Grazing in coastal grasslands
Bos, Daniël

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2002

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Download date: 08-12-2019
Abstract

We report on an aggregative response of Brent Geese to increased productivity of the vegetation during the growing season on agricultural fields on the island of Schiermonnikoog, the Netherlands. Plant standing crop was found to be maintained at low levels in the fields where geese activity focussed, whereas the remainder of the fields escaped herbivore control and developed a high standing crop. This pattern can be explained by the fact that the functional response of the geese is not monotonically increasing, but dome-shaped. As a consequence, continuously grazed swards are more suitable for feeding than temporarily ungrazed swards. We present an optimal foraging model showing that, beyond a threshold level, increased primary productivity leads to spatial heterogeneity in standing crop, under this assumption. Further increases in productivity lead to a progressive release of vegetation from herbivore control, which will develop a high standing crop. Interestingly, our model suggests that aggregative behaviour in herbivores only maintains the intake near the potential maximum if the environment is stable and predictable. Processes that disrupt an exact match between local primary production and consumption, like a misjudgement of patch quality by the herbivore, may lead to a less than optimal intake, as suitable vegetation becomes depleted.
Introduction

Prediction of the spatial distribution and the population numerical response of animal populations requires thorough understanding of the relationship between resource density and intake rate. For many species, vertebrates and invertebrates alike, this relation is a continuously increasing function and is then referred to as a functional response of Holling type II (Holling 1959; Spalinger & Hobbs 1992; Gross et al. 1993). There is wide recognition though, for the fact that the functional response may have an alternative shape (Abrams 1982; Hobbs & Swift 1988; Fryxell 1991), with profound consequences for the system under study. Herbivores, for example, may be confronted with a dome-shaped functional response for several reasons. With increasing resource density, the vegetation composition, structure and tissue quality change. Reduced energy absorption due to a declining digestibility (Fryxell 1991; Illius & Gordon 1991) is one of the better studied examples leading to a lower performance of ruminants at high resource densities, but more mechanisms have been identified, e.g. increased costs of locomotion or vigilance (van de Koppel et al. 1996), increased handling time (van der Wal et al. 1998) or reduced concentrations of nitrogen (Riddington et al. 1997; Hassall et al. 2001).

When higher rates of intake or absorption can be achieved at intermediate levels of resource density, herbivores are predicted to benefit from aggregation (McNaughton 1984; Fryxell 1991; Hutchings & Gordon 2001). Fryxell (1991) presented a model illustrating this phenomenon for a system without spatial heterogeneity. In this system, individual herbivores suffer from forage maturation due to excess forage production in relation to their consumption. Animals at higher densities keep the sward in a nutritious stage by repeated defoliation and thus facilitate each other. We studied an analogous case of herbivores in a productive environment, but included spatial heterogeneity. The motivation for constructing the model originated from field observations of spring-staging Brent Geese Branta bernicla bernicla, foraging on productive agricultural grassland along the coast of the Dutch Wadden Sea.

Geese rely heavily on forage of high quality (Owen 1980) and are, therefore, often observed on shortly grazed swards or newly emerging vegetation (Boudewijn & Ebbinge 1994). Several studies support the hypothesis that Brent Geese select swards in order to maximise intake of nitrogen (Ydenberg & Prins 1981; Hassall et al. 2001; Chapter 2) and that intake rate of nitrogen may actually decline at high levels of standing crop (van de Koppel et al. 1996; Riddington et al. 1997; van der Wal et al. 1998; Hassall et al. 2001). It is hypothesised that these processes may form the mechanism behind observed patterns of habitat use by geese during spring staging. In spring, the geese are confronted with increasing levels of primary production. As described by Spaans and Postma (2001), Brent Geese increase their grazing intensity as primary production increases. For this, they revisit an increasingly smaller share of the original area they utilised, with increasing frequency. When the geese depart for the breeding grounds at the end of May, a bi-modal pattern in sward structure has emerged with shortly grazed areas and large areas that are left ungrazed.
The objective of this paper is 1) to provide support for the hypothesised mechanisms with empirical data, 2) to simulate this pattern of use qualitatively in a model based on a dome-shaped functional response and 3) to explore the consequences of this concept using the model. The paper is organised in two sections, a field study and a modelling study. We will start with the field study, because the model is motivated by its results.

Field study

Methods

STUDY SITES
Field data on habitat use by Brent Geese in spring were collected on two barrier islands in the Dutch Wadden Sea, Texel (53°05’N, 4°50’E) and Schiermonnikoog (53°30’N, 6°10’E). Both islands have large tracts of embanked agricultural grassland (polder) and a different area of salt marsh. Schiermonnikoog is frequented by about 3,000 Brent (van der Wal et al. 2000) and up to 8,000 Barnacle Geese Branta leucopsis (Stahl 2001) during spring. The geese forage on polder grassland (270 ha) during early spring, but move to the marsh (1500 ha) in February/March (Barnacle Geese) and April (Brent Geese). The polder areas are used for grass production and cattle grazing by farmers and consist of homogeneous swards, containing mainly Lolium perenne and Poa trivialis. Fields are heavily fertilised with approximately 400 kg N.ha⁻¹ of artificial fertiliser in addition to the application of manure. On Schiermonnikoog the farmers have actively disturbed the geese in the polder during the months of April and May until 1999, but from the year 2000 onwards they have agreed to actually host the birds in the southern half of the polder. Approximately 10,000 Brent Geese stage on Texel during spring, mainly foraging in the Brent Goose reserve “Zeeburg” in the north-eastern part of the island. Adjacent to the reserve is a small (45 ha) ungrazed salt marsh that is only used to a very limited extent by the geese, as it is dominated by tall unpalatable plant species. The pastures in the reserve (110 ha) consist of homogeneous swards of Lolium perenne and Poa trivialis, that are managed by fertilisation (110 kg N.ha⁻¹) and aftermath grazing with livestock in order to accommodate the geese as good as possible. Disturbance to the geese is very limited because access for any traffic, including pedestrians is restricted.

FIELD PATTERNS
We counted Barnacle and Brent Geese in the polder areas of the Wadden Sea island Schiermonnikoog on a regular basis during the spring of 2000 and 2001, and attributed the birds to specific clearly delineated fields. The censuses were performed between 8.00 A.M. and 20.00 P.M. at different times for each count, and each count the whole polder area (290 ha) was scanned. In March, April and May 2000, we established transects through all pastures in the polder of Schiermonnikoog. At intervals of 10 m along these transects two measurements of canopy height were taken and accumulated
dropping density was estimated in a circular plot of 4 m². Dropping density is a reliable measure for the comparison of grazing intensity, since geese defecate at regular intervals (Owen 1971). Canopy height was measured with a 24 g, 20 cm diameter polystyrene disc that was dropped on the vegetation, sliding along a calibrated stick. The average canopy height was calculated for plots with and without fresh goose droppings.

**PATCH CHOICE EXPERIMENT**

At the Brent Goose reserve “Zeeburg” in the polder of the Wadden Sea island of Texel, we experimentally tested our hypothesis that swards of intermediate biomass are preferred over swards with higher values of biomass. For this, we excluded wild geese from small plots at 2 pastures that were known to be grazed intensively by geese, for 5 different periods of time. The plots were 16 m² in size and fenced using chicken wire of 50 cm high and 5 cm mesh size. The fences for the different treatments were erected 8, 5, 3, and 1 week(s) prior to May 7th 2000 and the control treatment was not excluded. The fields were managed according to standard practice by fertilising them with an artificial fertiliser (110 kg N.ha⁻¹). Each treatment was replicated four times at field I and three times of field II according to a randomised block design. At the 7th of May, all fencing was removed.

After removal of the fences, droppings were counted and removed daily in a 4 m² circular sub-plot, that was placed within each experimental plot and marked with an inconspicuous stick in the centre. Canopy height was measured every other day with five replicates per plot, using the method described above. Four sets of sods (10 cm x 10 cm) were taken from each plot and used to estimate the instantaneous rate of biomass intake (see below). Forage quality was measured as the nitrogen content of leaf tips (top 2 cm) from a mixture of the polder grasses. Forage quality samples were washed, air-dried at 70°C and nitrogen content was determined using an automated CNHS-analyser (Interscience EA 1110).

**INTAKE RATE**

Instantaneous intake rate of biomass was estimated, using three captive Brent Geese, brought individually into an experimental outdoor enclosure (4 m x 4 m) for the measurements. The geese were allowed to eat from sods of 10 cm x 10 cm, taken from the field plots, that were 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 during the trial, corrected for evaporation. Evaporation rate (g.s⁻¹) was estimated from the weight loss of a similar sod under the same circumstances. Time spent pecking per sod was carefully estimated by visual observation, supported by software that was specifically designed for the purpose, and summed to obtain an estimate of total pecking time (Tᵣ). The intake rate (g fresh.s⁻¹) was calculated by dividing removed biomass (Wᵣ) by total pecking time (Tᵣ). Each trial, one goose was offered one sod of each treatment at the same time, positioned in a regular grid but in random order. Each goose was used to test each of the sods at least once. The trials took place during the second week of May 2000. During the experimental trials and the 8 weeks before,
the geese were housed on grass in a 100 m² enclosure connected to the test area, and additionally fed with dried food pellets and grass presented as sods. Water was always available *ad libitum*. 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 from the Commission for the use of Animals in Experimental trials of the University of Groningen (DEC, permit no. BG07696/2382).

**DATA ANALYSES**

The average number of Brent and Barnacle Geese per field and per month in the polder of Schiermonnikoog was divided by the area of the fields they where observed upon during that month in order to estimate bird density. For the exclosure experiment in the polder of Texel, the accumulated number of droppings for the first week and the second week after the start of the experiment was used to estimate preference for the plots. Data on canopy height were averaged per plot to avoid pseudo-replication. These data were analysed using a Randomised Block ANOVA (Zar 1996). In this analysis ‘grazing treatment’ was entered as a fixed factor and ‘block’ was entered as a random factor. Instantaneous intake rate measurements were assumed to be independent measures and directly related to canopy height and the canopy height squared in a linear regression analysis. Count data were square-root transformed ($y' = \sqrt{(y+0.5)}$), to obtain homogeneity of variances. Statistical analyses were carried out with SPSS 10.1 (SPSS Inc.).

**Results**

**Field patterns**

In March of the years 2000 and 2001, almost all fields in the polder of Schiermonnikoog were frequented by geese, but towards May an aggregation was observed (Figure 5.1). In these months, a dichotomy arose between short-grazed areas and fields that were abandoned. In March the proportion of Barnacle Geese among all geese was still high (70% of total), but thereafter the majority of birds were Brent Geese. The canopy height of pasture fields that were maintained by the geese remained low (Figure 5.2) and was 4.9 ± 0.55 cm in May, while the canopy height in ungrazed fields increased sharply to 15.2 ± 0.36 cm (T-test, $t = 5.7, P = 0.001$). The average density of geese increased in both years (Figure 5.3A,B). This is especially clear if we focus on the field that was grazed until the end of May, as the average number of geese here increased by a factor 4 in 2000 and by more than a factor 2 in 2001, in spite of a decline in the total number of geese. The increased average density of birds was mainly caused by an increased presence in time, as the proportion of counts when birds were present on the field increased from 30% to over 80% of the counts. When birds were present, the average density of birds was constant at 128 ± 11 geese.ha⁻¹ (linear regression, effect of time: $F_{2,48} = 0.64$, n.s.).
Pattern of use in the Bancks polder, 2000

March (n=19)

April (n=25)

May (n=12)

Goose density (no.ha⁻¹.d⁻¹)

Figure 5.1 Maps of the average density of Brent and Barnacle Geese in polder fields on the island of Schiermonnikoog, illustrating the aggregation of geese over spring of the year 2000. The number of counts that were performed each month is indicated between brackets.

Figure 5.2 Development of canopy height (cm) in spring in the polder of Schiermonnikoog for the year 2000 on polder grassland that is either grazed (as observed from the presence of fresh droppings) or not grazed by geese. Significant differences are indicated using different letters ($P < 0.05$).
Intake rate and patch choice experiment

Canopy height on the experimental plots in the Brent Goose reserve on Texel, was positively related to green biomass (Pearson $r = 0.784$, $P < 0.001$, $n = 56$), and the plots that were excluded longest had significantly taller canopy height ($F_{4,30} = 3.39$, $P < 0.001$). The experiment took place at a moment when the geese had already started to leave the island and lasted two weeks (7 - 21st May 2000). Total grazing pressure was much lower during the second week and, therefore, the data were analysed separately for the two weeks. Preference, measured as accumulated grazing pressure, was highest for plots that had been excluded for a short period in the first (Figure 5.4A; $F_{4,24} = 3.39$, $P = 0.025$) as well as in the second week (Figure 5.4B; $F_{4,24} = 3.0$, $P = 0.037$) after opening of the exclosures. Instantaneous intake rate of matter, as measured using the captive Brent Geese, declined with canopy height (Figure 5.4C; linear regression, $F_{1,113} = 4.06$, $P = 0.046$, $R^2 = 0.034$), and so did nitrogen content (Figure 5.4D; linear regression, $F_{2,32} = 10.7$, $P = 0.02$, $R^2 = 0.402$).

Modelling study

The model

In order to better understand the spatial patterns described above on the basis of individual foraging decisions, we constructed a spatially implicit, discrete simulation model. The model consists of a large number of small patches. At the start of a time step, the ‘model geese’ redistribute over the patches according to expected intake rate. The biomass (B) in each patch changes due to time-dependent production and the total consumption by the geese present on this patch. A detailed description of the model assumptions is given below. An overview of the relevant model parameters and their reference values is given in Table 5.1.
Each time step of length $\Delta t$, the plant biomass (g.m$^{-2}$) in a patch changes due to production and consumption (formula 1).

$$\Delta B = [G(B,t) - N.F(B).t_{tot}]. \Delta t$$  \hspace{1cm} (1)

Here, $G(B,t)$ describe daily primary productivity (g.m$^{-2}$.day$^{-1}$) in relation to standing biomass and time of season (t, days). N is the number of geese present, F(B) is the intake rate per goose as a function of plant biomass (the functional response, g.s$^{-1}$, see below) and $t_{tot} = $ daylength. We are interested in a system where primary production increases systematically in the course of the season. In a first attempt, this relation was modelled as follows:

$$G(B,t) = G(t) = \gamma . (G_0 + G_1.t)$$  \hspace{1cm} (2a)

---

**Figure 5.4** The effects of temporary exclosure on goose grazing pressure (droppings.m$^{-2}$.day$^{-1}$) during the A) first and B) second week after opening of the exclosures (note that grass continued to grow and vegetation height is thus higher for each treatment in the second week), C) intake rate of biomass (mg dry.s$^{-1}$) and D) forage quality, measured as nitrogen content (%). Treatments that do not differ significantly share the same letter in panel A and B.
In words, primary productivity is independent of biomass, but increases linearly with time of season. The parameters (see Table 5.1) were chosen such that the productivity increases by a factor 2.5 from the start \((t=0)\) to the end \((t=90)\). The factor \(\gamma\) (gamma) was changed systematically in order to investigate the dependence of the simulation results on system productivity. In a second and more realistic attempt we used a modified logistic growth function to model primary production:

\[
G(B,t) = r(t). (B+B_0) \left( 1 - \frac{B+B_0}{K+B_0} \right)
\]  

where

\[
r(t) = \rho. \left( r_0 + r_1.t \right)
\]  

Table 5.1  Parameters used in the simulation model with units, reference value and the range over which parameters are varied.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Range</th>
<th>Min</th>
<th>Max</th>
<th>Reference value</th>
<th>Unit</th>
<th>Explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td></td>
<td>0.002</td>
<td>0.01</td>
<td>4.00E-03</td>
<td>(m^2.s^{-1})</td>
<td>search rate</td>
</tr>
<tr>
<td>(B_{(t=t_0)})</td>
<td></td>
<td>5</td>
<td>25</td>
<td>10</td>
<td>(g.m^{-2})</td>
<td>(initial) biomass density</td>
</tr>
<tr>
<td>(B_0)</td>
<td></td>
<td>20</td>
<td></td>
<td>(g.m^{-2})</td>
<td></td>
<td>crown or root-reserves that cannot be grazed</td>
</tr>
<tr>
<td>(\Delta t)</td>
<td></td>
<td>1</td>
<td>16</td>
<td>2</td>
<td>hours</td>
<td>time step size</td>
</tr>
<tr>
<td>(\varepsilon_{\text{max}})</td>
<td></td>
<td>0</td>
<td>0.5</td>
<td>0.2</td>
<td></td>
<td>potential variation around perceived intake rate in a patch</td>
</tr>
<tr>
<td>(F_{\text{min}})</td>
<td></td>
<td></td>
<td></td>
<td>10</td>
<td>(g \text{ Nitrogen.d}^{-1})</td>
<td>minimum required nitrogen consumption per goose</td>
</tr>
<tr>
<td>(\gamma)</td>
<td></td>
<td>1</td>
<td>5</td>
<td>3</td>
<td></td>
<td>index of productivity</td>
</tr>
<tr>
<td>(G_0)</td>
<td></td>
<td></td>
<td></td>
<td>2.40E-02</td>
<td>(g.m^{-2})</td>
<td>constant</td>
</tr>
<tr>
<td>(G_1)</td>
<td></td>
<td></td>
<td></td>
<td>4.00E-04</td>
<td>(g.m^{-2})</td>
<td>constant</td>
</tr>
<tr>
<td>(h_0)</td>
<td></td>
<td></td>
<td></td>
<td>100</td>
<td>(s.g^{-1})</td>
<td>constant in regression biomass-handling time</td>
</tr>
<tr>
<td>(h_1)</td>
<td></td>
<td></td>
<td></td>
<td>0.2</td>
<td></td>
<td>coefficient in regression biomass-handling time</td>
</tr>
<tr>
<td>(K)</td>
<td></td>
<td></td>
<td></td>
<td>200</td>
<td>(g.m^{-2})</td>
<td>vegetative carrying capacity</td>
</tr>
<tr>
<td>(t_{\text{tot}})</td>
<td></td>
<td></td>
<td></td>
<td>57600</td>
<td>(s)</td>
<td>daylength</td>
</tr>
<tr>
<td>(N)</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td>(starting) number of geese</td>
</tr>
<tr>
<td>(P)</td>
<td></td>
<td></td>
<td></td>
<td>500</td>
<td>7500</td>
<td>(m^2)</td>
</tr>
<tr>
<td>(p)</td>
<td></td>
<td></td>
<td></td>
<td>5</td>
<td>25</td>
<td>15</td>
</tr>
<tr>
<td>(q)</td>
<td></td>
<td></td>
<td></td>
<td>6</td>
<td>(%)</td>
<td>nitrogen content of the vegetation</td>
</tr>
<tr>
<td>(\rho)</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>(r_0)</td>
<td></td>
<td></td>
<td></td>
<td>4.20E-03</td>
<td>(g.m^{-2})</td>
<td>constant</td>
</tr>
<tr>
<td>(r_1)</td>
<td></td>
<td></td>
<td></td>
<td>2.00E-05</td>
<td>(g.m^{-2})</td>
<td>constant</td>
</tr>
<tr>
<td>(t)</td>
<td></td>
<td></td>
<td></td>
<td>0</td>
<td>90</td>
<td></td>
</tr>
</tbody>
</table>
Eqn. (2b) corresponds to the logistic growth equation for total biomass \( B + B_0 \), where \( B = B(t) \) refers to the vegetative biomass accessible to the herbivores while \( B_0 \) represents the crown or root-reserves of plants that cannot be grazed (Fryxell 1991). \( K \) is the vegetative carrying capacity. The optimum level of growth is found at \( B = 0.5(K - B_0) \). The intrinsic growth rate \( r(t) \) is assumed to increase linearly with time of season, and the parameters where chosen such that productivity increases by a factor 2.5 from the start \((t=0)\) to the end \((t=90)\), for a given level of biomass. The factor \( \rho \) was changed systematically in order to investigate the dependence of the simulation results on system productivity.

**INTAKE RATE**

Our description of the functional response \( F(B) \) of the herbivores was based on a Holling type II curve. However, we achieved a dome-shaped function by assuming a negative linear relationship between handling time \( h \) and biomass.

\[
F(B) = a.B.(1+a.h(B).B)^{-1} \tag{3a}
\]

with

\[
h(B) = h_o + h_1.B \tag{3b}
\]

As will be discussed below, there are several mechanisms that can lead to a dome-shaped response, and we have chosen for this alternative mainly for convenience. The maximum of the curve \( F(B) \) is located at \( B = \sqrt{(a.h_1)^{-1}} \).

**PATCH SELECTION**

The geese are assumed to make no travel costs and the criterion for patch selection is the perceived intake rate of biomass, under the condition that the expected intake and availability in the patch exceed a minimum level specified \( (F_{\text{min}}) \). Perceived intake rate differs from \( F(B) \) by \( \varepsilon \) (formula 3c), an error term randomly taken from a uniform distribution \( \varepsilon \in [-\varepsilon_{\text{max}}, \varepsilon_{\text{max}}] \).

\[
\text{preference} = F(B).(1+\varepsilon) \tag{3c}
\]

Most results presented are based on simulations with only one herbivore. We will later discuss the additional assumptions that were taken when models with multiple geese were studied.

**SPATIAL AND TEMPORAL SCALE**

We assume that geese are not constantly moving between patches, but rather utilise them for some time before moving on. Long step sizes, however, would constrain the herbivores in their ability to choose between patches. Hence, we assumed time step size to range between 1 hour and a complete daylight period of 16 hours. The choice of
the spatial scale of patches is very much intertwined with the decision on temporal scale, as small patch sizes would lead to artefacts caused by depletion, when time step sizes are large. In contrast, large patches lead to strong discretisation effects, as will be shown in the next paragraph. In the standard models presented here, patch size (p) varies between 5 and 25 m², while total area (P) is fixed at 500 m² for model runs with a single goose.

Simulation results

A single goose

The general pattern emerging from our model is a dichotomy between continuously grazed model patches and patches that are abandoned, sooner or later (Figure 5.5). From the start of a model run, the biomass in the patches continues to increase up to a level that yields the maximum intake rate. From that moment onwards, some patches are abandoned, not to be visited anymore during that model run and herbivore grazing intensity increases over time in the patches that are still grazed. The total number of patches that is grazed by the herbivore during the last phase of a simulation is lower when the system is more productive (Figure 5.6). Under these assumptions, the biomass density in the grazed patches is maintained at a value that is close to the optimum of the intake rate curve, as was illustrated in Figure 5.5. However, the model results depend to some extent on parameter values for patch size, productivity and error (ε\text{max}) in interaction with each other. The sensitivity of the model for these parameter is explored in Figure 5.7. Under low productivity (γ = 1), the herbivore is able to maintain low plant density in the entire area, and the consumption is constrained by primary production until the end of the simulation. Biomass is thus not over-abun-

![Figure 5.5](image-url)  

Figure 5.5  Biomass development over time in a few representative patches for a model run with default parameter settings and one goose.
dant, the maximum intake rate is not reached and no aggregation takes place. For that reason, variation in $\varepsilon_{\text{max}}$ or patch size hardly has an effect when $\gamma = 1$ (Figures 5.7A,B,C). Variation in time step size (Figure 5.7B) has little effect on the model outcome, under biomass-independent growth. Without error ($\varepsilon_{\text{max}} = 0$), the model is not sensitive to patch size or productivity (Figure 5.7A,C), but when the herbivore is not able to precisely distinguish between patches of different intake rate ($\varepsilon_{\text{max}} > 0$), this leads to focussing on a set of patches with combined area that yields insufficient primary production. The habitat is then slowly depleted and temporarily exploited at a level of biomass below that of maximum instantaneous intake rate. When patches are relatively large and production is high, these effects may be considerable (Figure 5.7C). The dynamics of this phenomenon are illustrated in Figure 5.8. When too many patches have escaped from herbivore control, the standing crop becomes depleted in the patches that are continuously grazed and the herbivore every once in a while visits a patch with high plant standing crop (Figure 5.8A). The situation of temporary depletion is sooner or later restored by the increase in primary production with time (Figure 5.8A). However, the intake rate is somewhat lower during this phase (Figure 5.8B), until the standing crop has recovered, while the number of patches used during the last two weeks (Figure 5.8C, note the time lag of two weeks) stops declining until that moment.

With primary production depending upon biomass, the sensitivity of the model to parameter values for patch size, time step size, productivity and error increases sharply (Figures 5.7D,E,F). Under most combinations of parameter values, the intake at the last day of a model run is considerably lower than the potential maximum, caused by depletion in the continuously grazed patches. Again, this is caused by the herbivores aggregating in a set of patches with combined area that yields insufficient primary pro-

![Figure 5.6](image_url)

**Figure 5.6** The effect of varying system productivity and error in perceived intake rate on the number of patches used during the last 2 weeks of a model run, for model runs with default parameter settings and one goose.
Figure 5.7  Sensitivity of model results to parameter variation in relation to system productivity: maximal error in perceived intake rate (A, D), step size (B, E) and patch size (C, F) under biomass independent (one set of results presented in A - C) and biomass dependent primary production (one set of results presented in D - F). Simulations where the bird did not survive are excluded (time step size $\Delta t = 8$ hrs and patch size $= 5 \text{ m}^2$).
Figure 5.8  Illustration of model behaviour under productive conditions ($\gamma = 4$) and relatively large patch size ($p = 25 \text{ m}^2$) leading to temporary depletion of the habitat, for a model run with one goose and $r_{\text{max}} = 0.2$. A temporary depletion is observed under high levels of production and large patch size, when the herbivores cannot exactly estimate the potential intake rate in a patch. A) The level of biomass in the patch that is selected by the herbivore, B) the realised nitrogen intake rate of the herbivore and C) the number of patches that are used during the previous two weeks for each time step.
duction. However, under biomass dependent primary production a positive feedback is triggered, leading to stronger depletion, given the assumption that the optimum level of biomass for primary production is higher than that for instantaneous intake rate.

SENSITIVITY FOR OTHER PARAMETERS
The sensitivity of the model for initial biomass and total area is low as long as they are above the minimum required for survival. A fivefold increase in these parameters, leads to deviations in the output parameters studied that are smaller than 3%. Changing the parameters of the functional response ($h_0$ and $h_1$) has an immediate effect on total consumption over spring and consumption at day 150, but the qualitative behaviour of the model remains unaffected.

MULTIPLE GEESE
Up to now, we only studied situations with a single herbivore. The situation may be different when multiple herbivores are in the system, and in order to check this possibility we also ran the model with the numbers of individuals ranging between one and fifteen. For model simulations with multiple geese, we increased the total area $P$ to 0.75 ha. When studying model systems with multiple herbivores, the order in which they are distributed may be very important, especially when direct interference is studied. We did not include interference in our model, and assumed a linear dominance hierarchy, as a result of which the geese were (re-)distributed over the model patches at each time step in the same order. For the present analysis the fate of individual geese and the consequences of this choice of hierarchy are not pursued any further.

Figure 5.9 The consumption per animal (g N.day$^{-1}$) in relation to herbivore numbers and the area of habitat that is maintained at the end of a simulation. Variation in the number of herbivores does not affect the intake per individual, but it does affect the total number of patches that are used in the last 2 weeks of a model run. Models are run with biomass independent growth, default parameter settings and a total area of 7,500 m$^2$. 
Model runs with multiple geese showed the same qualitative behaviour as those with a single goose. Figure 5.9 illustrates the effect of increasing the number of herbivores in the system for conditions of biomass-independent primary production. Per-capita consumption is not affected, as the increase in numbers is compensated for by an increased total area that is utilised. The same qualitative pattern is found under biomass dependent primary production.

**Discussion**

*Use of productive habitat in spring*

During spring, the geese in our simulation model as well as in the field, limit their use to a restricted area of the productive grassland and increase the intensity of grazing. Two processes could lead to such an increase in grazing intensity, namely an aggregation of herbivores into a more dense flock that spends the same amount of time, or a reduction in the revisitation interval (aggregation in space or time). The latter situation is most important in our field example from Schiermonnikoog (Figure 5.3). Aggregations of herbivores have been observed for many species of herbivore, such as Wildebeest *Connochaetus taurinus* (McNaughton 1976) or Red deer *Cervus elaphus* (Clutton-Brock *et al.* 1982). Possible mechanisms that lead to an aggregation of herbivores at swards of intermediate biomass are 1) spatial heterogeneity in forage quality, 2) the reduction of predation risk through enhanced predator detection or dilution and 3) a preference for continuously grazed swards (Fryxell 1991). Our experiment provides support for the interpretation that the observed aggregation by Brent Geese is caused by a preference for continuously grazed swards, due to declining rates of nutrient intake at higher levels of biomass (> 10 cm canopy height). Very similar experimental results were obtained by Wilmshurst *et al.* (1995) and Langvatn and Hanley (1993) for captive Red deer, by Gibb *et al.* (1997) for cattle, as well as by Bos *et al.* (chapter 2), Stahl *et al.* (2001) and Riddington *et al.* (1997) for wild geese. The consequence of this behaviour is an ‘escape’ of vegetation in areas that are left ungrazed.

*Declining nutrient intake rates*

Several reasons can result in a declining performance of the herbivores, when levels of biomass increase. In our experimental study, a decline in instantaneous intake rate of mass was observed (Figure 5.4C), presumably due to increased handling time. Such a decline in instantaneous intake rate has previously only been demonstrated for Wigeon *Anas penelope* (Durant 2001) and Barnacle Geese (van der Wal *et al.* 1998), but most of the functional response models published for herbivores (Spaling & Hobbs 1992; Gross *et al.* 1993; Illius & Gordon 1999; Schwinnig & Parsons 1999), follow the type II response as defined by Holling (1959). Above that, in our experiment, we also observed a small decrease in forage quality, measured as nitrogen content (Figure 5.4D), with increasing levels of biomass. The protein content and digestibility are
often related negatively to standing biomass (Riddington et al. 1997) and maturation stage (Demment & van Soest 1985; van Soest 1994). Hence, the intake rate of nitrogen or energy declines with biomass at the short (Hassall et al. 2001; Chapter 2) or the longer term (Arnold 1964; Fryxell 1991). Note that the formulation of the functional response used in the present model study yields equivalent results to the multiplication of a Holling II functional response with a function describing a declining forage quality with increasing biomass. Finally, there may be other factors leading to a lower performance of herbivores in taller swards, such as differences in vegetation composition or increased costs of locomotion and vigilance.

Model predictions

The inclusion of spatial heterogeneity in our model, in combination with a dome-shaped functional response leads to fundamentally different predictions than many of the existing alternative models. Under the assumption of a continuously increasing functional response (Ungar & Noy-Meir 1988; Vickery et al. 1995; Percival et al. 1996; Lang et al. 1997; Illius & Gordon 1999; Pettifor et al. 2000), the herbivores would be predicted to always select the patches with highest vegetation density. In the absence of strong interference, this leads to a homogenisation of biomass levels across patches (Sutherland 1996). In contrast, our model and that by Hutchings & Gordon (2001) predict the emergence of shortly grazed patches among otherwise ungrazed vegetation. In the field, such patterns have been described for cattle (Andresen et al. 1990; Gibb et al. 1997), geese (Spaans & Postma 2001) and sheep (Arnold 1964) at the scale of hundreds of meters, as well as for sheep at small (cm, Berg et al. 1997) to intermediate scales (m, Kiehl 1997).

Herbivores can increase their grazing intensity locally in response to increasing productivity, by the behavioural response of aggregation in space or time. This phenomenon was implied by Fryxell (1991), and specifically mentioned or modelled by McNaughton (1984), Arnold (1964) and Hutchings & Gordon (2001). In contrast to Hutchings & Gordon (2001) and Fryxell (1991) our model predicts that the intake per individual is independent of overall herbivore density, in highly productive habitat (Figure 5.7). The crucial difference is found in our assumption that the herbivores are able to relocate and re-graze previously visited patches. This is a reasonable assumption for geese in homogeneous polder grassland, given the fact that birds walking in flocks graze contiguous areas and that the birds are highly mobile. In the model by Hutchings & Gordon (2001), and the field data by Arnold (1964), sheep have lower performance at low stocking rate as the probability of encountering previously grazed patches is lower under these circumstances.

Effectively, when patches are abandoned, the consumption by the herbivores as a group is matched to the primary production in the continuously grazed area. In theory, the habitat could now be utilised at the level of biomass that would yield the maximum rate of intake. However, our simulation study shows that this situation only arises under the specific model assumptions of biomass independent primary productivity,
absence of travel costs and an error-free determination of patch profitability. A biologically realistic assumption of limited information, defined as an error in the perceived rate of intake of the model patches, leads to a certain degree of over-exploitation in the continuously grazed patches and a reduced intake. This effect is stronger at high levels of primary production and affected by the patch size used in the model. Due to limited information, the herbivores initially do not immediately respond to the fact that vegetation has grown beyond the optimum level of biomass. Then, after feeding for a while on an area larger than what would be ideal, they concentrate on an area that is smaller than the optimum size, given the current level of production and depletion occurs. Under biomass-dependent growth the effects of depletion can be very strong due to a positive feedback between biomass and primary production. The same phenomenon was observed by WallisDeVries (1996), and is partly related to the discrete character of the model (See box 5.1, page 107). However, it points at a more general finding that vegetation ‘escapes’ more easily than it is ‘recaptured’. Vegetation that has grown beyond the point of maximum intake requires relatively high grazing pressure before it can turn back to a state of low biomass. However, most of the grazing pressure is focussed on remaining patches in a low biomass state, and thus the net difference between growth and consumption is mostly positive. Any factor that disrupts an exact match between consumption and production either leads to a situation where the herbivores deplete the continuously grazed patches and feed with lower intake rate or where they are forced to eat with low intake rate at patches with high biomass levels. Examples of these factors are fluctuations in primary production, travel costs (WallisDeVries 1996), search time (Hutchings & Gordon 2001) and social interactions. In practice several processes can buffer these effects. Apart from increasing production over time, there can be a decreasing consumption due to emigration. In the case of the Brent Geese there is a continual movement towards the marsh habitat and staging sites that are further along the route to the breeding sites.

An implication of our concept is that small groups, or even individual herbivores, are predicted to be able to regulate vegetation density in highly productive systems. This is in contrast to predictions by van de Koppel et al. (1996) which state that the density of small herbivores will be low under conditions of high primary productivity. The apparent discrepancy with the model by van de Koppel et al. (1996) is found in the time scale that is considered. Van de Koppel et al. (1996) only allow for a population numerical response of the herbivores rather than an aggregative numerical response, and they implicitly assume that systems characterised by high primary productivity are also characterised by different successional stages of vegetation. We illustrate that, within a season, herbivores may be able to regulate vegetation density in a restricted area by an aggregative response. However, the limited grazing intensity in the remainder of the area can result in a vegetational change, rendering the habitat unsuitable in the long run. Temporary absence of herbivores for other reasons, e.g. breeding in the case of the Brent Geese can also allow vegetation succession to proceed (Adam 1990). Under these circumstances, the grazing system will remain stable only when the original composition of the sward is maintained by larger herbivores or farming activities.
The experiments by Stock & Hofeditz (2000) illustrate this process. After the removal of sheep at the salt marsh on the Hamburger Hallig (Germany), vegetation composition of the productive sward, once dominated by *Puccinellia maritima*, started to change and slowly lost its value for Barnacle Geese in autumn and spring.

**Model variations and limitations**

Productive habitats in which these processes occur are not isolated, but are often used in conjunction to other habitats. In our example of the Brent Goose, the productive polder grasslands are used in spring prior to moving to salt marsh habitat. Based on the theory of Ideal Free distribution (Fretwell & Lucas 1970), it is to be expected that the timing of a switch to alternative habitat is dependent upon the relative fitness, often approximated by the relative rates of intake, that can be achieved in either habitat. For conservation purposes it is desirable to be able to predict the timing of switches between habitat and the rates of intake achieved. However, the current model does not allow such a prediction as the effects of hysteresis lead to non-robust model behaviour. Especially under logistic growth, the results are dependent upon settings of the model that are not biologically relevant, such as model patch size and model step size. This problem is not encountered in models that use a continuously increasing functional response, or that analyse system behaviour under equilibrium conditions.

We suggest to explore next whether different foraging rules and different model structures would alter our conclusions and predict intake rate of herbivores in a robust and reliable manner. An example of such a model could be one in which patch-choice decisions are taken at multiple levels of scale, a suggestion that was also raised by Spalinger & Hobbs (1992), with small-scale displacements (e.g. by walking) between time steps and larger scale movements (e.g. flying) after longer time intervals. Such a model variation would obey the experimental result by WallisDeVries *et al.* (1999) that foraging selectivity is scale-dependent.

In contrast to the patch depletion models presented by Sutherland (1996), the effects of interference cannot be studied as easily in our patch model, under the assumption of a dome-shaped functional response and high primary productivity. The reason for this lies in the fact that the size of patches needs to be small and the number of patches high, in order to prevent artefacts of scale. As grazing in the patches with biomass densities lower than the optimum value for intake rate results in an homogenisation of patches with regard to biomass, there are many patches with only very little difference in potential (interference free) intake rate. Direct interference will lead to a dilution of birds over multiple patches, without affecting their intake, unless additional assumptions are made regarding interactions across patch boundaries. In spite of this, the grazing intensity per patch will remain the same, as individual birds will exert the same grazing pressure in a patch in multiple time steps as multiple birds would have exerted in a single time step.
Acknowledgements

We appreciate the help of many people involved in the data collection and especially Nicole Heuermann, Lutz von der Heyde, Conny Rothkegel and Maarten Loonen. We are grateful to the State Forestry Commission (SBB), Martin Eelman and Piet Postma, for permission to do experiments at the reserve ‘Zeeburg’ and to the farmers on Schiermonnikoog for allowing us presence on their land. The helpful discussions with Rudi Drent, Michiel WallisDeVries, Maarten Mouissie and Bernard Spaans were useful and enjoyable. We thank Dick Visser for preparing the graphs. This research was supported by the Technology Foundation STW, applied science division of NWO and the technology programme of the Ministry of Economic affairs.

References

Durant D (2001) Patterns and processes underlying the difference in the use of swards by grazing Anitdae. PhD thesis Université de La Rochelle, UFR de Sciences, La Rochelle


Spaans B, Postma P (2001) Inland pastures are an appropriate alternative for salt-mashes as a feeding area for spring-fattening Dark-bellied Brent Geese Branta bernicla. Ardea 89: 427-440


Vickery JA, Sutherland WJ, Watkinson AR, Lane SJ, Rowcliffe JM (1995) Habitat switching by dark-
bellied brent geese *Branta b. bernicla* (L.) in relation to food depletion. Oecologia 103: 499-508
in grazing herbivores. Oecologia 121: 355-363
elaphus*). Behav. Ecol. 6: 209-217
J. Appl. Ecol. 18: 443-453
Ecological theory predicts that herbivores can benefit from aggregation in productive habitat (McNaughton 1984; Fryxell 1991; Hutchings & Gordon 2001), when foraging efficiency decreases at high plant standing crop. By focusing on a limited part of the grazing area, a short sward is maintained, and intake is kept at a high level. Results of experimental field studies are in line with this hypothesis (Wilmshurst et al. 1995; Wilmshurst & Fryxell 1995), and aggregation is observed in the field (Spaans & Postma 2001). A spatially implicit simulation study, described in this chapter, indeed indicates that short-term foraging decisions, where herbivores consistently opt for swards with intermediate levels of biomass, may lead to patterns of aggregation in productive habitat. However, the simulation also revealed that, in spite of an over-abundance of food in the entire area, local depletion of standing biomass may take place in swards that are continued to be grazed by the herbivores. This phenomenon occurs when the area on which the herbivores have concentrated their grazing effort is too small to yield sufficient primary production to compensate for grazing losses, for instance due to a decrease in primary productivity, due to sub-optimal foraging decisions of the herbivore (Arnold 1964; WallisDeVries 1996), or due to an increase in herbivore numbers. The simulation results were sensitive to the values of patch size and time step size chosen, and insight in the robustness of these results is thus hampered by discretisation effects (this chapter). We thus seek analytical confirmation of the suggestion put forward in this chapter, that vegetation, once escaped to a state of high plant standing crop, may not easily be grazed back again to a state of low plant standing crop.

Following the framework of van de Koppel et al. (2002), we developed a spatially-implicit model of plant growth and herbivore grazing within a bounded area $D$. The net rate of change of plant biomass at a particular location $x,y$ within $D$ is described as:

$$\frac{dB}{dt} = G(B) - F(B)N$$

(1.)

where $G$ describes plant growth as a function of local plant standing crop ($B$), and $F$ describes consumption of herbivores as a function of local plant and herbivore density ($N$). We specified the model further by assuming that plant growth is maximal at low plant standing crop, and decreases linearly with increasing plant standing crop (Figure box5.1):

$$G(B) = r \left( \frac{1}{K} - \frac{B}{K} \right)$$

(2.)

Here, $r$ is a growth coefficient of the vegetation and $K$ is the carrying capacity. We assume that herbivore consumption rate first increases with plant standing crop, but later decreases due to constraints on intake (this chapter):

$$F(B) = \frac{aB}{1 + a(h_0 + h_1B)B}$$

(3.)

where $a$ is the search rate, and $h_0$ and $h_1$ are constants defining the handling time. More general, this phenomenon of a declining foraging efficiency could alternatively be caused by
constraints on digestion (Fryxell 1991) or a negative correlation between nutrient content and plant standing crop (Hassall et al. 2001). The consumption rate in vegetation with intermediate values of plant standing crop is thus higher than that in vegetation with high plant standing crop. Here, we assume that local herbivore density is proportional to the per capita herbivore consumption in the spot under consideration:

$$N = \alpha \cdot F(B)$$  \hspace{1cm} (4.)

This situation may arise, for example, when emigration from, or immigration to a patch are affected by the intake in that patch. The total amount of herbivores in the area can be expressed as the integral over the entire area \(D\), for both sides of the equation: \(\int \int N \, dx \, dy = \int \int \alpha F(B) \, dx \, dy\). By taking \(\alpha\) out of the integral and by dividing both sides by the size of domain, \(A\), we can express \(\alpha\) as \(N_{avg} / F_{avg}\), where \(N_{avg} = \int \int N \, dx \, dy / A\) and \(F_{avg} = \int \int F(B) \, dx \, dy / A\). Substitution in equation 4 now produces:

$$N = \frac{N_{avg}}{F_{avg}} \cdot F(B)$$  \hspace{1cm} (5.)

where \(N_{avg}\) refers to the average herbivore density over the area under consideration and \(F_{avg}\) equals the average intake in the entire area. This allows us to simplify the plant differential equation (1) to:

$$\frac{dB}{dt} = G(B) - F(B)^2 \frac{N_{avg}}{F_{avg}} = G(B) - C(B)$$  \hspace{1cm} (6.)

The function \(C(B)\) is the “consumption curve” (Figure box5.1) describing the local amounts of forage removed by herbivores as a function of its local availability and the average consumption rate in the entire area. The shape of this function resembles \(F(B)\), having the maximum at the same value of \(B\).

Because we are interested in a system where primary production generally increases in the course of the season, we now investigate the effects of increased primary productivity on the balance between local plant growth and herbivore grazing (Figure box5.1A). We assume that an increase in primary productivity is reflected in a proportional increase in both \(r\) and \(K\). If productivity is low (Figure box5.1A, solid line labelled ‘1’), only one equilibrium at low plant standing crop exists. At low productivity, herbivores are homogeneously distributed, and utilise the entire area. At intermediate levels of productivity there are two equilibria, one at high and one at low plant density (Figure box5.1A). At high levels of primary productivity, a situation may arise in which all vegetation is in a state of high plant density, indicated in Figure box5.1A by the one intersection of line ‘3’ with the consumption curve. In this situation the herbivores also use the entire area, but at low consumption rate per unit biomass. However, local intensification of herbivore grazing (aggregation) enables the herbivores to cope with these high levels of primary productivity up to a certain extent. The stippled line ‘b’ in Figure box5.1A refers to the upper level of primary productivity above which herbivores are not able to maintain a low plant density, and associated high consumption rates, in the entire area. After primary productivity has increased from low levels to this critical boundary level, a further increase in productivity leads to a spatial bifurcation in plant standing crop. According to our model, focusing of herbivore grazing allows a part of the vegetation to escape to high standing crop. We made one extra assumption, that patches of vegetation ‘escape’ from grazing one by one, and turn to a
state of high plant density, rather than all turning to the state of high plant density at once. So the herbivores aggregate on patches with low plant density, where consumption rates are highest, allowing them to maintain a short sward in that part of the area. The aggregation of herbivores, in response to the higher levels of primary production, leads to a change in the consumption curve, which is illustrated in Figure box 5.1B. The consumption curve becomes steeper. This means that more biomass is removed per unit area in the patches that are continued to be grazed. Mathematically, this is caused by a net decrease in average consumption, $F_{\text{avg}}$, because the herbivores spend part of the time foraging in patches with high plant density and associated low intake rate. With every subsequent increase in primary productivity, more patches escape from grazing and aggregation becomes more pronounced.

Figure box5-1  Plant growth and herbivore consumption for a small-scale location within the area of consideration. The straight lines represent plant growth ($G(B)$), lines 1, 2, 3, a and b), for different levels of productivity ($r$ and $K$), and the curves represent herbivore consumption ($C(B)$). A) Given a level of average consumption, the system may have one or two stable states, depending on the level of primary productivity. Stable states are indicated with black solid dots, an unstable state is given by an open circle. Lines 1, 2 and 3 refer to low, intermediate and high levels of primary productivity respectively. Stippled lines a and b refer to the boundary conditions of plant growth below and above which local plant density in part of the area switches to a different state. B) Aggregation by herbivores under increasing primary productivity is expressed in a steeper herbivore consumption curve, as indicated by the grey arrows.
The point that we would like to stress here is that there is a large ‘barrier’ for the herbivores to regain patches of vegetation that have turned to a state of high plant density. The primary productivity has to diminish below the level of consumption in the high biomass state, before vegetation in a patch will return to a low biomass state. This mathematical condition is indicated by the stippled line ‘a’ in Figure box5.1A. The critical level to which productivity has to decrease to allow the herbivores to ‘recapture’ vegetation in ungrazed swards (line ‘a’ in Figure box5.1A) is much lower than the critical level at which vegetation starts to ‘escape’ (line ‘b’ in Figure box5.1A). As a result, when part of the vegetation has escaped from grazing control following an increase in productivity, the vegetation is not recaptured when productivity returns to the former levels. Rather than that, a decrease occurs in plant density in the patches that are still under intensive herbivore grazing and, depending on the degree of the decline in productivity, this may lead to a decline in intake rate of the herbivores. This indicates that, in productive systems, a herbivore population is vulnerable to fluctuations in primary productivity, as loss of control over grazed swards cannot be easily regained.

In summary, the model analysis confirms that a hump-shaped functional response in herbivores leads to spatial bifurcation in plant standing crop at high levels of productivity. Beyond a threshold production level, increased primary production leads to a progressive release of vegetation from herbivore control. This vegetation will develop a high standing crop, unsuitable for herbivore grazing, whereas focusing of herbivore activity maintains a short sward in the remaining part of the vegetation. This way, herbivore foraging efficiency remains high, despite a distinct decrease in the overall suitability of the vegetation. However, the analysis indicates that temporary fluctuation in productivity, commonplace in natural environments, may lead to a less than optimal intake, as suitable vegetation becomes depleted. These findings support the results from the simulation study mentioned above (this chapter).

Acknowledgements

We would like to thank Franz J. Weissing and Max Rietkerk for their constructive comments that helped us to shape this study.