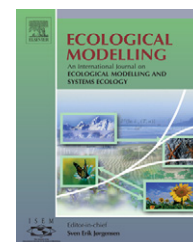


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Instantaneous intake rate of herbivores as function of forage quality and mass: Effects on facilitative and competitive interactions

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ABSTRACT

The functional response as the link between the consumer and its resource is a central issue in herbivore–vegetation interactions. Vegetation often consists of low and high quality tissue due to nutritional or structural differences. It has been observed that the instantaneous intake rate of herbivores decreases with decreasing forage quality. However, so far variation in forage quality is not explicitly considered when modeling this instantaneous intake rate. In this paper, we derive a model for the instantaneous intake rate depending on forage quality, i.e., the proportion of high quality tissue in the vegetation. In the model, a downward deflection of the functional response curve is caused by a reduction of the maximum consumption rate at high proportions of low quality tissue. The model gives a mechanistic explanation for decreasing intake rate with decreasing forage quality. Compared to a conventional functional response model with constant maximum consumption rate, a herbivore–grass model with the forage quality-dependent functional response leads to discontinuous changes in the vegetation and herbivore density. The effects hinge on the positive feedback between herbivore density and the proportion of high quality forage. Our analyses show that this positive feedback can explain the maintenance of lawn grass where a high herbivore density can maintain high quality forage. The model results indicate that depending on the coefficients of trophic conversion from resource to consumer, co-existence, facilitation and competitive exclusion between differently sized herbivore species can emerge.

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1. Introduction

The functional response as the link between the consumer and its resource is a central issue in herbivore–vegetation interactions. Many theoretical studies have explored the consequences of different shapes of the functional response on herbivores and their resources (Spalinger and Hobbs, 1992; Gross et al., 1993; Van de Koppel et al., 1996; Bos et al., 2004; Fortin, 2006). Also, much is known about the effects of forage

quality on passage (Allen, 1996), patch selection (Wilmshurst et al., 1995; Coppedge and Shaw, 1998; Wallis DeVries et al., 1999; Van der Wal et al., 2000; Fortin, 2002; Person et al., 2003), herbivore community assembly (Illius and Gordon, 1992; Belovsky, 1997; Mysterud, 2000), and daily intake (Wilmshurst et al., 1995, 1999; Van der Wal et al., 1998). However, few studies have considered forage quality as an explicit parameter affecting the functional response (Fryxell, 1991; Benvenuti et al., 2006; Drescher et al., 2006).

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At daily time scales, decreasing forage intake by herbivores from growing and maturing forage resources has been attributed to decreasing forage quality and consequent digestion constraints (Fryxell, 1991; Illius and Gordon, 1991; Hutchings and Gordon, 2001). For example, the high intake at intermediate forage mass is seen as the maximizing solution under ingestion and digestion constraints that can explain patch selection by red deer *Cervus elaphus* (Langvatn and Hanley, 1993; Wilmshurst et al., 1995). These studies do not, however, explicitly consider the effects of forage quality on the instantaneous intake rate, but mostly substitute forage mass for forage quality. Indeed, forage mass and forage quality can be related, but they are not always interchangeable, for example when considering the potentially negative effects of grazing on forage quality (Hamilton et al., 1973; Ayantunde et al., 1999; Orr et al., 2004; Animut et al., 2005). Since it has been observed that intake rate during short time spans can respond independently from forage mass to changing forage quality (Benvenuti et al., 2006; Drescher et al., 2006), the development of a model for the instantaneous intake rate as an explicit function of both forage quality and forage mass would be an important contribution to our understanding of the factors controlling intake behaviour.

As grass grows and matures, commonly its quality as forage for grazers decreases (Fryxell, 1991; Wilmshurst et al., 1995, 1999; Prins and Olff, 1998; Van der Wal et al., 1998; Hassall et al., 2001), which is mainly due to changes in the proportions of various plant parts and their nutrient contents. This can be illustrated by the decreasing proportion of leaves and the average nitrogen content in the plants (both indicating high forage quality) with increasing grass mass in a South African savanna (Fig. 1). Changes in forage quality can be the result of differential investment in stems or leaves due to competition for light when vegetation becomes more dense (Stobbs,

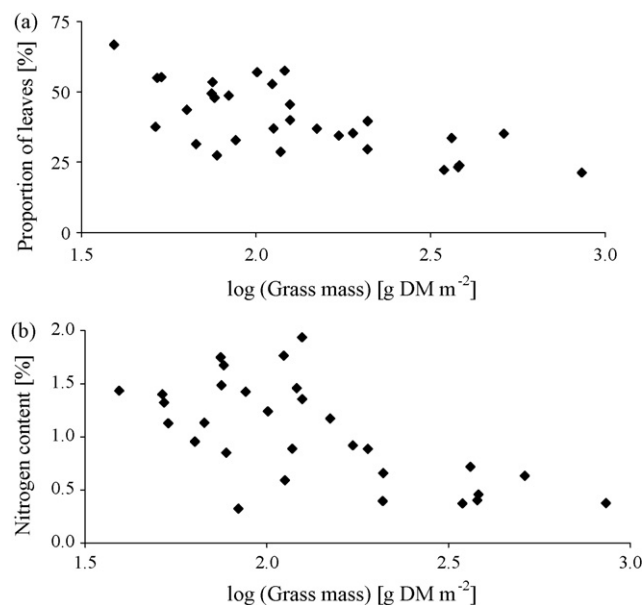


Fig. 1 – Decreasing (a) proportion of leaves and (b) average nitrogen content as a function of total grass mass in natural grasslands of a South African savanna in the late wet season (adapted from Drescher, 2003).

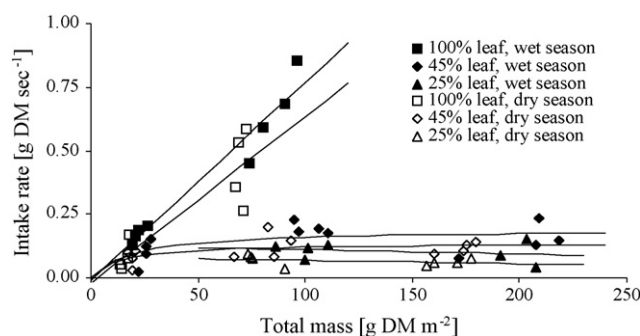


Fig. 2 – The functional response for cattle grazing on hand-constructed swards of *Panicum maximum* (Drescher et al., 2006) that differ in the proportion of high quality forage, i.e., leaf mass.

1973) or of selective grazing (Hamilton et al., 1973; Ayantunde et al., 1999; Orr et al., 2004; Animut et al., 2005). However, the mechanism by which decreasing forage quality affects the instantaneous intake rate at the scale of the grass sward has previously received little attention. A recent study on forage intake by large grazers demonstrated that the instantaneous intake rate depends both on the density and the proportion of high and low quality tissue in the vegetation, i.e., grass leaves and stems (Drescher et al., 2006, Fig. 2). The positive effect of density and proportion of leaves on bite rate and bite size leads to a higher instantaneous intake rate, while the effort to gather a fixed quantity of leaves depends on the density of stems in the sward. Thus, for a given total forage mass on offer, an increase in the proportion of low quality tissue depresses the instantaneous intake rate, which in turn leads to a decreased maximum consumption rate for that patch.

By formalizing the intake-depressing effect of increasing proportion of low quality forage in the grass sward, we derived a function for the herbivore instantaneous intake rate that explicitly depends on both forage quality and mass. Forage quality is defined here as the proportion of green leaf tissue, though nutritional differences are implicitly contained in this definition since green leaves tend to contain more available nutrients than stem tissue (Stobbs, 1973). We studied the effects of this functional response on large scale herbivore–grass dynamics using a simple model and compared it with a conventional functional response model. We included the forage quality-dependent functional response in a herbivore–grass model with two herbivore species sharing a common forage resource and used this model to investigate herbivore species interactions.

2. The model

2.1. The conventional functional response

The instantaneous rate of consumption by grazing herbivores is often described as a monotonically saturating function (type II curve, Holling, 1959), denoted as:

$$c(P) = c_m \frac{P}{P + k_1} \quad (1)$$

where $c(P)$ is the instantaneous consumption rate as a function of grass density P , c_m is the maximum per capita consumption rate, and k_1 is the half saturation constant, i.e., the grass density where the consumption rate is half of its maximum (Table 1). In this formulation, limited processing capacity causes the instantaneous intake rate to saturate at high grass density. However, the searching and handling times, which largely determine the shape of the functional response of the herbivore, are not explicitly considered. Patterns that fit Eq. (1) have frequently been found, particular in simple environments with only a single food type (Gross et al., 1993; McCoull et al., 1998; Koski and Johnson, 2002).

The rate of change of the grass and herbivore populations is generally represented by the following differential equations:

$$\frac{dP}{dt} = f(P) - c(P)N \tag{2a}$$

$$\frac{dN}{dt} = g(P)N \tag{2b}$$

where $f(P)$ describes grass growth as a function of grass density, N is herbivore density, and $g(P)$ is the per capita net growth rate of herbivores, i.e., their numerical response. The numerical response of herbivores is usually represented as:

$$g(P) = ec(P) - d \tag{3}$$

where e is the consumption-to-growth conversion coefficient and d is the specific herbivore loss rate (Table 1). Although this model assumes that the herbivore population reacts instantaneously to changes in grass biomass, it is often used to describe large scale herbivore–grass interactions (Van de Koppel et al., 1996; Farnsworth et al., 2002).

2.2. The forage quality-dependent functional response

Based on the findings of Drescher et al. (2006), we formulate the effect of the proportion of high quality tissue (p_H) on the functional response as an effect on the maximum consumption rate:

$$c_m(H, L) = c'_m \frac{p_H + k_2 c_{Lm}}{p_H + k_2} \tag{4a}$$

where $c_m(H, L)$ is the maximum consumption rate as a function of the proportion of high (H) and low (L) quality tissue, c'_m represents the effect of the proportion of high quality tissue on $c_m(H, L)$, c_{Lm} is the maximum consumption rate in the absence of high quality tissue expressed as a proportion of the maximum value of $c_m(H, L)$, and k_2 is the half saturation constant, i.e., the proportion of high quality tissue where $c_m(H, L)$ is half of its highest value. The maximum value of $c_m(H, L)$ is reached when $p_H = 1$. Therefore c'_m must be:

$$c'_m = c_{Hm} \frac{1 + k_2}{1 + k_2 c_{Lm}} \tag{4b}$$

so that the highest value for the maximum consumption rate ($c_m(H, L)$) is reached when the available forage consists of only high quality tissue ($p_H = 1$), and where c_{Hm} is the maximum consumption rate when there is only high quality tissue, which is expressed as a proportion of the maximum value of $c_m(H, L)$. Changes in the maximum consumption rate $c_m(H, L)$ as a function of the proportion of high quality tissue (Eq. (4b) substituted in Eq. (4a)) are illustrated in Fig. 3a.

The grass density P is the sum of the densities of high (H) and low (L) quality tissue. The proportion of high quality tissue thus is:

$$p_H = \frac{H}{H + L} = \frac{H}{P} \tag{5}$$

Table 1 – List of the used parameters and variables, their interpretation and units

P	Grass density (g m^{-2})
L	Density of low quality tissue (g m^{-2})
H	Density of high quality tissue (g m^{-2})
N	Herbivore density (g m^{-2})
c_m	Maximum per capita consumption rate ($\text{g g}^{-1} \text{d}^{-1}$)
k_1	Half saturation constant where the consumption rate is half of its maximum (g m^{-2})
e	Consumption-to-growth conversion coefficient (g g^{-1})
d	Specific loss rate of the herbivore (d^{-1})
c_{Hm}	Maximum consumption rate when the grass consists of only high quality tissue, i.e., $p_H = 1$ ($\text{g g}^{-1} \text{d}^{-1}$)
c_{Lm}	Lowest value for the maximum consumption rate in the absence of high quality tissue ($p_H = 0$), expressed as a proportion of the maximum consumption rate (-)
k_2	Half saturation constant where the maximum consumption rate is half of its highest value (-)
p_H	Proportion of high quality tissue (-)
m_L	Specific loss rate of stem biomass (d^{-1})
r_{Lm}	Maximum specific growth rate of stem biomass ($\text{g m}^{-2} \text{d}^{-1}$)
k_3	Half saturation constant where the specific growth rate is half of the maximum specific growth rate (g m^{-2})
r_H	Specific growth rate of leaf biomass ($\text{g m}^{-2} \text{d}^{-1}$)
m_H	Specific loss rate of leaf biomass (d^{-1})
e_H	Coefficient for the consumption-to-growth conversion for leaf biomass (g g^{-1})
e_L	Coefficient for the consumption-to-growth conversion for stem biomass (g g^{-1})
ρ_H	Proportion of high quality tissue in the diet of the herbivore (-)
β	Coefficient that represents the diet choice (-)

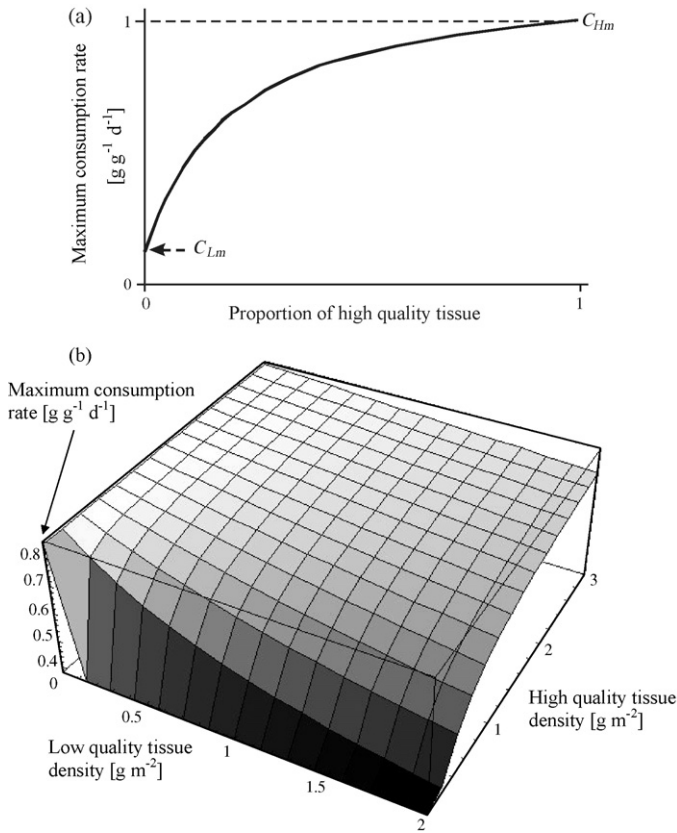


Fig. 3 – The maximum consumption rate $c_m(H,L)$ (Eq. (4b) substituted in Eq. (4a)) as function of (a) the proportion of high quality tissue (p_H) and (b) both the density of high quality tissue and low quality tissue (shaded area). Parameter values are: $c_{Hm} = 1.0$, $c_{Lm} = 0.1$, $k_2 = 0.2$.

The effects of the densities of high and low quality tissue on the maximum consumption rate $c_m(H,L)$ are illustrated in Fig. 3b. This figure shows several properties of Eq. (4). First, the maximum consumption rate is highest when the density of low quality tissue is zero (note that the model cannot produce the maximum consumption rate when the densities of both low and high quality tissue are zero). Second, when the grass density P remains constant, the maximum consumption rate increases following a saturating function with an increasing proportion of high quality tissue (see Fig. 3a). Third, when the grass density P remains constant, the maximum consumption rate decreases with an increasing proportion of low quality tissue (Drescher et al., 2006, Fig. 2).

Based on Eq. 4a and b, the average consumption rate of the herbivore $c(H,L)$ can be denoted as:

$$c(H, L) = c_m(H, L) \frac{P}{P + k_1} = c_{Hm} \left(\frac{1 + k_2}{1 + k_2 c_{Lm}} \right) \left(\frac{p_H + k_2 c_{Lm}}{p_H + k_2} \right) \times \left(\frac{H + L}{H + L + k_1} \right) \quad (6)$$

The effect of high and low quality tissue density on the functional response is illustrated in Fig. 4a. This figure shows that for swards with low densities of both high and low quality tis-

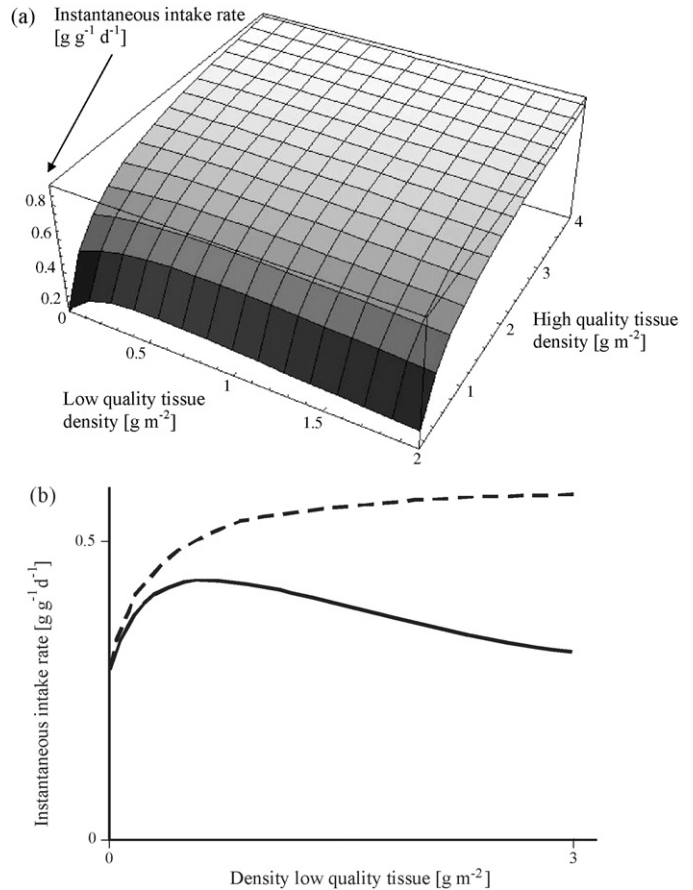


Fig. 4 – The consumption rate $c(H,L)$ (Eq. (6)) as a function of (a) both the density of low quality tissue and high quality tissue (shaded area), and (b) the density of low quality tissue. The solid line in (b) shows the consumption rate for increasing low quality forage tissue density while high quality tissue density remains constant (i.e., total forage mass increases but the proportion of high quality tissue p_H decreases). The dashed line in (b) shows the consumption rate when high quality tissue density increases faster than low quality forage tissue density (i.e., total forage mass increases and the proportion of high quality p_H increases). Parameter values in (a) and (b): $k_1 = 0.5$, $k_2 = 0.2$, $c_{Lm} = 0.05$, $c_{Hm} = 0.1$, solid line in (b): $H = 0.2$, dashed line in (b): $H = (0.2 + 0.2L)$.

sue, adding high quality tissue increases the consumption rate asymptotically. Adding low quality tissue, however, decreases the consumption rate after an initial increase, tracing a unimodal curve with the density of low quality tissue (Fig. 4b). Fig. 4 further shows that at all densities of low quality tissue, the consumption rate saturates for high densities of high quality tissue.

2.3. The herbivore–grass model

We use a simple model for analyzing the effects of the forage quality-dependent functional response on large scale herbivore–grass dynamics. The growth rate of grass stems (low quality tissue) is a positive function of leaf density (high

quality tissue). Since there is hardly any photosynthetically active material present when the leaf density is low, stem growth diminishes. Accordingly, the specific growth rate of stem biomass is modelled as:

$$r_L(H) = r_{Lm} \frac{H}{H + k_3} \quad (7)$$

where r_{Lm} is the maximum specific growth rate of stem biomass, and k_3 is the half saturation constant where the specific growth rate is half of the maximum specific growth rate. In the absence of herbivory, the rate of change of stem density (density of low quality tissue) is formulated as:

$$\frac{dL}{dt} = r_L(H) - m_L L \quad (8)$$

where m_L is the specific loss rate of stem biomass, i.e., a constant decay rate of ageing stem material. In the absence of herbivory, the rate of change of leaf density (density of high quality tissue) is formulated as:

$$\frac{dH}{dt} = r_H - m_H H \quad (9)$$

where r_H is the specific growth rate of leaf biomass, and m_H is the specific loss rate of leaf biomass, i.e., a constant decay rate of ageing leaves. Note that both the density of high and low quality tissue follows logistic growth. The grass density in the absence of herbivory at equilibrium (where the change in the state variables is zero, i.e., $dL/dt = dH/dt = 0$) is $P^* = H^* + L^*$, so that

$$H^* = \frac{r_H}{m_H} \quad L^* = \frac{r_H r_{Lm}}{m_L (k_3 m_H + r_H)} \quad (10)$$

The herbivore–grass model can now be formulated as:

$$\frac{dL}{dt} = r_L(H) - m_L L - (1 - \rho_H) c(H, L) N \quad (11a)$$

$$\frac{dH}{dt} = r_H - m_H H - \rho_H c(H, L) N \quad (11b)$$

$$\frac{dN}{dt} = (e_H \rho_H + e_L (1 - \rho_H)) c(H, L) N - dN \quad (11c)$$

where ρ_H is the proportion of high quality tissue in the diet of the herbivore and is based on the quality of the available forage. The parameters e_H and e_L are coefficients for the consumption-to-growth conversion for the ingested high and low quality tissue, respectively.

2.4. Analysis of the herbivore–grass model

We analyzed the herbivore–grass model with the conventional functional response (Eq. (1)) as well as with the forage quality-dependent functional response (Eq. (6)) and subsequently contrasted both approaches. In our analyses, we assumed that there is no active selection of high quality forage on the small scale, i.e., that the diet of the herbivores mirrors the local forage quality (so $\rho_H \approx p_H$).

First, the rate of change in the herbivore population (dN/dt , Eq. (11c)) was plotted as function of herbivore density (N) for

a constant density of low and high quality tissue. Second, we plotted the equilibria of the herbivore density and of the densities of low and high quality tissue ($dN/dt = dL/dt = dH/dt = 0$) as a function of the consumption-to-growth conversion coefficient for ingested low quality tissue (e_L). An increase in e_L , with constant e_H , means that the benefit of consuming low quality tissue is increasing. The effect of e_L is relevant since, for example, the magnitude of the difference between e_L and e_H can depend on the herbivore species (Belovsky, 1997). A decrease in the consumption-to-growth conversion coefficient (e_L) can also occur during times of the year when the protein content or digestibility of the ingested low quality tissue decreases. For example, the forage quality of leaves and stems decreases dramatically from the beginning until the end of the wet season, but more so for stems than for leaves (Stobbs, 1973).

Third, by adding another herbivore species (equal to Eq. (11c)) we turned the previously single consumer system into a two-consumer system in which both species have a forage quality-dependent functional response (Eq. (6)). The consumption-to-growth conversion is a function of the digestibility of the ingested forage; these coefficients might differ for differently sized herbivores. Consequently, we assume that the digestibility of low and high quality tissue is higher in large herbivores than in smaller herbivores (Poppi et al., 1981), and it follows that the consumption-to-growth conversion for the ingested low quality tissue (e_L) is higher in large herbivores than in smaller herbivores. We parameterized one herbivore species as being large-bodied and the other as small-bodied. For the large herbivore species, we varied the coefficient for the consumption-to-growth conversion for low quality forage (e_L), and for the small herbivores we varied the consumption-to-growth conversion for high quality forage (e_H). We assume that the consumption-to-growth conversion for the ingested high quality tissue (e_H) is larger in large herbivores than in smaller ones, though the magnitude of this difference is smaller for high quality tissue than for low quality tissue (Demment and Van Soest, 1985). We investigated the effects of the parameter changes on the position of so-called bifurcation sets, i.e., parameter values where the qualitative behaviour of equilibria changes (Edelstein-Keshet, 1988).

3. Results

3.1. Non-linearity in herbivore dynamics: the effect of the maximum specific growth rate of low quality forage (r_{Lm})

In the case of the conventional functional response (Eq. (1)), the rate of change in herbivore density is a unimodal curve where herbivore density is following logistic growth (Fig. 5a–c). Equilibria of the herbivore density are found where the rate of change in herbivore density meets the x-axis ($dN/dt = 0$). Increasing the maximum specific growth rate of low quality forage (r_{Lm}) causes the change of the stable equilibrium of herbivore density from lower to higher values of herbivore density (going from Fig. 5a–c). In the case of the forage quality-dependent functional response (Eq. (6)), a different pattern is observed. When increasing the maximum specific growth

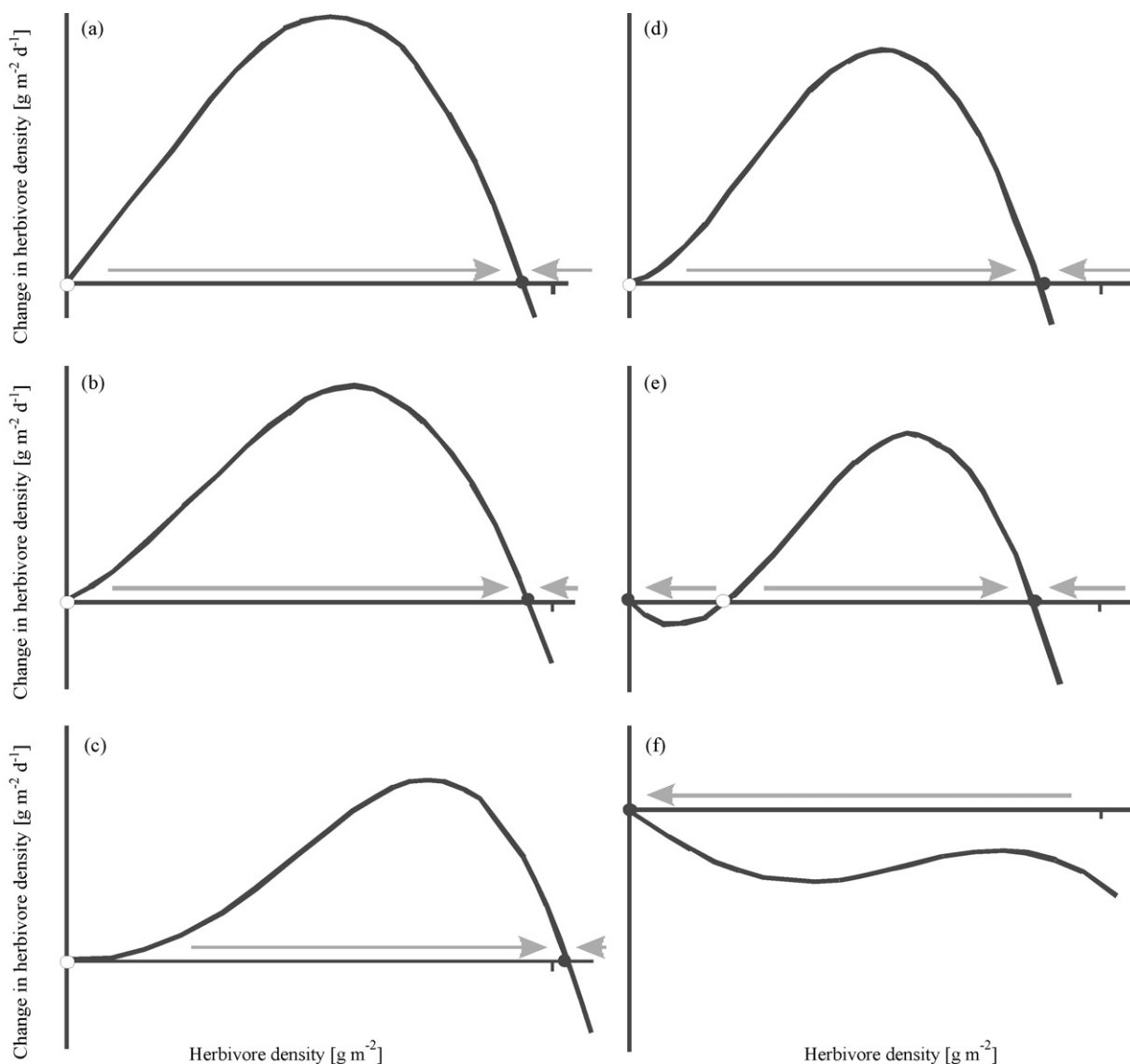


Fig. 5 – The rate of change in herbivore density (dN/dt , Eq. (11c)) as a function of herbivore density (N) for constant densities of low and high quality forage. Filled circles indicate stable equilibria, while open circles indicated unstable equilibria. Arrows indicate the directionality of dynamics. Fig. 5a–c show the rate of change in the herbivore population for a constant maximum consumption rate (Eq. (1)), while Fig. 5d–f show the rate of change in the herbivore population for a forage quality-dependent maximum consumption rate (Eq. (6)). Panels are ranked from top to bottom by increasing maximum growth rate of low quality tissue (stems). Parameter values are (a, d) $r_{Lm} = 0.5$, (b, e) $r_{Lm} = 0.8$ and (c, f) $r_{Lm} = 1.6$. Other parameter values are the same for top to bottom panels: $c_m = 1.0$ (for a–c), $c_{Hm} = 1.0$ and $c_{Lm} = 0.1$ (for d–f), $k_1 = 0.5$, $k_2 = 0.2$, $d = 0.06$, $m_L = 0.1$, $k_3 = 5$, $r_H = 0.9$, $m_H = 0.5$, $e_H = 0.1$, $e_L = 0.05$, $\beta = 100$.

rate of low quality forage (r_{Lm}) from low to intermediate levels, the trivial, unstable equilibrium at zero herbivore density (Fig. 5d) turns into a stable equilibrium and a new unstable equilibrium is formed (Fig. 5e). When herbivore density is below this new unstable equilibrium, herbivore density moves towards $N=0$. Above this threshold of the unstable equilibrium, a stable herbivore density is reached. This behaviour can be explained by the positive feedback between herbivore density and the proportion of high quality forage. When herbivore density is sufficiently high, herbivores can maintain a high proportion of high quality forage in the sward by remov-

ing plenty of grass biomass (both high and low quality forage). This stimulates the re-growth of young leaves and enables a high consumption rate, a situation that is reminiscent of herbivores foraging in grazing lawns (c.f. McNaughton, 1984). When herbivore density is low, though, decreased consumption allows for an accumulation of low quality tissue in the grass sward, i.e., an increase in the proportion of low quality forage with increasing grass biomass. The system then enters into a negative cycle of low herbivore density, decreasing forage quality, and decreasing consumption rate. We interpret this behaviour as a kind of Allee-effect, where low herbivore

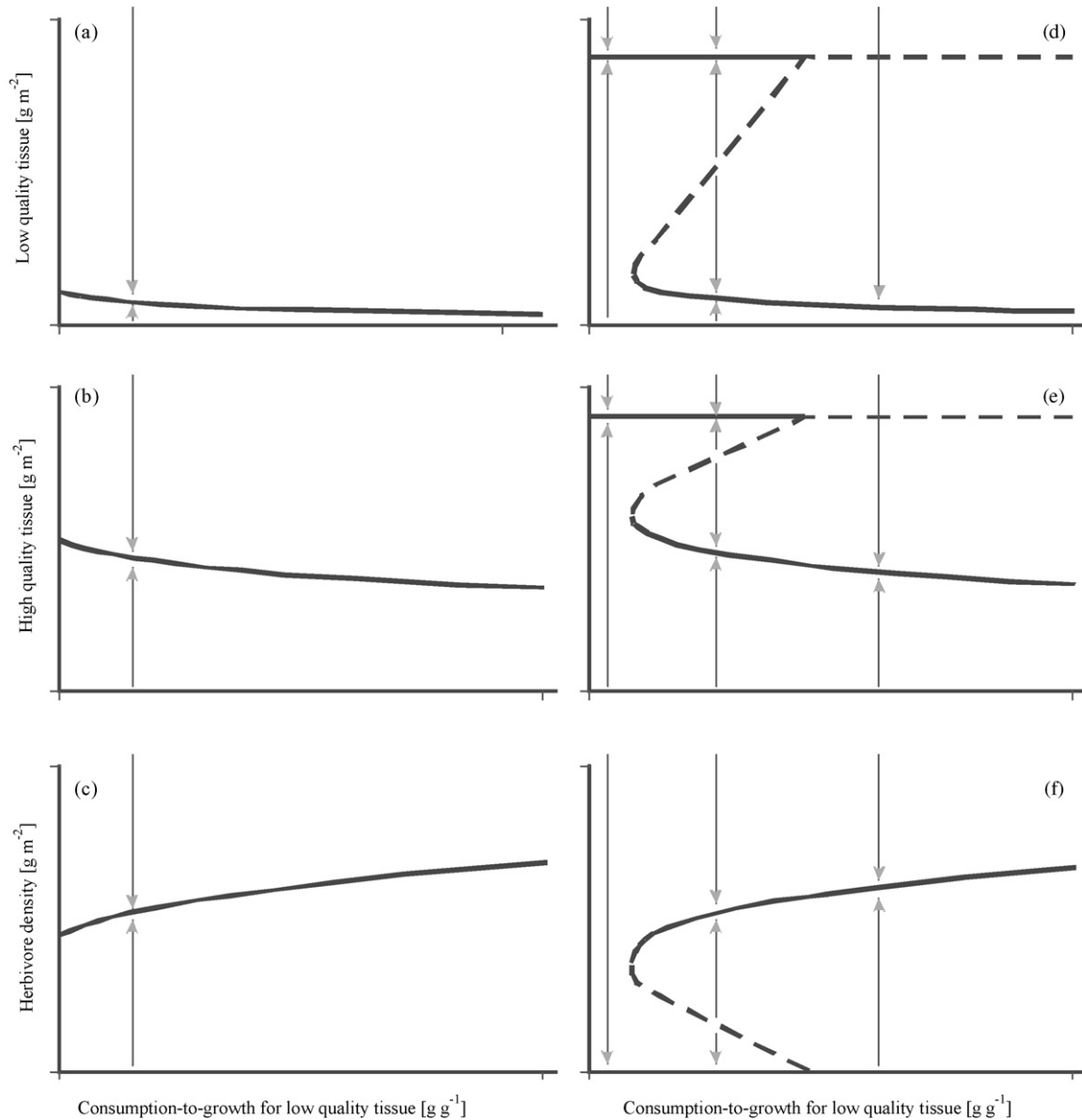


Fig. 6 – Changes in the equilibria of low and high quality forage and the herbivore density as function of the coefficient for the consumption-to-growth conversion for the low quality tissue e_L . Fig. 6a–c show the equilibria when the functional response with constant maximum consumption rate (Eq. (1)) is included. Fig. 6d–f show the equilibria for the system with the functional response with a variable maximum consumption rate (Eq. (6)). Here, the solid lines represent stable equilibria and the dashed lines the unstable equilibria. The arrows indicate the direction of development. The effects of e_L are shown on (a, d) the density of low quality tissue, (b, e) the density of high quality tissue, and (c, f) the density of herbivores. Parameter values are $c_m = 1.0$ (a–c) while $c_{Hm} = 1.0$ and $c_{Lm} = 0.1$ (d–f). Other parameter values are the same for all panels: $k_1 = 0.5$, $k_2 = 0.2$, $k_3 = 5$, $d = 0.06$, $m_L = 0.1$, $m_H = 0.5$, $r_H = 0.9$, $r_{Lm} = 0.5$, $e_H = 0.1$, $\beta = 100$.

densities cannot maintain the forage at high quality forage quality.

When the specific growth rate of low quality forage is increased from intermediate to high (Fig. 5f), the non-trivial stable equilibrium for higher herbivore density disappears, indicating that even high herbivore densities cannot maintain a high proportion of high quality forage in the grass sward. The decreasing forage quality leads to a decrease in consumption rate and ultimately to a local disappearance of the herbivores.

3.2. Non-linearity in herbivore dynamics: the effect of the consumption-to-growth conversion coefficient of low quality forage (e_L)

In the case of the conventional functional response (Eq. (1)), increasing e_L leads to rising herbivore density, since increasing sward biomass benefits the herbivores regardless of sward quality (Fig. 6a–d). In the case of the forage quality-dependent functional response (Eq. (6)), herbivore density shows discon-

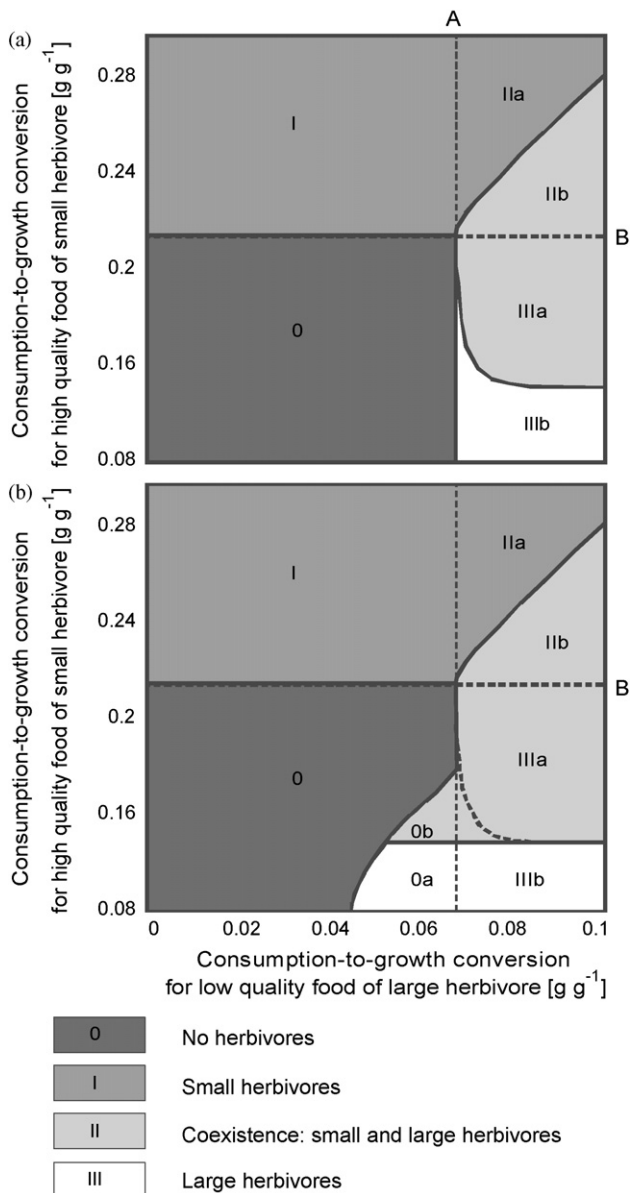


Fig. 7 – Parameter planes of the herbivore–grass model with two herbivore species, one large-bodied and one small-bodied. The investigated parameters are the consumption-to-growth conversion for low quality tissue (e_L) for large herbivores and the consumption-to-growth conversion of high quality forage (e_H) for small herbivores. Panel (a) shows density equilibria (presence or absence) reached from initially low herbivore densities (0.01 for both species), whereas panel (b) shows density equilibria (presence or absence) reached from initially high densities (10.0 for both species). Four regions of the parameter planes can be distinguished (0, I, II and III, separated by broken lines A and B) based on herbivore responses to changes in e_L and e_H in single-species systems. Line A indicates the threshold in e_L below which large herbivores disappear from the single-species system, while line B indicates a similar threshold in e_H for small herbivores. Regions 0, II and III can be further separated into sub-regions a and b, depending on the outcome of species interactions (competitive exclusion, co-existence, or facilitation). See

tinuous changes with changing e_L (Fig. 6f): there is one state without herbivores and another state with a high density of herbivores. For low levels of e_L , the herbivore density is zero. Under these conditions, even the positive effect of a high proportion of high quality forage is not sufficient to sustain a herbivore population. For higher values of e_L , the ingested forage provides sufficient nutritional benefits for herbivores to stay in the local system and they succeed to maintain a high proportion of high quality forage in the grass sward. A real-world example of these effects can be the seasonal change of e_L over time, for example as the quality of the low quality tissue (grass stems) declines with maturation. Under such conditions, herbivores cannot maintain the grass sward in a short “grazing lawn” stage with a high proportion of high quality tissue (leaves) and since the consumption rate is low, herbivore density will decrease and low quality stems will dominate the grass sward (Van der Wal et al., 1998).

3.3. Two herbivore species: competition and facilitation

We identified two parameters that are essential for herbivore species interactions: (1) the consumption-to-growth conversion of low quality forage (e_L) for large herbivores and (2) the consumption-to-growth conversion of high quality forage (e_H) for small herbivores. Depending on the values of these parameters, different types of species interactions emerge ranging from competitive exclusion, over co-existence, to facilitation. As an illustration, initially we divide the ranges of parameter values into four distinct regions (0, I, II, and III, Fig. 7a and b) based on the herbivore responses in single-species systems. Below threshold value A of parameter e_L (regions 0 and I, left of line A, Fig. 7a and b), the nutritional benefits from low quality forage are too low for the existence of large herbivores and they disappear from the system. Below threshold value B of parameter e_H (regions 0 and III, below line B, Fig. 7a and b), the benefits from high quality forage are too low for existence of small herbivores. Consequently, in single-species systems, large herbivores are excluded from region I, small herbivores are excluded from region III, both species are excluded from region 0, and both species can exist in region II. However, when the two species are sympatric, this picture changes and the effects of e_L and e_H interact with the initially densities of the herbivores in determining exclusion or co-existence of the species. We demonstrate the results of these interactions, by investigating the equilibrium densities (presence or absence) of large and small herbivores starting from initially low (0.01 for both species, Fig. 7a) and initially high (10.0 for both species, Fig. 7b) herbivore densities.

First, species interactions lead to exclusion of large herbivores from a part of region II (IIa, Fig. 7a and b). High nutritional benefits from high quality forage for small herbivores that result from high e_H enable them to competitively exclude large herbivores. However, if nutritional benefits from low quality forage for large herbivores that result from high e_L are suffi-

the results section for further explanations. Parameter values: $e_L = 0.0$ for small herbivores and $e_H = 0.1$ for large herbivores, $c_{Hm} = 1.0$, $c_{Lm} = 0.1$, $k_1 = 0.5$, $k_2 = 0.2$, $k_3 = 5$, $d = 0.06$, $m_L = 0.1$, $m_H = 0.5$, $r_H = 0.9$, $r_{Lm} = 1.0$, $\beta = 100$.

ciently high, both species can co-exist (IIb, Fig. 7a and b). These effects do not depend on initial herbivore densities.

Second, existence of small herbivores is facilitated by large herbivores in a part of region III (IIIa, Fig. 7a and b). Here, large herbivores increase the proportion of high quality forage, which is then exploited by small herbivores. This facilitation enables existence of small herbivores under conditions of e_H far below the threshold value B of the single-species system. The size of the parameter region for which large herbivores facilitate the existence of small herbivores increases from a situation with initially low (Fig. 7a) to initially high (Fig. 7b) herbivore densities. Only under the worst conditions (IIIb, Fig. 7a and b), small herbivores are still excluded from region III.

Third, neither small nor large herbivores can exist in region 0 in single-species systems or when the species are sympatric but starting with low initial densities (Fig. 7a). However, when starting with high initial densities (Fig. 7b), large herbivores can alter a forage resources by increasing the proportion of high quality forage and can invade the previously inaccessible resources despite low values of e_L (0a and b, Fig. 7b). Just as in region III, also in region 0 large herbivores facilitate the existence of small herbivores (0b, Fig. 7b), except for a region of lowest e_H (0a, Fig. 7b) from which small herbivores are still excluded.

4. Discussion

We derived an equation for the herbivore instantaneous intake rate depending on forage quality, i.e., the proportion of high quality tissue. Different from previous studies (Fryxell, 1991; Van de Koppel et al., 1996; Bos et al., 2004) we did not a priori assume a depressed consumption rate due to some negative effect of increasing forage mass on forage quality, for example due to digestive constraints (Fryxell et al., 2004). Instead, we are explicit that the instantaneous intake rate depends on the proportion and density of both low and high quality tissue (leaves and stems). A higher density and proportion of leaves increases bite rate and bite size (Illius et al., 1995), which leads to a higher instantaneous intake rate, while the effort to gather a fixed quantity of leaves increases with increasing density of stems in the sward (Drescher et al., 2006). Including our model for the instantaneous intake rate of herbivores in a herbivore–grass model yields alternate stable states under some conditions: one state in which the herbivores maintain a low standing crop and another state with dense vegetation that is unsuitable for herbivore grazing. This agrees with other studies including such a functional response (Van de Koppel et al., 1996). There are alternatives for modeling the numerical response of herbivores (e.g., Illius, 2006), but we believe that another formulation will yield no qualitative differences with our results. The downward deflection of our functional response model is caused by a depression of the maximum intake rate at high densities of low quality tissue due to increasing efforts of gathering and processing of forage parts (Drescher et al., 2006; Benvenuti et al., 2006). Since changes in the density of high and low quality tissue are linked to the growth of the overall forage resource (leaves plus stems), this model gives a more mechanistic explanation for decreasing instantaneous intake rates with increasing

forage mass than has been given so far (Fryxell, 1991; Van de Koppel et al., 1996; Bos et al., 2004). The mechanism that explains this decrease in consumption rate with decreasing proportion of high quality tissue as resource density increases enabled us to make predictions about the effect of body size that regulates consumption rate in our model (Gross et al., 1993; Prins and Olf, 1998). Large-sized animals have higher tolerance for low quality forage and their maximum consumption rate decreases slower with decreasing forage quality than for smaller animals. Therefore, large herbivore consumption rates should remain higher in low quality swards (i.e., with high biomass). This agrees with general observations that large herbivores can be found grazing in swards of high biomass with a relatively low proportion of high quality plant tissue.

These types of simple models require experiments to test their predictions. To test the proposed functional response model, different experiments have been conducted to measure the intake rate as function of grass biomass with varying fractions of leaves and stems (Drescher et al., 2006). Indeed depletion of the intake rate as function of forage quality was found (see also Fig. 2). Moreover, recent experiments with Canada geese (*Branta canadensis*) of different body mass showed that large geese exhibit a monotonically saturating function (type II), whereas smaller geese show a depression of the intake rate at swards with high grass biomass (Heuerman, 2007). Testing the herbivore–grass model is more difficult as it requires a large experimental set up to be followed over long periods of time. Van de Koppel et al. (1996) and Van der Wal et al. (1998) show convincingly that herbivore density decreases on swards with high grass biomass in which low quality stems dominate.

4.1. Co-existence

Our model predicts co-existence of two herbivore species sharing a common resource under a relatively narrow range of conditions. This region is defined by high values for both the conversion coefficients for high quality forage for the small herbivore (e_H) and for the conversion coefficient for low quality forage for the large herbivore (e_L). The surprising result of our work is that opposite to the findings of other studies (e.g., Wilson et al., 1999; Farnsworth et al., 2002; Cromsigt and Olf, 2006), we found that species co-existence is possible without partitioning of the forage resource. Differences in conversion efficiency of low and high quality forage between the two herbivore species seem to provide a nutritional niche sufficient for the co-existence of both species. Our finding is alike to the results of Loladze et al. (2004), who found that co-existence of two consumers foraging on one resource was made possible due to limited uptake of essential nutrients by both species. The region of co-existence found in our study is limited in favour of the small herbivores, because the growth of low quality tissue (stems) depends on the density of high quality tissue (leaves), but not the other way round. Because small herbivores utilize high quality tissue more efficiently than large herbivores, small herbivores increase their density faster than large herbivores and at the same time limit the growth of the low quality tissue, which could be more efficiently utilized by the large herbivores.

4.2. Facilitation

Current models of herbivore resource partitioning assume that species with larger body mass are able to digest lower quality forage than their smaller counterparts (Belovsky, 1997; Prins and Olff, 1998). For the larger herbivores, the benefits of consuming low quality forage are larger than for small-sized herbivores. Our model predicts that when the large herbivore conversion coefficient for low quality forage (e_H) is sufficiently high, large herbivores can invade areas with low forage quality. The indiscriminate consumption of both high and low quality forage by the large herbivore (no diet selection, $\rho_H \approx p_H$) is stimulating the growth of high quality tissue more than that of low quality tissue, thus improving overall forage quality (Edelstein-Keshet, 1986). This process results in swards of sufficiently high forage quality for the persistence of smaller herbivore species with a narrower tolerance for forage quality. It enables the small herbivores to exist under conditions (low e_H) under which they could not exist if they were the only herbivore species and therefore provides a more mechanistic explanation for the often suggested process of facilitation (Arsenault and Owen-Smith, 2002; Farnsworth et al., 2002). A similar result to ours has been found by Farnsworth et al. (2002), who stated that facilitation of small-sized herbivores by large herbivores is possible provided that small herbivores have a larger consumption-to-growth conversion of high quality forage (e_H).

4.3. Differences between our approach and diet choice models

Previous foraging models that included variation in forage quality made use of the diet choice concept (e.g., Fryxell and Lundberg, 1994; Farnsworth et al., 2002). In these models, one forage type is more attractive to the herbivore than another, possibly due to higher nutritional value. Both forage types can occur with different densities and may have different encounter probabilities. In these models, a change in the density of one forage type can lead to sudden changes in the diet of the herbivore. Herbivores, however, take thousands of bites each day, typically covering a wide range of forage types. The profitability of each bite depends on forage type, forage age, and environmental factors such as soil nutrient availability. Information about bite quality is available to the herbivore only with a time-delayed feedback after digestion and integrated over a large number of bites. It seems thus unlikely that herbivores have a detailed knowledge of the nutritional value of individual bites, which they could use to make instantaneous decisions on diet choice (Prins and Olff, 1998). Furthermore, in grass swards, different forage types (high and low quality tissue) are intimately mixed and cannot easily be separated. Hence, the opportunity for diet selection is physically limited and virtually every bite closely resembles the composition of the local grass sward. Consequently, selection for high quality forage is excluded from our model since we assumed that the diet of the herbivore mirrors the locally available forage quality ($\rho_H \approx p_H$). This is not to say that herbivores cannot learn or base foraging decisions on previous experience. However, foraging is a hierarchical process (e.g., Bailey, 1996) with active selection occurring at the

patch scale or higher (Fryxell et al., 2004), while foraging at the micro-scale is mainly governed by the physical properties of the forage resource and the mechanics of forage consumption (Illius et al., 1995). Our model of the forage quality-dependent functional response thus reflects reality more accurately than current models of instantaneous diet choice. Future studies of our forage quality-dependent response as part of the hierarchical foraging process could lead to further improvements of our model.

4.4. Variation in diet quality and spatial scale

Large-sized herbivores have large intake demands and are more efficient in the use of low quality forage than smaller sized herbivores (Belovsky, 1997; Prins and Olff, 1998). Also, large herbivores have larger mouth parts, presumably making plant part selection difficult. For large herbivores, it might therefore neither be possible nor necessary to select a high quality diet from complex grass swards with a mix of low and high quality components. Smaller herbivores, however, that are less tolerant of low forage quality and have lower intake demands, can be expected to strive for a high quality diet. Despite these presumed differences between herbivores of different size, for our analyses we assumed that there is no diet selection by either herbivore species ($\rho_H \approx p_H$). Admittedly, our assumption that $\rho_H \approx p_H$ is a simplification of the real system: in grasslands with pronounced vertical or horizontal heterogeneity, to some degree smaller herbivores might achieve a higher quality diet by selecting parts of the sward strata (horizontally or vertically structured) with higher than average forage quality (Stobbs, 1973), while larger herbivores might achieve a higher quality diet by selecting at larger spatial scales, e.g., at the patch level or landscape level (Fryxell et al., 2004).

Such issues could be addressed, for example by reformulating our herbivore–grass model as a spatially explicit model. With such a model, also the effects of the size of patches of high or low forage quality on herbivore foraging behaviour and dynamics could be investigated. We speculate that small herbivores can tolerate occasional bites of low forage quality without intake reducing effects of digestive limitation. Extended series of only low quality bites, however, might depress diet quality temporarily under a threshold of digestive tolerance. In other words, it is not only important what the average diet quality over a longer time period is, but also how short-term variation in diet quality is temporally distributed. We would expect that, if patch size is limited, small herbivores may be able to tolerate the inclusion of low quality forage patches in their foraging bouts. With increasing patch size, however, forage quality from low quality patches might depress diet quality of whole foraging bouts below the threshold of digestive tolerance. The strength of selection for high quality patches should thus increase with increasing patch size (Wallis DeVries et al., 1999).

4.5. Applicability of our findings to other trophic interactions

We discussed the applicability of our forage quality-dependent functional response to explain the co-existence of herbivores

and the role of facilitation. These findings could help to explain the rich grazer species assemblages, for example in Africa (Prins and Olff, 1998; Arsenaul and Owen-Smith, 2002). Moreover, it helps to understand under what conditions lawn grasses appear and can be maintained (McNaughton, 1984).

The forage quality-dependent functional response (Eq. (6)) gives an explanation for the decrease of consumption rates with decreasing resource quality that is not necessarily linked to resource density. We believe that our findings have applicability to other trophic interactions than the one we studied. In a literature review, we found several examples of predator–prey relationships where the prey population consists of at least two prey types differing in quality with effects for the predator. Reason et al. (1998) reported on the variation in pathogen susceptibility of African armyworm larvae that can be susceptible or resistant types and thus vary in resource quality for the pathogen (White and Wilson, 1999). It was found that the resistant host type could stabilise unstable host–pathogen interactions. Engelmayer (1992) and Czesny et al. (2001) studied the behaviour of piscoid predators and found them foraging less effectively when the proportion of low quality prey increased. Sarma et al. (1998) found that increasing the proportion of high quality prey led to an increased numerical response of a rotifoid predator. Dicke et al. (1990) and Eubanks and Denno (2000) investigated predator–prey relationships in aracoid predators and found that the predator numerical response depended on prey type, though prey preference was related to other characteristics.

The unifying feature of these cases is that the consumer has limited ability to process information about prey quality at the moment of prey capture. We suggest that our perspective has general relevance under conditions that reduce a consumer's ability to make diet choice decisions and can help explaining dynamics and discontinuous changes in many predator–prey relationships, from infectious diseases over carnivorous predators to herbivores.

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