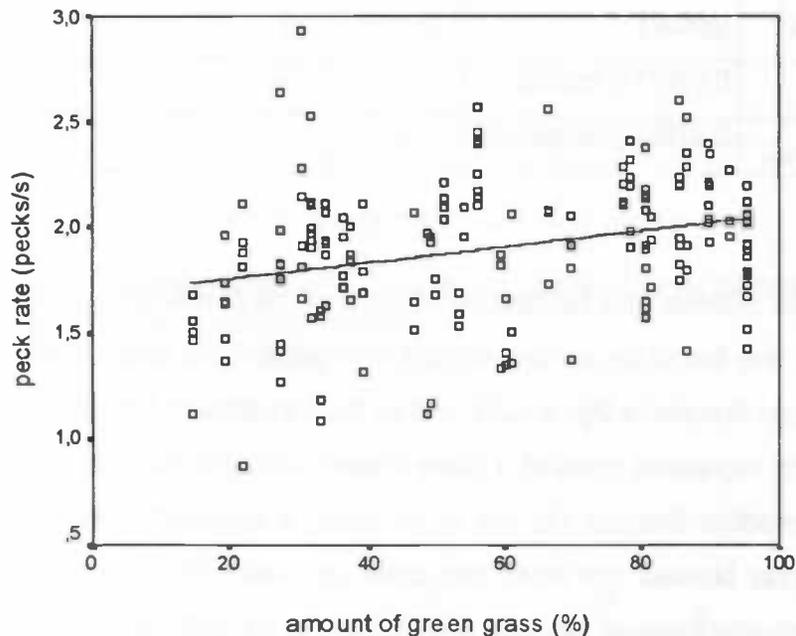


Figure 4.29: Influence of the percentage of green grass on the peck rate for the brents on *Puccinellia* ($p < 0.001$, $R^2 = 0.07059$, $F = 16.14$, $d.f. = 173$, $y = 0.0038x + 1.6862$)

Biomass and intake rate: the functional response

The instantaneous dry matter intake rate can by definition be explained as the product of bite size and peck rate. In relation with other variables there was a significant influence of the interaction between biomass of grass and the plant species and of the fixed factors plant species and fertilization (table 4.19).

Table 4.19: GLM-model for the determination of the intake rate by plant characteristics

| variable | coefficient | F | d.f. | p |
|----------------|-----------------------|-------|------|-------|
| constant | 4.287 | | | |
| fertilization | 2.158 | 8.191 | 1 | 0.004 |
| plant species | 0.128 (polder) | 4.988 | 2 | 0.007 |
| | -4.411 (Festuca) | | | |
| plant species* | 0.00571 | 4.368 | 3 | 0.005 |
| biomass grass | (polder) | | | |
| | 0.03671 (Festuca) | | | |
| | 0.01069 (Puccinellia) | | | |

The regression between total biomass as measure of plant availability and intake rate was significant for only two of the six combinations of vegetation and goose species (table 4.20.), for the brents on *Puccinellia* (figure 4.30) and for the barnacles on the polder (figure 4.31). In both cases the regression revealed a dome-shaped functional response with highest intake rates at intermediate biomass. For non of the cases a significant relationship between the amount of grass biomass and intake rate could be found. For *Festuca rubra* there was a positive relationship between biomass and intake rate for both species as well as for the barnacles on *Puccinellia* but they were not significant (figure 4.32). And there was a negative trend in the relation between biomass and intake rate of the brent geese on the polder (figure 4.33).

Table 4.20: Regression lines for the relation between total biomass and intake rate.

| vegetation | goose species | regression line | F | d.f. | R ² | p |
|-------------|---------------|-------------------------------------|------|------|----------------|-----------|
| Puccinellia | Brents | $y = -0.0005x^2 + 0.1177X + 2,709$ | 4.02 | 172 | 0.03364 | 0.0195 ** |
| Puccinella | Barnacles | $y = 0.0251x + 2.1079$ | 2.11 | 60 | 0.01780 | 0.1520 |
| Festuca | Brents | $y = 0.0123x + 3.4469$ | 2.56 | 110 | 0.01132 | 0.1347 |
| Festuca | Barnacles | $y = 0.0274x - 0.3563$ | 2.41 | 38 | 0.03445 | 0.1303 |
| polder | brents | $y = -0.0133x + 6.4331$ | 2.89 | 295 | 0.00635 | 0.0901 |
| polder | Barnacles | $y = -0.0004x^2 + 0.1228X + 0.6395$ | 5.63 | 110 | 0.04673 | 0.0047 ** |

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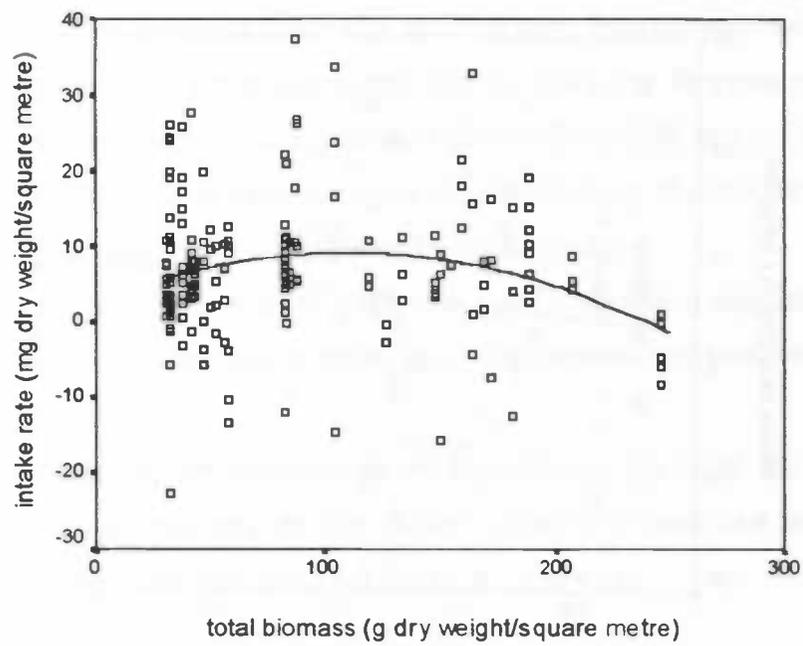


Figure 4.30: Quadratic regression between total biomass and intake rate for the brents on *Puccinellia* – the dome shaped functional response

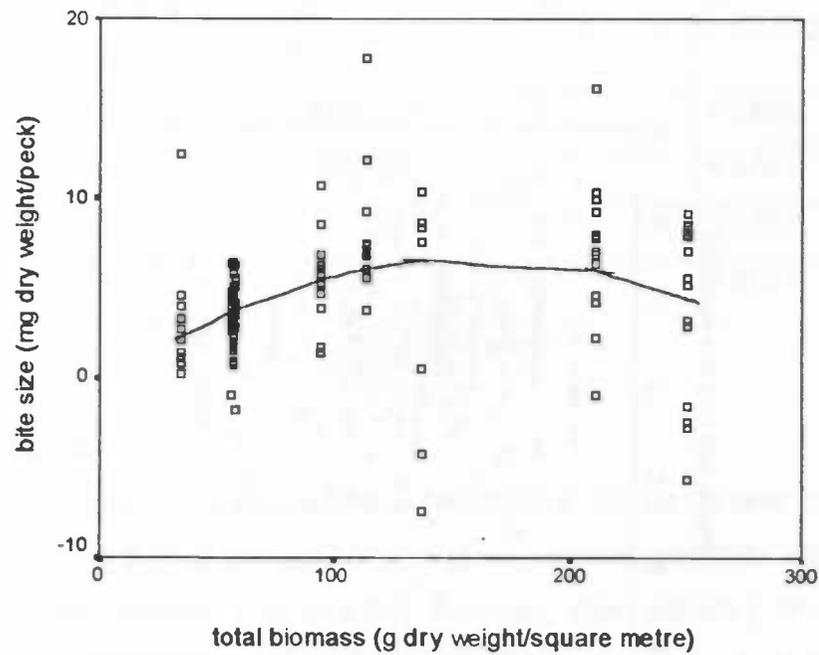


Figure 4.31: Dome-shaped functional response for the barnacles on the polder

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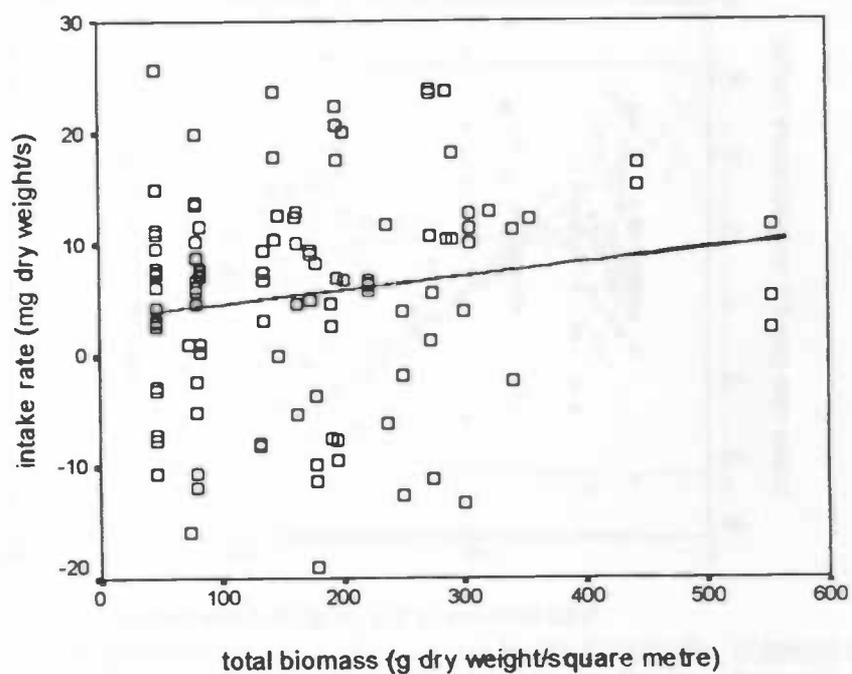


Figure 4.32: Functional response for the brents on *Festuca*, the regression line was not significant.

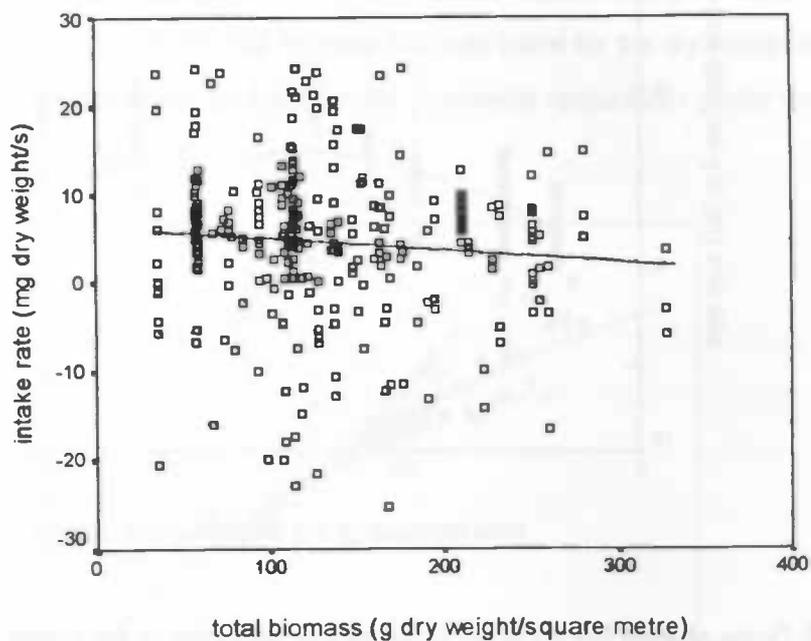


Figure 4.33: Decreasing functional response for the brents on the polder. The regression line was not significant ($p = 0.090$).

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The intake rate could also be related to bite size and peck rate. But both variables are ratios that share either the numerator or the denominator with the intake rate. Regressions between such variables have been discussed controversially (PRAIRIE & BIRD, 1989, JACKSON & SOMERS, 1991 KENNEY, 1991). Besides that all three original variables (number of pecks, foraging time and weight removed) involved have been shown to be highly correlated.

Nevertheless the influence of both variables on the intake rate is of interest, especially referring to the question whether the instantaneous intake rate can be predicted from peck rates that can be measured in the field.

If the interaction between bite size and peck rate was excluded from the model, the intake rate could be explained by peck rate and bite size and the interaction between total biomass and bite size and total biomass and peck rate ($p < 0.001$ for all, table 4.21).

Table 4.21 : GLM-model for the influence of bite size, peck rate and total biomass on the intake rate

| variable | coefficient | F | d.f. | p |
|--------------------|-------------|----------|------|---------|
| constant | -4.832 | | | |
| bite size | 1.753 | 4729.107 | 1 | < 0.001 |
| peck rate | 2.765 | 187.756 | 1 | < 0.001 |
| bite size*biomass | -0.00161 | 107.687 | 1 | < 0.001 |
| peck rate* biomass | 0.002905 | 13.847 | 1 | < 0.001 |

Bite size and intake rate:

Bite size had an significant positive effect on intake rate (figure 4..34). On the other this was a spurious correlation due to the fact that both variables share a common nominator with a large measurement error term (PRAIRIE & BIRD, 1989). But many other authors (for example SPALINGER & HOBBS, 1992) have found the same relationship between bite size and intake rate.

Thus the bite size predominantly influenced the intake rate and explained the dome-shaped functional response: the intake rate increased with bite size as biomass increased and at high biomass both bite size and intake rate decrease again while the peck rate decreases with increasing biomass.

4. Results

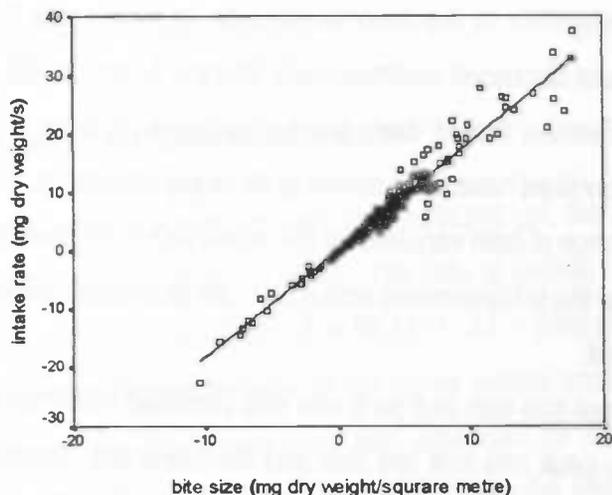


Figure 4.34: Relation between bite size and intake rate for the *Puccinellia*, obtained with the brent geese. ($p < 0.001$, $R^2 = 0.95010$, $F = 3294.16$, $d.f. = 173$, $y = 1.8323x + 0.3018$)

Protein intake rate:

The protein intake rate was closely related to the dry matter intake rate (figure 4.35). Therefore it showed the same relation to the total biomass that was found for the dry matter intake rate. Only the optima of the dome-shaped functions for *Puccinellia* respectively polder were shifted to a slightly lower biomass.

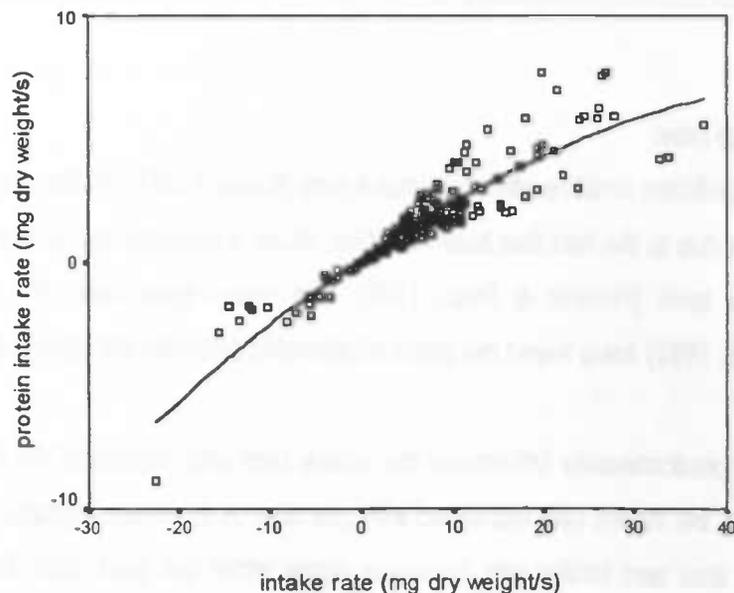


Figure 4.35: Correlation between dry matter intake rate and protein intake rate for *Puccinellia*, brents. ($p < 0.001$, $R^2 = 0.8454$, $F = 470.26$, $d.f. = 172$, $y = -0.0021x^2 + 0.2491x + 0.1749$)

Influence of protein content and intake rate on preference

Unfertilized *Puccinellia*

If two unfertilized turfs were compared with each other both the ratio of the protein content and the ratio of biomasses had an influence on the proportion of pecks. While the protein content had a positive relation with preference the proportion of pecks was lower for the turf with the higher biomass. The slope ($=b$) for the regression between natural logarithm of the ratio of biomasses and the natural logarithm of the ratio of pecks taken from turfs was -0.9817 ($R^2 = 0.13147$, $p < 0.001$, $F = 78.863$, $d.f. = 52$). This indicated (negative) matching. The slope for the ratio of protein contents was 2.0113 ($R^2 = 0.12067$, $p < 0.001$, $F = 71.499$, $d.f. = 521$). The protein intake rate showed positive matching with the preference ($R^2 = 0.04455$, $p < 0.001$, $F = 24.29462$, $d.f. = 521$, $b = 0.9375$). There was no significant relation between the preference and the intake rate ($R^2 = 0.00309$, $p = 0.2046$). The preference showed a high sensitivity for the protein content and matching with the biomass and the protein intake rate (figure 4.36).

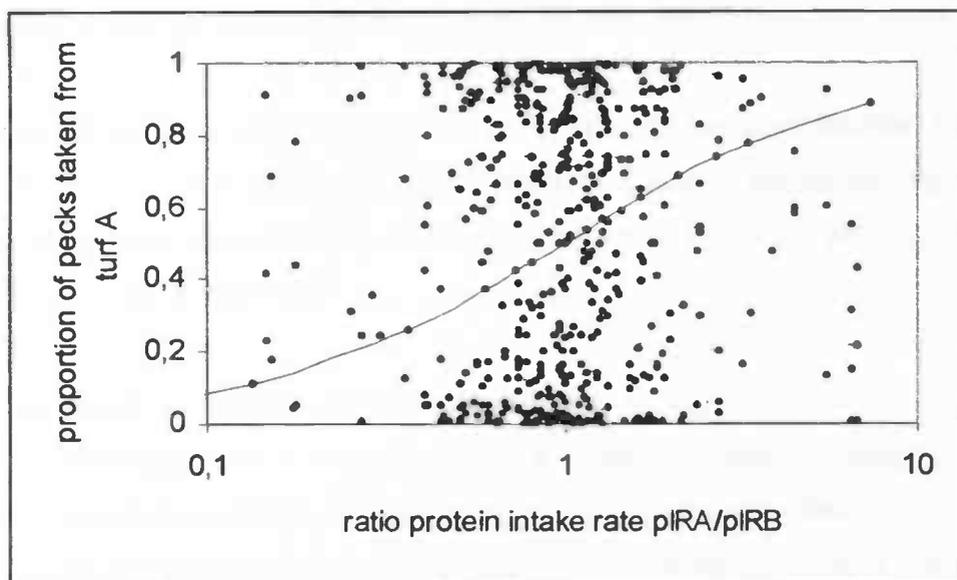


Figure 4.36: Relative preference for a turf in relation to the ratio of protein intake rates of two turfs

unfertilized *Puccinellia*.

Fertilized *Puccinellia*

The ratio of the protein content could explain the choice between two fertilized turfs best ($b = 3.9192$, $R^2 = 0.15674$, $p < 0.001$, $F = 20.26$, $d.f. = 109$) while the ratio of biomasses had hardly any influence ($b = -0.4543$, $R^2 = 0.005325$, $p = 0.0148$, $F = 6.13$, $d.f. = 109$) on the preference.

4. Results

The ratio of protein intake rate ($p = 0.2291$, $R^2 = 0.01324$) and the intake rate ($p = 0.5938$, $R^2 = 0.00262$) showed no relation with the ratio of pecks.

Comparison between fertilized and unfertilized *Puccinellia*

If the geese had to choose between a fertilized and an unfertilized turf, the ratio of biomasses was completely insignificant ($R^2 = 0.0001$, $p = 0.8648$). The ratio of protein contents influenced the choice ($b = 3.4414$, $R^2 = 0.22310$, $p < 0.001$, $F = 86.1511$, $d.f. = 300$) of the animal, which meant that the fertilized turf was chosen because of the higher protein content. The influence of the intake rate and the protein intake rate were also significant for the intake rate ($R^2 = 0.01534$, $p = 0.0314$, $F = 4.67389$, $d.f. = 300$, slope 1.4028) and the protein intake rate ($R^2 = 0.10470$, $p < 0.001$, $F = 35.08467$, $d.f. = 300$, slope 0.6774). The slope and therefore the sensitivity of the preference was largest for the relation between preference and protein content.

5. Discussion

5.1 *Functional response*

The correction factor calculated to improve the estimation of the evaporation resulted in a reduction of variance of bite size and intake rate as well as in a reduction of the number of negative values. But still negative values were left in the analysis. The choice of a smaller range of values would not have resulted in better results because the smaller the sample the more single values influence the results. But nevertheless the not very accurate measurement of the amount of plant material consumed by the animals affects all intake rate and bite size values. This causes a relation between the two factors, that is much stronger than probably really present. Consequently both intake rate and bite size show very similar relations with other factors. A possibility to overcome this interrelation between intake rate and bite size is the six-bite technique developed by LACA et al. (1992, as cited by UNGAR, 1996). Here the animal is only allowed to take very few bites to determine the bites size and afterwards the intake rate is measured.

The difficulty to determine intake rates and bite sizes accurately has been described by other authors, too. So ILLIUS et al. (1999) could only detect a preference for patches with high intake rates by taking mean values from several special intake-rate trials and not with those values derived from the choice experiment.

For the process of diet selection the long term intake rate in respects to a day or a week is much more elucidating but it is nearly impossible to measure. Therefore investigation have focussed on the short term intake rate. From measurements of short term intake rates and daily activity budgets the daily food intake can be estimated. Furthermore short term intake rates can provide useful information about the diet selection in relation to certain characteristics of the sward and behavioral aspects like bite size and peck rate. But diet selection in terms of choice of different food plants is effective on a different time scale. Here postingestive processes also play an important role and the uptake of a sufficient amount of nutrients and energy within the digestive capacity of the animal.

By definition intake rate can be expressed as product of peck rate and bite size. In distinction to the functional response this is called the arithmetic response. Both variables can be predicted

by biomass but there is not always a simple linear relation between biomass and either bite size or peck rate.

Bites were shown to increase with biomass. This relationship has been found by a lot of authors and it seems quite clear why: if the plant size or the plant density increases the animal is able to take up more biomass per bite until the maximum bite volume is reached.

This might be disguised in this study because especially at high biomass (*Festuca* and *Lolium/Poa*) long parts of the plants were removed but not really eaten. Part of the very long leaves were spilled on the ground but they could not be assigned to one of the turfs.

On the polder there was no relation found between biomass and bite size for the brent geese, the bite size was rather constant. For the brents on *Puccinellia* and for the barnacles on the polder the bite size decreased again after a maximum bite size was reached of 5.3 respectively 6.2 mg dry weight/peck.

But why should the bite size decrease at high biomasses? At high biomass turfs there is typically also a large amount of dead material present. The smaller bites might reflect a more careful selection of plant parts at these turfs. This relation has been found for sheep (PRACHE et al., 1998) which took smaller bites to ingest only the more nutritious leaves. In this case the intake rate does not influence the choice but the selected plant (part) influences the intake rate. If the intake rate decreases because of smaller bites this can be compensated by a higher peck rate, longer grazing bouts or a higher energy/nutrient content of the ingested food as seen for the sheep.

A big difference between geese and many other large (i. e. vertebrate) herbivores is that their bites are rather small. They are not able to incorporate more than one to a few leaves within a single bite. This is the prerequisite to a much higher selectivity than possible for many large grazers.

The peck rate or more general the bite rate is determined by searching and handling. As biomass increased, the peck rate decreased linear for all three vegetation types and both goose species. This decrease in peck rate is normally attributed to an increase in handling time because it should take longer to remove and to swallow larger bites since bite size increases with biomass. But not in all cases there was a significant direct relationship between peck rate and bite size which could be assumed if peck rate decreases with biomass and bite size increases until a certain biomass. On the other hand the relation between bite size and bite rate is probably not that close for geese because they do not have to chew their bites.

Nevertheless not only the size of the bite determines the peck rate but also a searching component which might also cause a decrease in bite size at high biomass. This can also be measured as step rate. This searching component is important in a vegetation with a lot of dead or unpalatable material in it. There is an asymptotic increase of peck rate with the percentage of green grasses and a decrease with the amount of dead material. If the goose has to search for the next palatable bite because the green material is covered dead material the peck rate decreases.

Optimal biomass in terms of intake rate

The results for the functional response were rather unclear: A significant dome shaped relation between dry matter intake rate and the biomass was only found in two out of six cases. For the other types no significant relations could be found, the trends were either a positive or a negative relation. What does that mean? The dome-shaped functional response is at least very clear for the barnacle geese on the polder while the trend was similar for the brents if the Texel-experiments were excluded from the analysis. For the later there was a decreasing trend. But although the increase of the intake rate with biomass was not significant the possibility of an asymptotically increasing (type II) functional response cannot be excluded. The functional response might depend very much on the specific characteristics of a vegetation or plant species and therefore it might look different for various grasses. A distinct functional response it has already been shown for herbs compared to algae (TRUDELL & WHITE, 1981), which is of course a systematically much broader range.

The functional response for the protein intake rates was found to be closely related to the relation of biomass and dry matter intake rate. Although the optima for the protein intake rate were at slightly lower biomass than the optima for the intake rate both were higher than the preferred biomass.

5.2 Preference

Geese and other herbivores have been shown to prefer low to intermediate biomass or vegetation height. This has been attributed to a low foraging efficiency of small herbivores like geese and hare in dense vegetation as described by VAN DER WAL et al. (1998). A bottom up control of the vegetation is assumed, which means that the herbivores are forced to leave an area if the vegetation height exceeds a certain value. This leads to a concentration of grazers in special areas, so called grazing lawns, where the vegetation is maintained by consecutive grazing at a sufficient low height. Other possible explanations that came up for a preference for relatively short or intermediate vegetation height were be that potential predators are harder to spot, walking is more difficult, handling of the meal becomes difficult and the quality decreases due to maturation of the plants.

The captive geese generally preferred also not the turfs with the highest biomass during the trials. But because of the size of the turfs they were able to walk around them and there was no necessity to walk through the vegetation. For the same reason it can be assumed that the possibility to discover a potential predator was not reduced if the geese were feeding from turfs with high vegetation.

Most authors have tried to explain preference either by dry matter intake rate maximization or by nutrient intake rate maximization. Both variables could not explain the choices made by the geese sufficiently in most cases. The geese prefer in general turfs of lower biomass than those that would offer optimal intake rates and also lower than those that offer optimal protein intake rates.

Instead of the intake rate the quality in terms of the protein content of the food plants played an important role in the determination of the preference. The larger the differences in the protein content the more this criterion dominated the choice of the geese. This was very obvious when fertilized and not fertilized turfs are compared with each other.

What are the different effects of quality and intake rate?

In general the geese do preferred turfs low biomass and high quality. Both factors are normally interrelated because the protein content decreases as the plants grow and the amount of

structural components increases. But fertilization changed the relation between protein content and biomass. Fertilized turfs are preferred by the geese over not fertilized, although and or because the vegetation/biomass is higher. The fertilization can alter the preferred biomass as described by RIDDINGTON et al. (1997). This switch of preference at fertilized sites is possible because the quality does not restrict the diet selection and this might enable the geese to follow an intake rate maximization tactic. This is not possible at not fertilized patches were the need of a sufficient protein intake interferes with the intake rate maximization.

Turfs with higher biomasses were preferred which still contain a lot of protein and also offered higher intake rates. But although the preference switches to higher biomasses, not the very high biomasses are preferred. This means that even though the absolute protein intake per second or minute might be higher at higher biomass, the geese still prefer lower biomass turfs that offer less protein per time scale. But although these turfs offer lower intake rates they contain more protein in relation to other plant components which means a higher digestibility. HASSAL et al. (2001) showed that the application of fertilized uncoupled the relation between biomass and protein content but it did not prevent a decrease in digestibility in terms of breaking strain with increasing biomass. And as geese have very short gut retention times of only 90 to 120 minutes the digestible efficiency is rather low and this could explain their preference for highly digestible food.

Although the relation between preference and higher intake rates on fertilized turfs could not be directly shown it still provides a reasonable explanation for the behavior observed. The large measurement error might disguise some relations between intake rate and other factors. And not the actual energy intake rate was determined but the dry matter intake rate. High dry matter intake might not completely match with high energy intake especially at higher biomass.

Something else that is quite important to keep in mind is the time scale of the investigation. VILLALBA & PROVENZA (2000) discussed the influence of postingestive feedback on the foraging behavior. This can only be detected if the animals continuously feed on a certain vegetation for at least a few days. But then they found that the intake rate on the food source increases after the animals had been injected with starch while it stayed at the same level for animals that had been injected with water. "Thus, in horizontally heterogeneous pastures of similar quality, animals may be able to access the reward from a patch by sensing the rate at which food can be obtained from the patch, and modify their preferences accordingly" (DISTEL et al., 1995).

However, when sward quality is variable, nutrient composition can be even more important than structure in determining preference. Tall or short swards may be preferred when their nutritional quality is higher. Food that yield lower intake rates can be preferred by lambs fed unbalanced basal diets when those foods provide ratios of energy/protein closer to the lamb's nutritional needs.

Another problem also concerns the time scale. Different authors have stressed the necessity to determine the question whether animals really maximize their intake rate or nutrient intake rate on a longer time scale. On a short time scale of seconds or minutes the digestibility and gut passage time are not included in the optimality model. But these factors might reduce the profitability of some high intake rate forages.

Why is it necessary for the geese to optimize their intake of energy or nutrients?

Herbivores have a low quality diet and they have to spend long time of the day foraging. therefore they are very vulnerable to changes in intake rate and quality because it is not that easy for them to compensate for lower quality or decreased intake rate by simply foraging more and longer. Furthermore the fitness of an animal directly can be affected by its intake rate.

A correlation between higher intake rates and improved lifetime reproductive success has been shown in zebrafinches (LEMON & BARTH, 1992). Higher intake rates can result in larger amounts of body reserves. The accumulation of body reserves is crucial for migration and breeding and the geese with the largest amount of body reserves have greater reproductive success (EBBINGE et al., 1982).

Possible cues for selection

What kind of cues do the geese use to decide which plant species or which patch to prefer? the factor biomass was related to all parameters in the functional response and also to the preference. Nevertheless the protein content respectively the application of fertilizer was able to change the preferences in relation to biomass. How do the geese detect quality differences? There are indications that geese and other wildfowl are able to distinguish grasses of different quality by their colour. But they might also be able to measure the protein content while eating. This could explain the frequent switches between the turfs to compare the different patches. These consecutive tests of possible food plants are called sampling and sampling is quite

frequently seen in wild animals, too. The necessity to sample was often made responsible for partial preferences. Preferences are regarded to be partial if the patch or food plant that seem to have the highest profitability is not consumed exclusively but also other plants, plant parts or plant sizes are included in the diet. This was found sheep which could have maximized their energy and protein intake by eating only clover also showed partial preferences (NEWMAN et al, 1994).

Why do partial preferences occur that frequently?

Many authors have come up with explanations for not optimal choices as the partial preferences are also called. One possible reason are measurement errors of the observer which were quite obvious for the estimation of the correct amount of weight removed and therefore for the intake rate and the bite size. Because of this large and obvious inaccuracy all statements concerning bite size, intake rate and protein intake rate have to be handled very cautious. Related to this issue is the argumentation that the factor that really determines the preference of the focus animals was not even measured but completely overlooked. In this context supplementary nutrients are always mentioned. For example have the turfs that originated from the same plots really been homogeneous?

Partial preferences have also been regarded as discrimination errors made by the animal. This argument can be modified to the "simple fact of life" as discussed by (HANLEY 1997). The optimization of the diet is assumed to be too complex, especially for herbivores. The environment changes continuously and in too many to make it possible for an animal to determine the optimal choice at each single moment. To keep track of all the developments of the current and future food plants the animals have to sample all the plants in a relatively short time scale. the only other possibility to cope with a constantly changing (food) environment are simple rules of thumb that fit for most situation. But if something like rules of thumb occurs then the foraging efficiency is not optimized over a short period but probably over weeks or longer. Simple rules of thumb might provide an alternative to complex behaviour patterns which assume a higher learning capacity to allow the development of behavior patterns based on trial and error. EDWARDS et al (1997) for example could train sheep to form associations between certain swards and food rewards.

Mixed diets cant also be explained by matching. The animals might include different food plants in the diet relative to their profitability. This kind of matching could be found for the relative

preference for certain *Puccinellia*-turfs in relation to the difference their protein intake rates or biomass. From complete indifference to perfect matching, increasing sensitivity to an complete exclusion of all other than the most profitable food source there is a wide range of possible behavioural responses.

Nevertheless many of the approaches assume a certain amount of sampling to account for spatial variance and variance over time in quality and other factors. This necessity of sampling is also indicated by the fact that the geese switch habitats during late winter/early spring according to the quality of the vegetation (PRINS & YDENBERG, 1985) which has to be checked every now and then to determine the right date of the switch. And this does not only hold true for the choice between polder and salt marsh or *Festuca* and *Puccinellia* but also for the different feeding areas within a specific vegetation type. This continuous sampling was maybe reflected by the grazing pattern the geese showed during the trials, the fact that they taste from all the turfs that are offered.

Grazing pattern and sampling

The geese obviously first went around between the turfs and tasted from all of them.

And although the geese visited most turfs during the first round they took more pecks from the preferred turfs. The others were only visited for a few pecks to sample the vegetation and they were often not visited again in a later round.

It is hard to say anything about the turfs that were left out, did that happen by accident or were they ignored on purpose? Or as JÓNSDÓTTIR VIVAS et al. (1991) wrote „It is often difficult to distinguish between an animal not discovering or actively rejecting a food item.” But it seems that the geese do not necessary have to taste all of the turfs, they can also distinguish the different vegetation types by sight as seen at the polder – *Festuca* – *Puccinellia* comparison. During these trials in many cases only the three turfs of the preferred vegetation type have been eaten from.

No matter if the geese ate only from two or three or from all nine turfs, the motivation was highest at the mixed trials with all three vegetation types. This phenomenon was also describes by PETERS et al. (2000), who found that slugs consumed more food when they had the choice between various food species.

The second type of experiments that confirms this was the control experiment where the motivation was very low. The control experiments indicated that the first turf was preferred but was not true for the rest of the experiments. This might be due to the homogeneity of turfs which is of course the requirement of a control experiment. If the turf the goose is feeding on right now is compared to those visited before there is a tendency to leave earlier if all other turfs offer the same quality/intake rate. If there are different turfs on offer, the goose stays proportionally longer/takes more pecks from relatively better turfs and proportionally less from those that are lower in quality/intake rate. For wild geese this would mean that they can move on continuously in a homogenous vegetation because after the next step the vegetation will probably be right the same. In a heterogeneous environment it is advantageous to stay in patches that are better than the average. Since the control experiments took place in between the row of experiments and not in advance the geese might have been searching for better patches. SPALINGER et al. (1988) reported that they were not able to do alternate trials with different plant species because then the deer refused to eat from the less preferred plants and kept on searching for the more palatable species that had been there during the trial before.

Motivation

Besides individual differences in the foraging motivation of the geese the motivation at the various experimental types reflected the preference in the experiments. This is also indicated by two cases of successive trials with the same goose but different turfs, first *Lolium/Poa* and afterwards *Puccinellia*. While their feeding motivation for polder was already gone, they still liked to feed from *Puccinellia*-turfs which indicates higher preference.

Salt marsh or polder?

There is an ongoing discussion about the reasons for the switch from the polder of Schiermonnikoog to the salt marsh during March and April. First the barnacle geese leave the polder and a little bit later the brents do the same.

During the spring 2000 for the first time not all brent geese left the polder to feed on the salt marsh. A reason for this might have been the fact that the chasing and scaring by the farmers was less intensively than during other years. This shows that it might be possible for the geese to get along mainly on a *Lolium/Poa* diet during spring on Schiermonnikoog. On other islands

like Texel the brents feed on the polder the whole spring because there are no salt marshes at all. Still the question has to be answered which geese stayed in the polder, are they able to reproduce successfully or where do the less successful individuals?

An important fact that makes the geese leave the polder might be the high growth rate there at the end of spring. This causes the grasses to grow beyond the profitability-threshold of the geese very quickly. After this threshold is passed the vegetation becomes unsuitable for the geese. To avoid that the geese concentrate during spring more and more on a few pastures, which are kept short while all the others grow. After a pasture has escaped the grazing control the geese are not able to come back. In a cold spring the geese leave the polder later than in warmer springs (PRINS & YDENBERG, 1985). During cold years not only the growth rates in the salt marsh are lower and therefore the profitability for the geese, the growth rates are also low in the polder. This makes it possible for the geese to control the area for a longer time. The growth rates of the plants determine how much the geese have to concentrate to maintain a sufficient short sward. There might be a simple goose density that cannot be exceeded because of competition between the individuals. From a certain point on it might be more profitable to feed in lower goose densities on the salt marsh which is easier to manage because the growth rates there are lower. It is still controversial whether geese that only feed on the polder are able to raise young successfully but there are indications that this is possible. Because of the fast growth in the polder area the geese are not able to come back to the polder after they have left the area for a few days. This explains the sudden switch to the salt marsh, maybe also at the point when it becomes necessary to control the recourses there, too.

Additionally the salt marsh does not only offer *Puccinellia* and *Festuca*, but also two favorite food plants, *Plantago maritima* and *Triglochin maritima*. These two species do not occur in such a large amount as the grasses do but they occur within the island zone between *Puccinellia* and *Festuca*. PROP & DEERENBERG (1991) concluded that the geese cannot maintain and improve their body condition beyond mid of May without consuming *Plantago* and *Triglochin*. But these two food plants are mainly monopolized by the dominant individuals in a flock and only those return with offspring to the wintering grounds.

While the barnacle geese exhibited a distinct preference for the polder during the polder-*Festuca-Puccinellia* comparison, the preference of the brents seemed irregular. But the observed could be compared with the switch of the wild geese although two of the captive geese showed several consecutive switches in comparison to a sudden switch of the wild

geese. How can the frequent switch between the vegetation types be explained, which occurred not only between successive trials but also within one trial between polder and *Puccinellia* and to a smaller extent also *Festuca*? Was this due to a It might also reflect the fact that a massive sampling to determine the right moment to switch from polder to salt marsh. In general this behaviour indicates that the switch to the salt marsh cannot only be explained by less disturbed area the geese find there.

Later during the season the brents did not only show a lower motivation at *Festuca*-trial but also at the polder-trials with the Texel-turfs. The wild barnacles were observed to feed much more in the *Festuca*-area than the brents do and they switch to the polder earlier than the brents but still the captive barnacles kept on feeding from the polder. On the other hand at the end of April, at the time when the experiment was conducted, the wild barnacles started their migration to the breeding grounds.

While the switch occurred step by step for the juvenile brents, the two adult brents switched from polder to *Puccinellia* and back. Is this an example for sampling (as it occurred in all trials in general) which is of course necessary to determine the right point to switch or is that the consequence of a preference for mixed diets. This is probably not possible in that extent for the wild geese because of the distance between the different feeding areas. This can be substituted by the fact that the barnacles meet at roost-places after a foraging period and these can serve as sources of information about potential feeding areas (YDENBERG et al., 1983). But in general sampling should be demanded also to find new food plant in terms of discovering *Plantago* and *Triglochin* on a smaller range. On the salt marsh during May the protein content of the *Puccinellia* was higher than of the *Festuca*, this explains the preference of the geese for *Puccinellia*.

Did the captive geese behave similar to wild geese?

One of the important thing in this respect is the time scale of the investigation. The trials started in the second half on April and the barnacle geese left the island at the end of April to migrate to their breeding grounds. This could provide an explanation for the low motivation of the barnacles during the salt-marsh trials which took place in May.

Nevertheless parallels could be seen between the behavior of wild and captive geese. *Festuca* was more or less ignored by the captive geese, for the wild geese, especially the brents, it is regarded as a substitute for *Puccinellia* during years in which the later does not provide enough food. The only areas that was visited by the wild geese quite frequently and that was also preferred by the captive geese was the oldest part of the grazed salt marsh, the OBK. Also the switch from the polder to the salt marsh was reflected during the foraging trials of the brent geese.

White was captured only a few weeks before the experiments started and despite the fact that this goose had to get used to the enclosure and experimental procedure, it behaved not significantly different from the other (brent) geese, except for the fact that its foraging motivation was lower, more comparable to that of the barnacle geese.

The next thing that has to be taken into consideration is the fact that not all wild geese can make their own foraging choices. They are animals that live in large groups, and within the group only high ranking animals, which are normally pair with many goslings, are able to monopolize the best patches, on the salt marsh these are patches that contain *Plantago maritima* and *Triglochin maritima*. In this relation the animals are able to make optimal decisions which they cannot make in the wild. On the other hand even if the choices on offer are beyond the optimal one would still claim that they chose for the best that is possible.

This can be related to the preference for turfs that were sprayed with fresh water in comparison to salt water. TIMMER (1989) found that pairs of brents and barnacles both also spent more time foraging on areas that had been sprayed with fresh water instead of salt water. If brents and barnacles were able to feed together in the same enclosure, the barnacles still consumed more of the fresh water grass while the brents were found on the salt-water-sprayed part due to the competition with the larger and stronger barnacles. Additionally they have salt glands and therefore the possibility to cope with higher salt concentrations of their food plants.

5.3 Conclusions

The preference in terms of the switch to different food plants the during the season and this could not be explained in terms of protein content or intake rate. Within a certain vegetation type the selection seemed follow two principles: first the plants with the highest protein content are selected and within the high-quality plants the ones that might also offer higher intake rates.

5.4 Recommendations

For exacter values of intake rates and bite sizes a better estimation of the evaporation is inevitable and therefor it is necessary to run experiments in the lab under controlled conditions. But that would a completely different approach because it means more stress for the animals. And this might in turn change the results. Other possibilities would be to make the trials as short as possible and to avoid any solar radiation.

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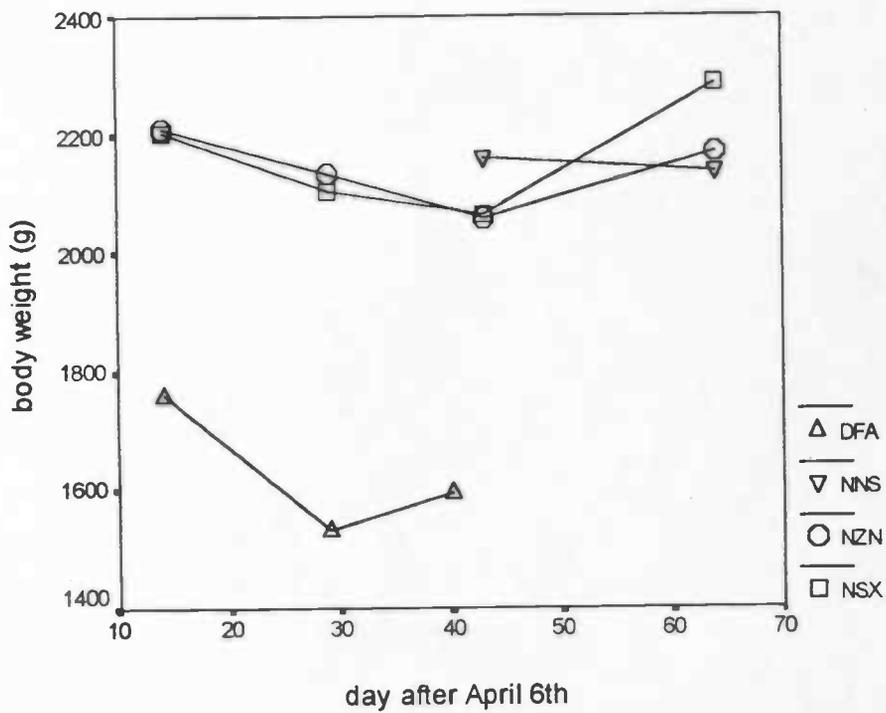
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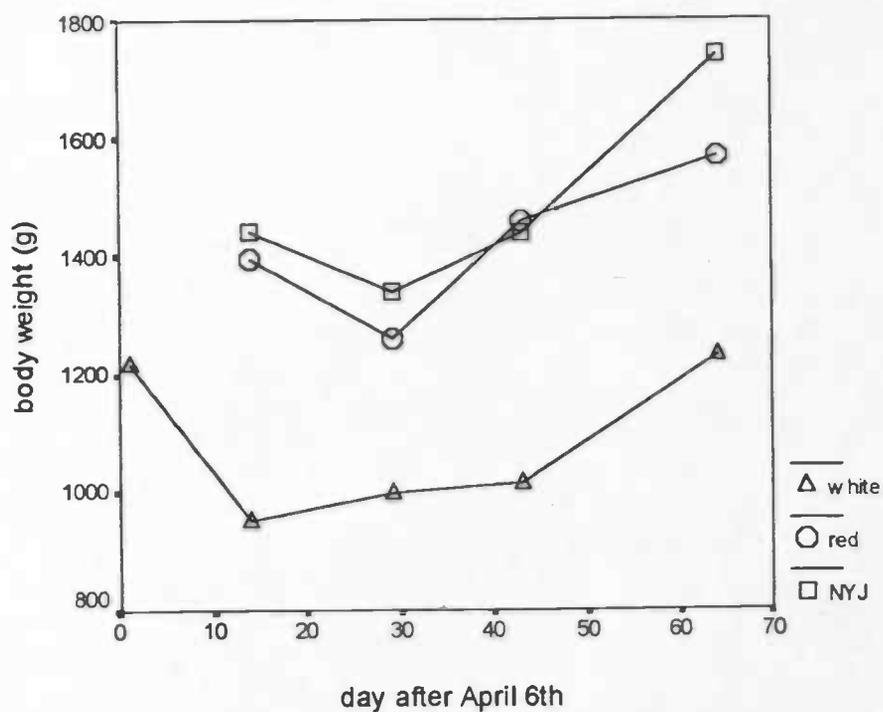
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8. Appendix



Weight development of the barnacle geese



Weight development of the brent geese