Grazing in coastal grasslands
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Abstract

We have studied the relative importance of food biomass and food quality for habitat preference in Brent Geese by manipulating these parameters. Levels of biomass and food quality, measured as nitrogen content, were independently enhanced by temporary exclosure from grazing and addition of artificial fertiliser in a full-factorial experiment. Instantaneous intake rate increased linearly with sward height, over the range of values studied. Patch preference, as determined from the number of aggressive interactions and bird density for wild Brent Geese, was however highest for plots with the highest nitrogen content. Grazing pressure, measured as dropping density, showed the same pattern. Only the number of interactions was measurably affected by sward height in addition to the effect of nitrogen content. These results complement earlier work (Riddington et al. 1997; Hassall et al. 2001) by demonstrating that, even at low values of sward height, food quality is an important parameter determining patch choice. Our results are consistent with the expectation that patch choice is influenced by nitrogen intake rates and they provide an explanation for distribution patterns of Brent Geese on agricultural grasslands and the sequence in which pasture and marsh habitats are utilised in spring.
Models of patch choice in herbivores are in most cases based upon a relationship between intake rate and biomass of food (Turner et al. 1993; Percival et al. 1996; Percival et al. 1998; Pettifor et al. 2000). Often, the shape of this functional response is assumed to decelerate towards a plateau according to the disc-equation (Holling 1959; Spalinger & Hobbs 1992; Gross et al. 1993; Ginnett & Demment 1995). Under this assumption, classical theory predicts that herbivore density will reach its maximum at the highest standing biomass (Oksanen et al. 1981). This generalisation however does not fit the empirical facts. Accordingly, Fryxell (1991), corroborated by van de Koppel et al. (1996), provided a theoretical framework to account for the effect of food quality on resource acquisition in herbivores. He showed that aggregation of ruminants at intermediate levels of biomass can result from spatial variation in food quality and from forage maturation effects, under the assumption that food quality declines with increasing biomass. Experimental work by Langvatn & Hanley (1993) and Wilmshurst et al. (1995) on red deer *Cervus elaphus* support the model prediction that intermediate levels of biomass will be preferred over patches with high biomass, if the intake rate of energy or protein is higher in these patches.

The average quality of the diet is negatively related to body size in mammalian (Prins & Olff 1999) and avian (van Eerden 1997) herbivores. Small herbivores, such as lagomorphs and herbivorous waterfowl, are therefore even more likely to be influenced by differences in food quality than the large ruminants. In waterfowl, the digestion of food is poor due to a relatively short digestive tract and high passage rates (Prop & Vulink 1992). This makes them more sensitive to food quality than expected according to body size (Sedinger 1997). Geese, for example, typically feed on high quality food (Owen 1980). Indeed, many field studies show relationships between foraging decisions of waterfowl and food quality: At the diet level, geese are observed to choose those components that yield the highest energy and protein intake rate (Prop & Deerenberg 1991). At the patch level grazing pressure and nitrogen content of food are highly correlated (Ydenberg & Prins 1981; Teunissen et al. 1985; Vickery et al. 1994). And also at the scale of staging sites, e.g. the island of Schiermonnikoog, could the habitat choice be related to protein content (Prins & Ydenberg 1985) and to digestibility (Boudewijn 1984). In many of these examples, however, the analysis is confounded by differences in plant production, standing biomass and presumably, the intake rate of food. It is, therefore, difficult to determine to what extent foraging decisions are affected by intake rate of food and food quality.

Recent work by Riddington et al. (1997) and Hassall et al. (2001) showed the importance of nitrogen constraints for patch choice in Brent Geese *Branta bernicla bernicla*. In their study with wintering Brent Geese on coastal grasslands in Britain, birds preferred short swards over tall swards under unfertilised conditions, due to a negative correlation between nitrogen content and sward height. The lifting of this constraint by fertilisation resulted in a preference for tall swards. They formulate their findings in relation to the forage maturation hypothesis, by arguing that swards of intermediate
length are preferred due to opposing constraints associated with sward height. At low sward heights intake rate forms an important constraint, while nitrogen content and digestive constraints become important at taller swards.

We quantitatively elaborate upon their concept by manipulating the same parameters under different circumstances. Our study focuses on the spring situation, where levels of sward height are generally low. The birds are also in a different physiological state, as they have to acquire fat reserves for spring migration and breeding (Ebbinge & Spaans 1995). Following Riddington et al. (1997) and Hassall et al. (2001), we started from the premise that both food quality and biomass will affect patch choice and that intake rate will be positively related to biomass. We studied the relative importance of these variables at a low range of sward heights by experimentally manipulating them within a single plant community. The preference for patches was estimated from behavioural measures as well as from grazing pressure for wild Brent Geese, and we established the relationship between biomass and intake rate of food using captive animals. After McKay et al. (1994) and Hassall et al. (2001) who stressed the importance of protein acquisition for Brent Geese, we will use nitrogen content as a measure of quality throughout the present paper. The relationship between nitrogen content and other measures of food quality will later be discussed.

### Study area

The experiment was carried out at the cattle-grazed salt marsh (400 ha) of Schiermonnikoog (53°30’N, 6°10’E), a barrier island in the Dutch Wadden Sea. Numbers of Brent Geese staging on Schiermonnikoog range between 2,000 and 4,000 during spring (van der Wal et al. 2000b). For a detailed description of the salt marsh see Olff et al. (1997). In early spring the geese spend most of the time foraging in the embanked polder (270 ha), but towards May a gradual shift to the salt marsh is observed. Barnacle Geese Branta leucopsis (Prins & Ydenberg 1985) are also important herbivores utilising the marsh, leaving the island around mid April (Stahl 2001). Although European brown hares Lepus europaues are abundant at some of the ungrazed sites, their density at the cattle-grazed salt marsh was relatively low when the experiment was performed. The grazed salt marsh is grazed with cattle from the end of May until November at a stocking rate of 0.5 cow.ha⁻¹ and harbours a mosaic of plant communities (van Wijnen et al. 1997). The plant communities here, that are characterised by Festuca rubra and Puccinellia maritima, experience the highest grazing pressure of the whole island by Brent Geese in May (unpublished data).
Methods

Twenty-eight plots of 2m by 6m were selected within the Juncetum gerardi and the Puccinellietum maritimae plant communities, in areas on the cattle-grazed salt marsh. The communities were dominated by short *Festuca rubra* (41%), *Juncus gerardi* (20%) and *Puccinellia maritima* (15%), and known to be frequently visited by Brent Geese. The plots were homogenous with respect to vegetation composition and height. Subdivision into 7 replicate blocks of 4 plots each was made, where plots within a block were nearer to each other than to plots in adjacent blocks. Average distance between plots in a block was approximately 4 m. Four different treatments were assigned randomly to these plots, within a block. These treatments included fertiliser application and temporary herbivore exclosure in a full factorial way. This resulted in plots of high biomass with high quality (fertilised & excluded, FE), high biomass and low quality (unfertilised & excluded, UE), low biomass and high quality (fertilised & grazed, FG) and finally low biomass with low quality (unfertilised & grazed, UG). Fertilisation was accomplished using a commercial fertiliser (*CaCO3.NH4NO3*, 27%), dissolved in 0.5-liter water and sprayed over the vegetation, resulting in a net addition of 25 g of N.m⁻². Geese and hares were excluded for 3 - 4 weeks using chicken wire (5 cm meshwidth, 50 cm high). The experiment was carried out in two series. The first 3 complete blocks (12 plots) received the treatments April 1st 1998. The second series of 4 blocks (16 plots) was treated April 5th. An observation tower was placed within a distance of 100 m from the plots and behavioural data of the geese were recorded, starting from the moment that the exclosures were removed. Observations started April 22nd and May 5th for the first and second series, respectively.

Vegetation analysis

The day before the exclosures were removed, the available biomass and the sward height were measured. Aboveground biomass was estimated by randomly taking one sod of 10 cm x 10 cm per plot and cutting it to ground level. The material was sorted to live and dead material, washed, dried at 60°C for 48 hours and weighed. Using a PSII field spectrometer (ASD, Boulder), reflectance values were measured for red and infra red light, and an index of green biomass was calculated (Normalised Difference Vegetation Index, NDVI, Esselink & van Gils 1985). The development of live standing biomass over time was monitored by measuring the green biomass-index at weekly intervals. Live biomass was positively correlated to the green biomass-index (Pearson $r^2 = 0.46, P < 0.01, n = 28$). Sward height was measured with a 24 g, 20 cm diameter polystyrene disc that was dropped on the vegetation, sliding along a calibrated stick that rested on the ground. Sward height was linearly related to biomass of live leaves (g dry mass.m⁻²) ($y = 0.099+0.32x, r^2 = 0.84, P < 0.001$) and to the green biomass-index (value) ($y = 0.68+0.048x, r^2 = 0.42, P < 0.001$). In most analyses, sward height is therefore used as an index of the quantity of food available. On a more detailed level, growth and depletion were measured using the leaf-length of individually marked
Foraging behaviour of Brent

From dawn to dusk, the experimental site was observed. Goose density and number of agonistic interactions were recorded at regular intervals by sequentially scanning each plot and observing it for ten seconds (see Teunissen et al. 1985). An agonistic interaction was defined as a sudden interruption of the current behaviour of an individual to try and chase another until the previous behaviour is resumed. Interaction frequency was assessed by dividing the number of interactions by the number of birds present in the plot. Average bird density was calculated by dividing the total number of birds observed in each plot by the total number of times that at least one goose in the plot was counted. Visit time (bird minutes) was calculated by multiplying the amount of time that geese were present at individual plots with the average bird density in the plot, per hourly interval. We collected data on step and peck rates per plot at regular
intervals, for as many individual animals as possible. Step and peck rates were determined by measuring the time required for 10 steps and 50 pecks, respectively, using a chronometer. We were able to observe the second series of the experiment for 15 days, but practical reasons limited the observation period for the first series to three subsequent days. At the end of each day, droppings were counted on the entire experimental plots and removed. Grazing pressure was defined as the rate of accumulation of droppings per unit area per day.

Instantaneous intake rate of food was estimated, using a pair of captive Brent Geese, brought into an experimental chamber for the measurements. These geese were allowed to eat 50 pecks from a sod of 10 cm x 20 cm, taken from the field plots, that was weighed before and after the trial to the nearest 10 mg (Sartorius pro 32/34F). Removed biomass (Wr, g fresh weight) was measured as the weight loss of the sod (g) during the trial, corrected for spilled food (g) and evaporation (g). Evaporation rate (g. s\(^{-1}\)) was estimated from the weight loss of the same sod in the same room, during five minutes prior to the trial, and multiplied by the duration of the trial (s) to obtain an estimate of evaporation (g). Time spent pecking per individual was carefully estimated using video recordings of the feeding trials and summed to obtain an estimate of total pecking time (T\(_p\), s). The intake rate (g fresh. s\(^{-1}\)) was calculated by dividing removed biomass (Wr) by total pecking time (T\(_p\)). Sods were provided to the geese in random order, with a constant interval of 20 min. During the experimental trials and the 8 weeks before, the geese were housed in a 2 m x 2 m indoor facility and additionally fed with dried food pellets and grass presented as sods. Light followed a diurnal cycle mimicking outside circumstances. The geese had been captured from the wild in 1996 and had been housed in a large open aviary until 8 weeks before the experimental trials. All catching, handling and non-invasive experimentation with captive geese in this study was conducted under a permit from the Dutch Ministry of Agriculture, Nature Management and Fisheries and a DEC permit of the Commission for the use of Animals in Experimental trials of the University of Groningen. (DEC No BG07696).

Data analyses

Data were averaged per plot to avoid pseudo-replication and analysed using a Randomised Block ANOVA (Zar 1996). In this analysis ‘fertilisation’ and ‘grazing’ were entered as fixed factors and ‘block’ was entered as a random factor. When appropriate, data were square root transformed \((y' = \sqrt{(y+0.5)})\), to obtain normality and homogeneity of variances. Percentage values routinely were Arcsine transformed. Post-hoc comparisons between the four treatments were carried out using Tukey’s honestly significant difference test. When the assumptions of parametric ANOVA could not be met, a non parametric Friedman ANOVA and associated post hoc comparisons (Zar 1996) were used instead. Changes in peck and step rate over time were investigated to study depletion effects. For this, a multiple linear regression was carried out, with treatment as a factor and time (cumulative hours of observation after start of the experiment) as a covariate. The foraging parameters peck rate, step rate
and intake rate were related to vegetation height, nitrogen content and the interaction between them, using backward multiple regression, eliminating variables when they were not significant at the 0.05 level. Finally, we used the number of interactions, bird density and the grazing pressure as parameters of preference and tested for the effect of vegetation height, nitrogen content and the interaction between them, using backward multiple regression. In these regression analyses we corrected for differences between the two series by incorporating series as a fixed factor. Statistical analyses were carried out with SPSS 8.0 (SPSS Inc.).

Results

Treatment effect on the vegetation

At the onset of observations, after removal of the exclosures, a significant difference in total live biomass was found between excluded plots (UE,FE) and those that received continuous grazing (UG,FG; F1,18 = 12.4, \(P < 0.05\), see Table 2.1). Both other indices of food biomass, the green biomass-index and sward height revealed the same pattern. Parameters of food quality were also strongly related to the treatments. Foodplants in fertilised plots (FG,FE) had a higher nitrogen (F1,18 = 130, \(P < 0.001\)) and water content (F1,18 = 154, \(P < 0.001\)) than plants in unfertilised plots (UG,UE). A significant interaction (F1,18 = 10.7, \(P < 0.05\)) between fertilisation and grazing arose as the nitrogen content was enhanced by grazing in unfertilised plots. The distribution of nitrogen over the different chemical compounds was hardly affected by the treatments, although unfertilised plots had a slightly enhanced proportion of insoluble nitrogen. Nitrate was virtually absent in all of the samples, averaging 0.3% on dry weight basis. The content of non-structural carbohydrates (starch and soluble sugars) and hemicellulose was lower in the fertilised & grazed treatment (FG, Tukey, \(P < 0.05\)), but the other treatments were not significantly different. No differences in plant species abundance were observed between the treatments.

Behavioural parameters and grazing pressure

Total visiting time increased gradually over time, although at different rates for each treatment (Figure 2.1A,B). Fertilised treatments had higher bird densities (F1,18 = 28.4, \(P < 0.001\), Table 2.1) and received higher grazing pressure (square root transformation, F1,18 = 93, \(P < 0.001\)). The percentage of grazed leaves of \(P.\ maritima\) and \(F.\ rubra\) corresponds closely to grazing pressure (Table 2.1). The frequency of agonistic interactions per individual goose present on the plot did not differ between treatments. The higher bird densities (Table 2.1) and the higher visiting times (Figure 2.1) were, however, reflected in greatly enhanced total number of observed interactions per plot, under fertilisation (square root transformation \(F_{1,15} = 14.5, P < 0.01\)). There was a good correlation between the sum of interactions and grazing pressure (Pearson correlation coefficient = 0.48, \(P < 0.05\), n=22). Previous exclusion of grazing had no
## Sward characteristics

<table>
<thead>
<tr>
<th></th>
<th>Unfertilised</th>
<th>Fertilised</th>
<th>Test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Grazed</td>
<td>Ungrazed</td>
<td>Grazed</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>UG</td>
<td>s.e.</td>
</tr>
<tr>
<td>Sward height (cm)</td>
<td>28</td>
<td>1.8</td>
<td>0.1 a</td>
</tr>
<tr>
<td>Vegetation index (value)</td>
<td>28</td>
<td>0.8</td>
<td>0.0 a</td>
</tr>
<tr>
<td>Dead biomass (g dw.m⁻²)</td>
<td>28</td>
<td>0.2</td>
<td>0.1</td>
</tr>
<tr>
<td>Live biomass (g dw.m⁻²)</td>
<td>28</td>
<td>0.7</td>
<td>0.1 ab</td>
</tr>
<tr>
<td>Cover of Juncus (%)</td>
<td>28</td>
<td>18.9</td>
<td>4.2</td>
</tr>
<tr>
<td>Cover of grasses (%)</td>
<td>28</td>
<td>55.6</td>
<td>3.7</td>
</tr>
<tr>
<td>Nitrogen content (mg.g dw⁻¹)</td>
<td>28</td>
<td>31.9</td>
<td>1.5 a</td>
</tr>
<tr>
<td>Juncus. gerardi</td>
<td>21</td>
<td>38.8</td>
<td>2.0 ab</td>
</tr>
<tr>
<td>Prop. of insoluble nitrogen (%)</td>
<td>16</td>
<td>83.0</td>
<td>0.2 ab</td>
</tr>
<tr>
<td>Acid Detergent Fibre (ADF) (%)</td>
<td>7</td>
<td>19.8</td>
<td>19.7</td>
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<tr>
<td>Water content</td>
<td>27</td>
<td>64.9</td>
<td>0.7 a</td>
</tr>
<tr>
<td>Non-structural carbohydrates +hemi-cellulose (mg. g dw⁻¹)</td>
<td>16</td>
<td>348.0</td>
<td>15.5 a</td>
</tr>
<tr>
<td>Leaf elongation (mm.day⁻¹)</td>
<td>16</td>
<td>1.4</td>
<td>0.2 a</td>
</tr>
</tbody>
</table>

### Foraging parameters

<table>
<thead>
<tr>
<th></th>
<th>Unfertilised</th>
<th>Fertilised</th>
<th>Test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Grazed</td>
<td>Ungrazed</td>
<td>Grazed</td>
</tr>
<tr>
<td>Peck rate (sec.peck⁻¹)</td>
<td>22</td>
<td>0.4</td>
<td>0.0</td>
</tr>
<tr>
<td>Step rate (sec.step⁻¹)</td>
<td>21</td>
<td>1.7</td>
<td>0.3</td>
</tr>
<tr>
<td>% of leaves grazed day⁻¹</td>
<td>16</td>
<td>0.8</td>
<td>0.2 a</td>
</tr>
<tr>
<td>Bird density (no.plot⁻¹)</td>
<td>28</td>
<td>0.6</td>
<td>0.3 a</td>
</tr>
<tr>
<td>No of interactions (total over observation period)</td>
<td>22</td>
<td>2.2</td>
<td>0.7 a</td>
</tr>
<tr>
<td>Interaction frequency (no.bird⁻¹.10 seconds⁻¹)</td>
<td>22</td>
<td>0.04</td>
<td>0.0</td>
</tr>
<tr>
<td>Intake rate (g fresh.s⁻¹)</td>
<td>16</td>
<td>0.02</td>
<td>0.00 a</td>
</tr>
<tr>
<td>Grazing pressure (droppings.m⁻².d⁻¹)</td>
<td>Geese</td>
<td>28</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td>Hares</td>
<td>28</td>
<td>0.02</td>
</tr>
</tbody>
</table>
Table 2.1  Mean values of sward and foraging parameters for different treatments. Values that do not share the same superscript letter are significantly different from each other. Test results for the effect of manipulation by grazing and fertilisation are indicated by abbreviating the factors in the variance analysis as follows: F = fertilisation, G = grazing and F*G is the interaction between fertilisation and grazing. Levels of significance are indicated using asterisks: * = 0.05, ** =0.01 and *** = 0.001. RB refers to a non-replicated randomised block ANOVA and F refers to Friedman ANOVA.

Figure 2.1  Measures of the use of the experimental treatments over time A) Cumulative grazing pressure (droppings.m^{-2}) by Brent Geese, B) cumulative visit time (bird minutes) on the plots expressed on an hourly basis, C) Normalised Difference Vegetation Index (NDVI), the ratio of red and infrared light reflected by the vegetation. This index is an estimator of live standing biomass. fertilised & excluded (FE); fertilised & grazed (FG); unfertilised & excluded (UE) and unfertilised & grazed (UG).
significant effect on bird density, number of interactions and grazing pressure. Hare grazing intensity was low compared to goose grazing, and concentrated on fertilised & excluded plots (FE).

Fertilisation had a significant effect upon step rate (Table 2.1) by geese. With increasing nitrogen content of the grasses, the step rate is observed to decrease (multiple linear regression: \( r^2 = 0.33, P < 0.01 \)). Peck rate was not affected by any of the treatments. Instantaneous intake rate increased linearly with biomass, within the range of biomass densities encountered (multiple linear regression: \( F_{1,14} = 55.2, P < 0.001 \), Figure 2.2). This is mainly explained by an increase in bite size, with increasing levels of biomass (data not shown). Nitrogen content was not important in explaining variation in intake rate.

In three cases during the first series of observations, we were able to follow specific family units or a particular individual goose for some time. The birds were recognisable from their behaviour and family composition and monopolised certain plots for considerable time (Figure 2.3). Plot FE2, the second replicate of the fertilised & excluded treatment, was at first occupied by a pair with an aggressive male. The male of this pair was seen to threaten other birds up to 10 m away from his female, and effectively monopolised the plot for more than three hours. It was taken over after a heroic fight, by a family of five, which had already spent 15 minutes at the fertilised & grazed plot FG1 immediately before that. This family maintained control over the plot for two hours, until all birds in the area departed due to disturbance (helicopter). Both the pair and members of the succeeding family performed short excursions to adjoining plots with different treatments. These excursions never lasted longer than 2 minutes. Another family of five occupied plot FE3 during both days for periods of more than two hours.

Figure 2.2 The relationship between intake rate (g fresh.s\(^{-1}\)) and biomass on offer (g dw.m\(^{-2}\)). Each data point represents the mean of a duplicate measurement; \( y = 0.00045x -0.00043, r^2 = 0.0792, P < 0.001 \).
Development in plant growth and depletion over time

Over the experimental period the differences in the green biomass-index between treatments tend to disappear (Figure 2.1C), to a large extent because of a net decline in aboveground biomass in the fertilised & excluded plots (FE) in both series. Episodes of decline in biomass are apparent in the fertilised treatments (FE, FG), coinciding with periods of grazing, but unfertilised plots (UE, UG) hardly show such decline because the intensity of use is much lower. Throughout the experiment however, differences in biomass between the grazing treatments remain present and the rank order of the treatments in terms of biomass largely remains the same. There is a parallel increase in grazing pressure (Figure 2.1A) and visiting time (Figure 2.1B) among treatments. Leaf elongation in the fertilised treatments (FE, FG) did not differ significantly from the unfertilised & excluded treatment (UE, Table 2.1).

Preference in relation to biomass and quality

The three parameters of patch preference by geese that we used in this analysis (see Methods) are significantly related to nitrogen content of the main food species, when correcting for the differences between the series (Table 2.2). An interaction between sward height and nitrogen content did not contribute to explaining any of the variation in patch preference. Some of the variation in the total number of interactions could be explained by sward height (24%) in addition to nitrogen content (40%).
Discussion

Patch preference

The experimental manipulations resulted in clear differences in food quality between treatments, as measured in terms of nitrogen content, while vegetation composition was not significantly altered. Fertilised plots had higher values of nitrogen than unfertilised treatments. Levels of biomass were also affected by the treatments. Biomass was linearly related to instantaneous intake rate (Figure 2.2). In this range of sward heights Hassall *et al.* (2001) also found a linear relationship. By breaking the correlation between biomass and quality, we can now investigate their relative importance.

We evaluate three parameters of preference. Two of these, bird density and the total number of interactions are considered measures of instantaneous preference. The geese used fertilised plots in higher densities and were more active in defending those plots than unfertilised ones (Table 2.1). Grazing pressure provides a measure over a longer term, and showed the same pattern (Table 2.1). The uniformity in response at different time scales argues against an overriding effect of depletion or production. Such effects were also not detectable from a changing pattern of visits to the treatments over time (Figure 2.1A,B), or changes in peck and step rate over time. Depletion, therefore, does not appear to affect our conclusions.

Some of the fertilised plots were monopolised by a particular family unit of geese, for several successive grazing bouts (Figure 2.3). These individual observations support our other indices of preference, as dominant pairs are apparently willing to defend our manipulated plots. A similar phenomenon was observed by Stahl *et al.* (2001) and Prop & Loonen (1989), who clearly demonstrated that resources are not divided equally over flock members. Flocks consist of markedly different individuals and some of these individuals may have a profound effect on population dynamics (Teunissen *et al.* 1985) or habitat choice.

Both the factorial models (Table 2.1) and the regression models (Table 2.2) indicate a large effect of food quality, measured as nitrogen content, on patch preference by Brent Geese. This result helps us to further elaborate upon the conceptual model put forward by Riddington *et al.* (1997) and Hassall *et al.* (2001). In their experiments,

### Table 2.2

Summary of the multiple linear regression models relating the three parameters of patch preference to sward height and nitrogen content of the grasses. For each significant variable the estimated coefficients are given.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Intercept Sward height</th>
<th>Nitrogen content Fest./ Pucc.</th>
<th>Series</th>
<th>$r^2$</th>
<th>$P$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bird density</td>
<td>-0.11 n.s.</td>
<td>0.09</td>
<td>-1.15</td>
<td>0.57</td>
<td>0.01</td>
<td>28</td>
</tr>
<tr>
<td>Sum of interactions</td>
<td>-47.00 9.76</td>
<td>1.13</td>
<td>n.s.</td>
<td>0.53</td>
<td>0.01</td>
<td>22</td>
</tr>
<tr>
<td>Grazing pressure</td>
<td>-2.43 n.s.</td>
<td>0.05</td>
<td>1.20</td>
<td>0.57</td>
<td>0.01</td>
<td>28</td>
</tr>
</tbody>
</table>
they found a preference for short sward heights under unfertilised circumstances, because of a negative correlation between sward height and nitrogen content. Elimination of this correlation by fertilisation led to a preference for tall swards. Riddington et al. (1997) propose that intake rate of nitrogen is the criterion for geese to select patches. This idea is graphically illustrated in Figure 2.4. According to the concept of Riddington et al. (1997), the product of nitrogen and intake rate (nitrogen intake rate, mg N.s⁻¹, Figure 2.4B) has an optimum at intermediate sward height as a result of a decelerating functional response (type II response of Holling 1959) and a declining N content of food
(Figure 2.4A). By fertilising the sward, this optimum disappeared in the experiment performed by Riddington and Hassall. At short sward heights (to the left of the optimum) the main constraint for the geese is imposed by intake rate, in their results. Our experiment was performed in this low range of sward heights, and we also demonstrated that intake rate increased strongly with sward height in this range. In spite of this, we find a strong effect of nitrogen content, rather than vegetation height. In our case, the levels of nitrogen differed by a factor two between fertilised and unfertilised treatments, while this difference was small in the experiment of Riddington and Hassall at low sward heights. So, as long as the differences in nitrogen content are large enough, the Brent Geese respond to it, even at low values of sward height. We thus strongly support the hypothesis by Riddington et al. (1997) and Hassall et al. (2001) that it is both food quantity and quality that determines patch choice in geese. The relationships between our parameters of preference and the product of nitrogen content and intake rate (nitrogen intake rate, mg N.s⁻¹), are highly significant (Linear regression, P < 0.001, Figure 2.5 A,B), and provide a better fit than regression models with nitrogen content alone as the independent variable. So, we have further proof that food quality plays an extremely important role, even at low sward heights. The role of food quantity will be more prominent when differences in nitrogen content are smaller relative to differences in intake rate, as was found by Hassall et al. (2001).

Stahl (2001) reported on two experiments on the marsh at Schiermonnikoog in which levels of biomass and quality were manipulated analogous to the present study. Her findings confirm our results that parameters of food quality affect patch choice in Brent Geese to a greater extent than do levels of biomass. In addition to that she demonstrated the existence of facilitative and competitive interactions between the different species of herbivore on the marsh. Brent Geese were shown to prefer patches that were previously grazed by Barnacle Geese with intermediate grazing pressure. Reasons for this were the higher nutrient levels in these patches, in spite of lower levels of biomass. High grazing pressures by hare, however, coincided with lower goose grazing pressure, presumably due to depletion effects.

Food quality and intake rate

There is controversy, extensively discussed by van der Wal et al. (2000a) and Hassall et al. (2001), about which currency to use in studies dealing with food quality for herbivores. The set-up of our field experiment enabled us to separate effects of increased biomass availability from food quality in general. The measures of quality in our experiment are all correlated, except for the non-structural carbohydrates and hemicellulose, which were considerably lower in the fertilised & grazed (FG) treatment. In all treatments, nitrogen content was high. The lowest value observed was still above the minimum required values suggested for Brent Geese (Prop, pers. comm.) and poultry (NRC 1994). We cannot from these results comment further upon the relative importance of the different quality parameters. The quality parameters of Juncus gerardi, both nitrogen content and ADF, reacted to the treatments in the same way as the grasses
and reached the same levels. The geese probably do not need to distinguish between these food plant species in this period of the year.

There is, however, clear consensus about the phenomenon of a declining quality with increased standing biomass (van Soest 1994; Wright & Illius 1995; Riddington et al. 1997) and this has far reaching ecological consequences, in view of the fact that herbivores are sensitive to these differences (Wilmshurst et al. 1995; Wilmshurst & Fryxell 1995; Stahl 2001; Hassall et al. 2001). Fryxell (1991) provided a model illustrating that ruminants benefit from aggregating at patches of intermediate biomass, because of a declining digestibility at higher levels of forage density. Van de Koppel et al. (1996) showed that the density of small herbivores has an optimum over a gradient of biomass, assuming that foraging efficiency is maximal at intermediate levels of standing biomass. Such a decrease in foraging efficiency may not only stem from declining

Figure 2.5 The relationship between nitrogen intake rate (mg N s⁻¹) and A) grazing pressure (linear regression $r^2 = 0.553, P < 0.001$) B) the total number of interactions observed per day of observation (linear regression $r^2 = 0.623, P < 0.001$, one datapoint is excluded from calculation of this regression line with the justification that this plot was hardly visited during observations).
food quality at high levels of biomass. Van der Wal et al. (1998) for example, demonstrated how increased handling time and search effort, caused by differences in sward structure, led to lower efficiency. Other factors may involve differences in vegetation composition or increased costs of locomotion and vigilance in taller swards. Our results exemplify the concept outlined by van de Koppel et al. (1996) by pointing at the importance of nutrient intake rate rather than simply food biomass intake rate. Small herbivores may choose to forage in areas of lower standing crop because of higher nutrient intake rates.

From patch to habitat use

The results of this experiment contribute to our understanding of the patterns of habitat use that are observed in Brent Geese. During spring large differences exist between habitats in timing of plant growth (Bakker et al. 1993) and food quality of alternative foodplants (chapter 3). By their own grazing, geese affect the growth stage of plants and their quality as food (Ydenberg & Prins 1981; Stahl 2001, Table 1). In time and space, the spring staging areas are therefore not homogeneous with respect to food quality. Patch choice was demonstrated to be strongly affected by parameters of food quality (this experiment; Ydenberg & Prins 1981; Riddington et al. 1997; Stahl 2001). We therefore agree with Hassall et al. (2001) that, under these circumstances, food quality should be included in models of habitat use for geese and other small herbivores. Declining nutrient intake rates with increasing levels of standing crop may explain observed patterns of habitat use within initially homogeneous agricultural grassland. Over spring, Brent Geese were observed to aggregate at a smaller surface, with increasing primary production (chapter 5; Spaans & Postma 2001). This leads to a dichotomy in areas with an intensively grazed short sward and areas with tall sward heights that are left ungrazed. The hypothesis that this pattern emerges because of declining nutrient intake rates with increasing levels of standing crop is supported by field experiments using short term exclosures (chapter 5). Wild Brent Geese had higher grazing intensity in plots of intermediate biomass, where both intake rates and nitrogen content are higher. Alternative hypotheses, that this pattern is emerging due to spatial heterogeneity in food quality or avoidance of predation risk, need not be invoked, but may nonetheless be useful in explaining the geographical location of the patches that are being maintained.

During spring, the birds utilise pasture and marsh habitat in an order that is the reverse from that in autumn. In autumn the switch from marsh to pastural land has been explained by Vickery et al. (1995) by the depletion of food plants in the preferred marsh habitat. In this depletion model, no parameter of quality needs to be invoked according to the authors, although they admit that plant quality and profitability will determine the ranking of habitats in terms of preference. When the birds move back to marsh habitat in spring they exchange productive areas with high values of standing biomass (99 g dry.m$^{-2}$ ± 48 st. dev. in April, unpublished data) for habitat with limited food availability (6-12 g dry.m$^{-2}$ ± 6-11 st. dev. in April, unpublished data). This
particular switch in spring cannot be explained using the depletion model by Vickery et al. (1995). Our experiment does provide an explanation, since quality differences within or among habitats may lead to higher instantaneous nutrient consumption rates in spite of lower levels of standing crop. An additional explanation for birds switching habitat in spring can be found in different levels of disturbance, as described for Barnacle Geese on our study island by Prins & Ydenberg (1985). Lower levels of disturbance on the marsh, as compared to the pasture area, allow the birds to improve their utilisation of food plants by grazing more selectively. In this view, the nutrient absorption rates on the marsh are higher due to improved digestion, in spite of lower levels of standing crop. Both explanations are not mutually exclusive, but stress the relative importance of food quality in patch choice by Brent Geese.

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Brent Geese in flight above the biological field-station "de Herdershut" on Schiermonnikoog, moving between polder and salt marsh (photo J. Stahl).