Dark-bellied Brent geese aggregate to cope with increased levels of primary production

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We report on an aggregative response of Dark-bellied 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 a decreased efficiency of grazing in vegetation with a high standing crop. In other words, 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 a model showing that, for a dome-shaped functional response, optimal foraging under increasing primary productivity leads to spatial heterogeneity in standing crop. Beyond a certain threshold value, a further increase in productivity leads to a progressive release of vegetation from herbivore control and to the development of a high standing crop. Interestingly, our model suggests that only in a stable and predictable environment the aggregative behaviour of herbivores is able to maintain the intake rate close to its potential maximum. Misjudgement of patch quality by the herbivore or any other process disrupting the match between local primary production and consumption leads to a less than optimal intake, as suitable vegetation becomes depleted. This has important implications for ecological inferences, such as the prediction of carrying capacities in herbivore-dominated ecosystems.

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Predicting the spatial distribution and dynamics of animal populations requires a thorough understanding of the relationship between resource availability and intake rate, the so-called functional response. For many species, vertebrates and invertebrates alike, the functional response, is an increasing function (Holling 1959, Spalinger and Hobbs 1992, Gross et al. 1993). There is recognition though that for a number of plant-herbivore systems the functional response is dome-shaped, i.e. decreasing at high resource densities (Abrams 1982, Hobbs and Swift 1988, Fryxell 1991), a fact that may have profound consequences for the dynamics of plant–herbivore systems. A decline in the functional response may reflect the change in vegetation composition, structure and tissue quality with increasing resource density. For example, reduced energy absorption due to a declining digestibility may lead to a lower performance of ruminants at a higher standing crop (Fryxell 1991, Illius and Gordon 1991). Other mechanisms underlying a decline in the functional response are 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).

Geese rely heavily on forage of high quality (Owen 1980) and are therefore often observed on shortly grazed swards or newly emerging vegetation (Boudewijn and Ebbinge 1994). Several studies support the hypothesis that dark-bellied Brent geese *Branta bernicla* (L.) select short swards in order to maximise intake of nitrogen (Ydenberg and Prins 1981, Hassall et al. 2001, Bos 2002) 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). We hypothesize that these processes form the mechanism behind aggregated 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), dark-bellied 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.

If the highest rates of intake or absorption are achieved at intermediate levels of resource density, herbivores are predicted to benefit from aggregation (McNaughton 1984, Fryxell 1991, Hutchings and Gordon 2001). Fryxell (1991) presented a model illustrating this phenomenon. In this model, individual herbivores suffer from forage maturation when forage production exceeds forage consumption. Animals at higher densities keep the sward in a nutritious stage by repeated defoliation and thus facilitate each other. Here, we also consider the effects of aggregative grazing in a productive environment. In contrast to Fryxell's study, we include spatial heterogeneity. We will demonstrate that spatial heterogeneity may be of great importance, since focussed grazing leads to a patchy vegetation of alternating ungrazed patches and young swards. We relate the modelling part of our study to observations on spring staging dark-bellied Brent geese foraging on productive agricultural grassland along the coast of the Dutch Wadden Sea. The objective of this paper is (1) to describe patterns of habitat use by Brent geese on a Dutch Wadden sea island, (2) to infer the shape of the functional response curve of the geese from experiments, (3) to include the resulting dome-shaped functional response curve in a spatially-implicit optimal foraging model, and (4) to explore the implications of this model for both the geese and the vegetation. The paper is organised in two sections, a field study and a modelling study. We start with the field study, because the model is motivated by its results.

Field study

Methods

Study sites
Field data on habitat use by dark-bellied 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 dark-bellied Brent geese (van der Wal et al. 2000) and up to 8,000 barnacle geese *Branta leucopsis* (Bechst) (Bos and Stahl 2003) during spring. The geese forage on polder grassland (290 ha) during early spring, but move to the marsh (1500 ha) in February/March (barnacle geese) and April (dark-bellied Brent geese). The polder areas are used for grass production and cattle grazing by farmers and consist of homogeneous swards, containing mainly *Lolium perenne* (L.) and *Poa* sp. 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 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 dark-bellied 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* sp. that are managed by fertilisation (110 kg N ha^{-1}) and aftermath grazing with livestock in order to accommodate the geese. Disturbance of the geese is very limited because access for pedestrians and traffic is restricted.

Field patterns
We counted barnacle and dark-bellied 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 am and 8:00 pm at different times for each count. At 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 assessed in a circular plot of 4 m^2. 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 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 m^2 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, while the geese were not excluded in the control treatment. 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 in field I and three times in field II using a randomised block design. On May 7th, all fencing was removed.

After removal of the fences, droppings were counted and removed daily in a 4 m^2 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 × 10 cm) were taken from each plot and used to estimate the instantaneous rate of biomass intake (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 dark-bellied Brent geese, brought individually into an experimental outdoor enclosure (4 × 4 m) for the measurements. The geese were allowed to eat from sods of 10 × 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 (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 estimated by visual observation, supported by software that was specifically designed for the purpose, and summed to obtain an estimate of total pecking time (s). The intake rate (g fresh s^{-1}) was calculated by dividing removed biomass by total pecking time. In each trial, a 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 m^2 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 analysis

The average number of dark-bellied 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 goose density. For the exclosure experiment in the polder of Texel, the accumulated number of droppings for the first week and for 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 (Fig. 1). The average density of geese in those fields that were visited in the month concerned increased in both years (Fig. 2 A,B). This is especially clear if we focus on the single field that was grazed until the end of May (marked by an 'M' in Fig. 1). On that field, goose density increased fourfold in 2000 and more than twofold in 2001, despite of a decline in the total number of geese (Fig. 2 A,B). Towards the end of May, a dichotomy
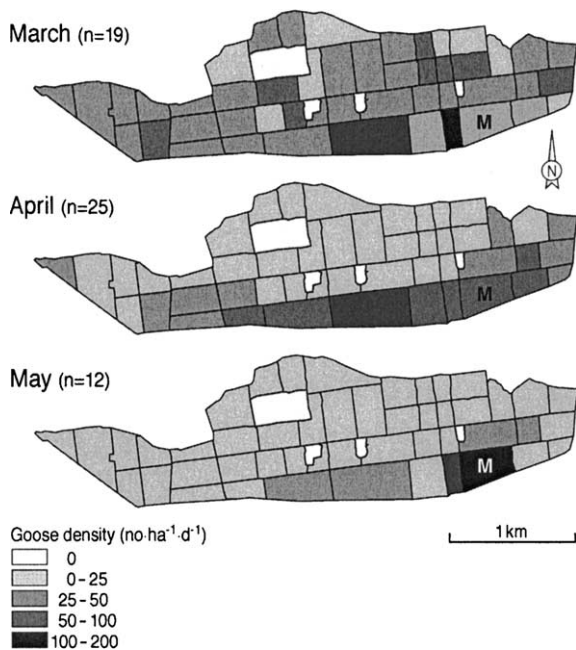
Fig. 1. Maps of the average density of dark-bellied Brent and barnacle geese in polder fields on the island of Schiermonnikoog, illustrating the aggregation of geese over spring of the year 2000. The number of counts that were performed each month is indicated between brackets. The specific field that was grazed until the end of May is marked with and 'M' (Fig. 2).
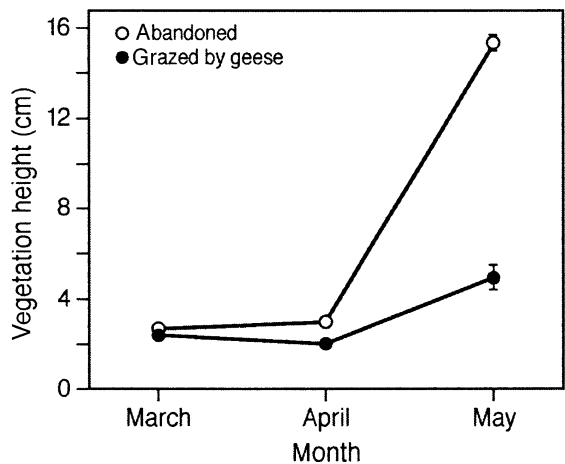

Fig. 3. Development of canopy height (cm) in spring in the polder of Schiermonnikoog for the year 2000 on polder grassland that is either grazed (with fresh droppings) or not grazed by geese. Error bars indicate the standard error, but are in most cases smaller than the size of the symbol.

arose between short grazed areas and fields that were abandoned. The canopy height of fields that were maintained by the geese remained low and was 4.9 ± 0.6 cm in May 2000, while the canopy height in ungrazed fields increased sharply to 15.2 ± 0.4 cm (Fig. 3).

Intake rate and patch choice experiment

On the experimental plots in the Brent goose reserve on Texel, those plots having been excluded longest had significantly taller canopy height ($F_{4,30} = 25.2$, P < 0.001, $R^2 = 0.771$). Canopy height was positively related to green biomass (Pearson r = 0.784, P < 0.001, n = 56). The experiment took place in a period when the geese had already started to leave the island and lasted two weeks (May 7–21, 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 (Fig. 4A; $F_{4,24} = 3.39$, P = 0.025) as well as in the second week (Fig. 4B; $F_{4,24} = 3.0$, P = 0.037) after opening of the exclosures. Instantaneous intake rate of biomass, as measured using the captive dark-bellied Brent geese, declined with canopy height (Fig. 4C; linear regression $F_{1,113} = 4.06$, P = 0.046, $R^2 = 0.034$), and so did nitrogen content (Fig. 4D; linear regression $F_{1,33} = 5.9$, P = 0.02, $R^2 = 0.153$).
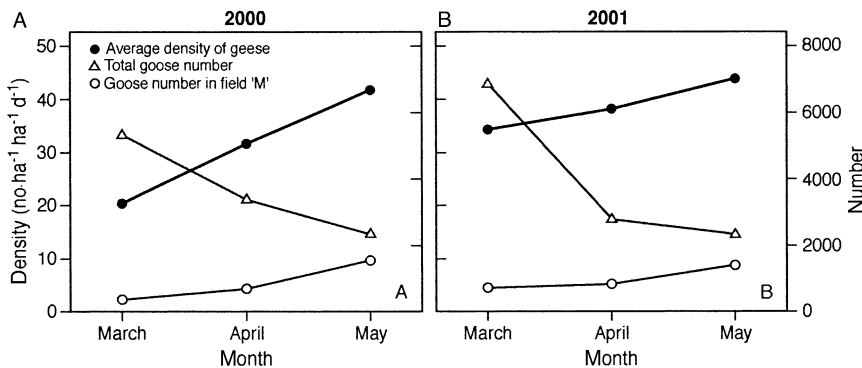

Fig. 2. Development in goose numbers and goose density (dark-bellied Brent plus barnacle geese, No ha^{-1} d^{-1}) in spring in the polder of Schiermonnikoog for the years (A) 2000 and (B) 2001. 'Average density of geese' refers to those fields only that were visited by geese in the month concerned, 'Goose number in field 'M'' refers to the single field that remained under grazing by geese until the end of May in both years (Fig. 1).

Fig. 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).
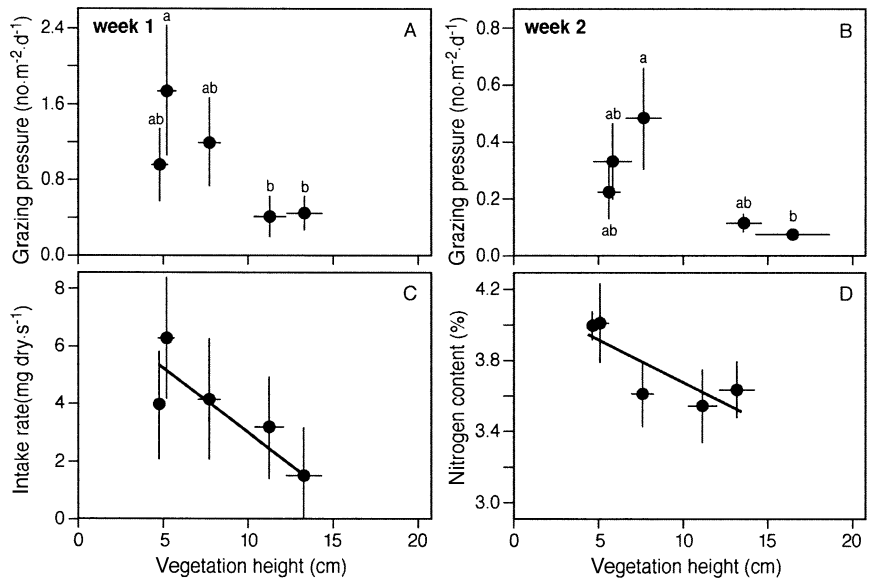
Modelling study

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. In the model, there is a large number of small patches, each characterized by a certain biomass density B. We simulate a whole season that is divided into time steps of length Δt. At the start of a time step, the model 'geese' redistribute over the patches according to expected intake rate. The biomass 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 1.

Vegetation growth
During each time step, the plant biomass (g m^{-2}) in a patch changes due to production and consumption:

$$\Delta B = [G(B, t) - NF(B)d]\Delta t \qquad (1)$$

Table 1. Parameters used in the simulation model with units, reference value and the range over which parameters are varied.

Parameter	Range		Reference value	Unit	Explanation
	Min	Max			
a	0.002	0.01	4.0E-03	m^2 s^{-1}	search rate
$B_{(t=t0)}$	5	25	10	g m^{-2}	(initial) biomass density
B_0			20	g m^{-2}	crown or root-reserves that cannot be grazed
Δt	0.125	1	0.5	day	time-step size
ε_{max}	0	0.5	0.2	–	variation around perceived intake rate
F_{min}			10	g nitrogen d^{-1}	minimum required nitrogen consumption
γ	1	5	3	–	index of productivity
g_0			2.4E-02	g m^{-2}	constant
g_1			4.0E-04	g m^{-2}	constant
h_0			100	s g^{-1}	constant in regression biomass–handling time
h_1	0.2	1	0.5	s g^{-2} m^2	coefficient in regression biomass–handling time
K			200	g m^{-2}	vegetative carrying capacity
d			57600	s	daylength
N	1	15	1	No.	(starting) number of geese
A	500	7500	500	m^2	total area
p	5	25	15	m^2	size of patch
q			6	%	nitrogen content of the vegetation
ρ	1	5	3	–	index of productivity
r_0			4.2E-03	g m^{-2}	constant
r_1			2.0E-05	g m^{-2}	constant
q			1.25E-04	No.$^{-1}$	interference-effect on intake
t	0	90		day	time

Here, G(B,t) describes daily primary production (g m^{-2} day^{-1}), which is dependent on standing biomass B and time of season t (days). N is the number of geese present in the patch, F(B) is the instantaneous intake rate per goose (g s^{-1}), which is a function of plant biomass (the functional response; below) and d indicates daylength (s). We are interested in a system where primary production increases systematically in the course of the season. In a first attempt, we assume that this increase is linear and independent of standing biomass:

$$G(B, t) = \gamma(g_0 + g_1 t) \tag{2a}$$

The parameters g_0 and g_1 were chosen such that the productivity increases by a factor 2.5 from the start (t = 0) to the end (t = 90) of the season (Table 1). The parameter γ 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:

$$G(B, t) = r(t)\,(B + B_0)\left(1 - \frac{B + B_0}{K + B_0}\right) \tag{2b}$$

Eq. 2b corresponds to the logistic growth equation for total biomass $B + B_0$, where B 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 carrying capacity of vegetative biomass. Notice that, for any given value of t, G(B,t) is maximized for $B = \frac{1}{2}(K - B_0)$. We assume that the intrinsic growth rate r(t) increases linearly with time of season, i.e.

$$r(t) = \rho(r_0 + r_1 t), \tag{2c}$$

where the parameters r_0 and r_1 are again chosen such such that, for a given level of biomass, productivity increases by a factor 2.5 from the start (t = 0) to the end (t = 90) of the season (Table 1). The parameter ρ was changed systematically in order to investigate the dependence of the simulation results on system productivity.

Intake rate
There are many ways to model a dome-shaped functional response. We modelled F(B) by a modified Holling type II curve (Case 2000), with fixed area of discovery a but a varying handling time h:

$$F(B) = \frac{a\,B}{1 + a\,h(B)B} \tag{3a}$$

The handling time was assumed to increase linearly with standing biomass:

$$h(B) = h_0 + h_1\,B \tag{3b}$$

For the functional response curve (Eq. 3a), intake first increases with biomass until it reaches a maximum at

$B_{max} = \sqrt{(a\,h_1)^{-1}}$. Beyond this value, intake decreases with biomass.

Patch selection
When a single herbivore is foraging in our model, it tends to be "ideal" and "free" in the sense that it omniscient concerning the state of all patches, that it is free to move without travel costs, and that it tends to choose the patch with the highest expected intake rate (i.e. the patch with maximal F(B)). However, to make our model more realistic we assumed that the herbivores cannot estimate expected intake rate with perfect accuracy. At the start of each time step, each patch i with biomass B_i is assigned a preference value

$$P_i = F(B_i)\,(1 + \varepsilon_i) \tag{4}$$

where the error term ε_i is drawn at random from a uniform distribution over an interval $[-\varepsilon_{max}, \varepsilon_{max}]$. The herbivore then forages on the patch with the highest value of P_i. Besides being more realistic, this procedure also assures that initially identical patches can develop differently due to small judgement errors.

To study potential aggregation effects, we also considered several herbivores foraging in the same area. Modelling such a situation is inherently more difficult, since expected intake rate on a patch (and hence the preference value of a patch) does not only depend on standing biomass but also on the presence and density of other herbivores in the patch. Hence, the decision of each herbivore on where to forage should also reflect the decision of other herbivores. To avoid these complications as far as possible, we assumed a linear dominance hierarchy that remains constant throughout the season. At the start of a time step, the individual on top of the hierarchy selects a patch as if it were foraging in isolation. It also gets the intake rate corresponding to this patch, irrespective of the presence of others. Each following individual then makes its choice, one after the other, taking into account that the biomass-intake in the patch is reduced by the number N_i of individuals that are present in the patch:

$$F(B, N_i) = (1 - N_i q)\frac{a\,B}{1 + a\,h(B)B} \tag{5}$$

Here q is a parameter quantifying the strength of interference.

Spatial and temporal scale
In our model, the herbivores do not move constantly between patches, but they rather utilize a given patch for a certain time period Δt. This generates discretisation effects, since two patches with the same initial biomass, one grazed and the other not, may differ substantially in biomass at the end of the grazing period. This difference is proportional to the length of the time period and it is

of higher relative importance in case of small patch sizes. Hence, a proper choice of the temporal scale (i.e. time step Δt) and the spatial scale (i.e. patch size) are of crucial importance to avoid model artefacts. Moreover, the effects of both scales are intertwined, small patch sizes requiring small time steps. In our simulations, the time step ranged between 0.125 and 1.000 (a complete daylight period). Patch size varied between 5 and 25 m^2. In case of a single goose, the total area was fixed at 500 m^2, while in case of multiple geese a total area of 7500 m^2 was chosen.

Simulation results

Figure 5 illustrates the model behaviour for the special case of a single foraging goose. At the start of the season, the herbivore visits all patches repeatedly, thereby keeping the standing biomass at a relatively low level. In the course of time, however, plant productivity slowly increases. As a consequence, standing biomass also increases, until the level B_{max} is reached that corresponds to the maximum of the dome-shaped functional response curve. From that moment onwards, some patches are abandoned, since patches with a biomass density substantially above B_{max} are less profitable (and, hence, less preferred) than patches with biomass density at or slightly below B_{max}. As a consequence, a clear-cut dichotomy develops between patches that are kept at a low biomass due to ongoing grazing and patches that escape grazing pressure since they are abandoned at some stage during the season.

In the simulation run of Fig. 5, the biomass density in the grazed patches is maintained at a value that is close to B_{max}. Accordingly, the herbivore manages to maximize intake rate even in a long-term perspective. This, however, is by far not always the case, and the intake rate can be substantially lower than the theoretical maximum $F(B_{max})$ throughout a major part of the season. This is illustrated for a different simulation run by Fig. 6, which shows how the escape of patches from herbivore control (Fig. 6A) leads to a temporal decrease in intake rate (Fig. 6B). 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. The situation of temporary depletion may sooner or later be restored by the increase in primary production with time. In the period until recovery of the standing stock, however, the intake rate of the herbivore is lowered to a certain extent.

Whether or not the herbivore is able to maintain its intake rate close to maximal level is strongly dependent on the assumptions concerning plant growth (Eq. 2a vs 2b) and the choice of model parameters. To illustrate this point, Fig. 7 shows the consumption of the herbivore towards the end of the season (day 90) for various scenarios. Intake rate at the end of spring staging is of particular importance for the breeding success of geese (Ebbinge and Spaans 1995), but the reader should keep in mind that the choice t = 90 is somewhat arbitrary.
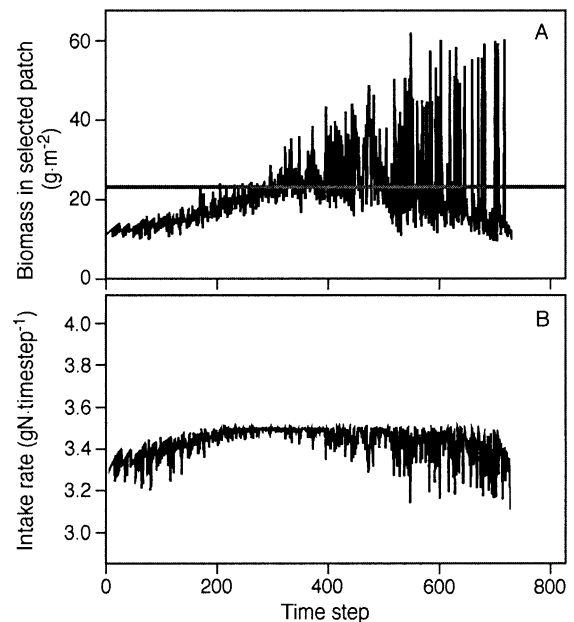
Fig. 6. Illustration of model behaviour under productive conditions ($\gamma = 4$) and relatively large patch size ($p = 25$ m^2) leading to a temporary depletion of the habitat, for a model run with one goose and $\varepsilon_{max} = 0.5$. (A) Biomass density in the patch that is selected by the herbivore in the given time step. The horizontal shaded line indicates the level of biomass that would yield a maximal intake rate. (B) The realised nitrogen intake rate of the herbivore.
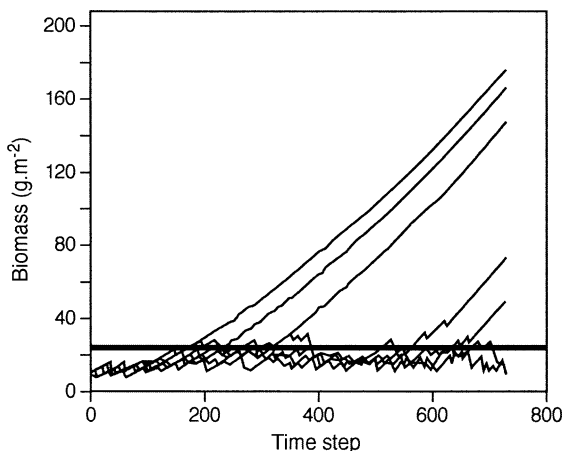
Fig. 5. Biomass development over time in a few representative patches for a model run with default parameter settings and a single goose. The horizontal shaded line indicates the level of biomass that would yield the maximal intake rate.
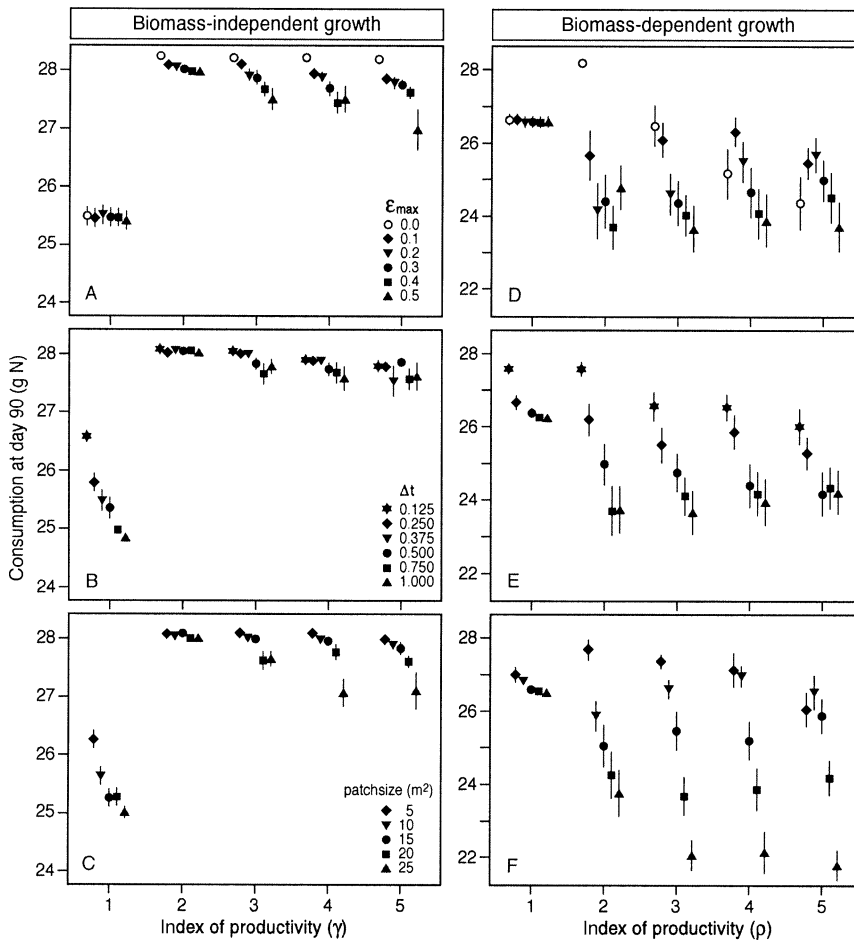
Fig. 7. Dependence of the nitrogen consumption of a single goose at the end of the season (day 90) on the model parameters. In panels (A) to (C), biomass growth is density-independent, while it is given by a modified logistic growth equation in panels (D) to (F). Shown are the effects of the maximal error in perceived intake rate (ε_{max}, panels (A) and (D)), time-step size (Δt, panels (B) and (E)), and patch size (p, panels (C) and (F)). Data are based on 1800 model runs. Simulations where the goose did not survive are excluded (time-step size $\Delta t = 0.5$ hrs and patch size $= 5$ m^2, n $= 30$ simulations). Error bars indicate the standard error.

Panels (A) to (C) in Fig. 7 focus on scenario (2a) where plant growth is assumed to be density-independent (the simulations in Fig. 5 and Fig. 6 were based on this scenario). At low productivity ($\gamma = 1$), the herbivore is able to maintain plant density at a low level in the entire area. Until the end of the season (day 90), the consumption is constrained by primary production. Biomass is thus not over-abundant, the potential maximum intake rate is not reached and no patches escape grazing. For higher values of γ ($\gamma \geq 2$), plant productivity is sufficiently high to ensure that eventually the critical biomass density B_{max} is reached, where some patches are abandoned. The herbivore is able to keep the grazed patches at the level B_{max}, yielding a maximal intake rate, provided that the profitability of patches can be predicted without error ($\varepsilon_{max} = 0$). At higher error rates, the intake rate achieved towards the end of the season can be substantially lower (Fig. 7A). Intake rate is also negatively affected by a coarse temporal scale (Fig. 7B) and/or a coarse spatial scale (Fig. 7C).

When primary production is density dependent (Eq. 2b), the sensitivity of the simulation results to changes in the parameter values increases sharply (panels (D) to (F) of Fig. 7). Under most combinations of parameter values, the intake at the last day of a model run is substantially lower than the potential maximum $F(B_{max})$. As in the simulation of Fig. 6, this is caused by depletion in the continuously grazed patches. Again, the herbivore focuses on a set of patches with combined area yielding insufficient primary production. In contrast to the situation in Fig. 6, however, vegetation recovery may be much slower if not impossible in case of density dependent primary production. In fact, a positive feedback is triggered, since higher levels of depletion lead to lower plant production, at least in case that B_{max} is smaller than $B = \frac{1}{2}(K - B_0)$, the biomass at which primary biomass production is maximized.

With respect to the other model parameters, the model outcome is quite robust (as long as system productivity is above the minimum required for survival). For example,

a fivefold increase in initial biomass or total area leads to deviations in the model output that does not exceed 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 90, but the qualitative behaviour of the model remains unaffected.

Up to now, we focused on a system with a single herbivore. However, model runs with multiple geese showed the same qualitative behaviour as those with a single goose. Fig. 8 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

Pattern formation in the vegetation

Under the assumption of a continuously increasing functional response (Ungar and Noy-Meir 1988, Vickery et al. 1995, Percival et al. 1996, Lang et al. 1997, Illius and Gordon 1999, Pettifor et al. 2000), plant–herbivore theory predicts that herbivores should always select patches with highest vegetation density. In the absence of strong interference, this leads to a homogenisation of biomass levels across patches (Sutherland 1996). Our results show that the inclusion a dome-shaped functional response leads to fundamentally different predictions. Our model predicts the emergence of shortly grazed

Fig. 8. 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.

patches alternating with ungrazed vegetation patches, which conforms the results of Hutchings and Gordon (2001). As productivity increases, the geese limit their habitat use to a restricted area of the productive grassland and increase the intensity of grazing, which allows them to maintain a high intake rate of high quality forage. Model predictions were in agreement with observed aggregation of goose grazing in our field study. In other field studies, the phenomenon of pattern formation has been described for cattle (Andresen et al. 1990, Gibb et al. 1997), geese (Spaans and 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).

Preference for continuously grazed swards

Aggregations of herbivores have been observed for many species of herbivore, such as wildebeest *Connochaetus taurinus* (Burchel) (McNaughton 1976) or red deer *Cervus elaphus* (L.) (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 trough enhanced predator detection or dilution and (3) a preference for continuously grazed swards (Fryxell 1991). Our experiment provides support for the third explanation: the observed aggregation by dark-bellied Brent geese is caused by a preference for continuously grazed swards. 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 (2002), Stahl (2001) and Riddington et al. (1997) for wild geese. The consequence of this aggregation is an "escape" of vegetation in areas that are left ungrazed.

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 biomass was observed (Fig. 4C), presumably due to increased handling time. Such a decline in instantaneous intake rate has previously only been demonstrated for wigeon *Anas penelope* (L.) (Durant 2001) and barnacle geese (van der Wal et al. 1998). Most of the functional response models published for herbivores (Spalinger and Hobbs 1992, Gross et al. 1993, Illius and Gordon 1999, Schwinning and Parsons 1999), follow the type II response as defined by Holling (1959). Above that, we also observed a small decrease in forage quality, measured as nitrogen content (Fig. 4D), in our experiment, 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 and van Soest 1985, van Soest 1994). Hence the intake rate of nitrogen
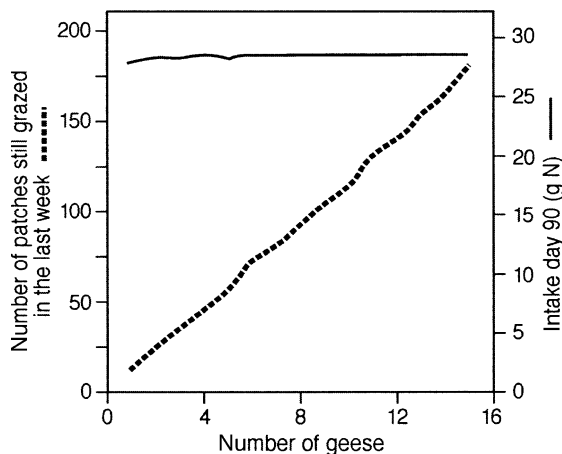
or energy declines with biomass at the short (Hassall et al. 2001, Bos 2002, this study) or the longer term (Arnold 1964, Fryxell 1991). Finally, there may be other factors leading to a lower performance of herbivores in taller swards, such as differences in vegetation composition or increased costs of locomotion and vigilance.

Model prediction: intake independent of overall herbivore density

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), specifically mentioned by Arnold (1964), McNaughton (1984) and modelled by Hutchings and Gordon (2001). In contrast to Fryxell (1991) and Hutchings and Gordon (2001) our model predicts that, in a highly productive habitat, the intake per individual is independent of overall herbivore density (Fig. 8). 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 geese walking in flocks graze contiguous areas and that geese are highly mobile. In contrast, the sheep studied by Arnold (1964) and modelled by Hutchings and Gordon (2001) have lower performance at low stocking rate, as the probability of encountering previously grazed patches is smaller under such circumstances.

Model prediction: overexploitation in continuously grazed patches

By abandoning patches, the herbivores as a group might be able to match their consumption to primary production in the continuously grazed area. One might expect the herbivores to restrict their habitat use to such an extent that they are able to realize the potential maximum rate of intake. However, our simulation study shows that this situation only arises under highly specific assumptions, such as density-independent primary productivity, absence of travel costs and an error-free determination of patch profitability (Fig. 7A). For example, imperfect information, resulting in an erroneous judgement of expected intake rate, 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 is 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. Nonetheless, it points at a more general finding that vegetation 'escapes' more easily than it is 'recaptured' (Bos 2002). 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 in patches that are in a high-biomass state. 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 to a situation 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 and 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 dark-bellied Brent geese there is a continual movement during spring towards the marsh habitat and staging sites that are further along the route to the breeding sites.

Dynamic implications of herbivore aggregation

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 on a restricted part of the area. 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. It is an apparent discrepancy related to the time scales that are considered, and the processes occurring at these time scales. Van de Koppel et al. (1996) present a graphical analysis of herbivore distribution under the assumption of a dome-shaped functional response. Their analysis deals with time scales of multiple years over which vegetation succession becomes relevant. The numerical response, in their analysis, is limited to a population numerical response, 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. This is true for the livestock–ungrazed salt marshes

they study, where succession is caused mainly by a continual increase in nutrient availability over time (Olff et al. 1997). Our model illustrates 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 indeed 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 dark-bellied 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 (Stock and Hofeditz 2000, van der Wal et al. 2000, Bos et al. 2002, van der Graaf et al. 2002).

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