

# The stability of grazing systems revisited: spatial models and the role of heterogeneity

S. SCHWINNING\* and A. J. PARSONS†

\*Department of Biology, University of Utah, Salt Lake City, UT 84112, USA and †AgResearch Grasslands, Private Bag 11008 Palmerston North, New Zealand

## Introduction

In 1975, Noy-Meir presented a comprehensive, graphical stability analysis for plant–herbivore interactions. Inspired by the analysis of predator–prey interactions by Rosenzweig & MacArthur (1963), he cast the model in the form of ordinary differential equations, representing grazing as a homogeneous process in space and continuous in time (Noy-Meir 1975). His analysis demonstrated that a continuously grazed ecosystem may have multiple stable states and may be ‘discontinuously stable’ (see also reviews by May 1977; Tainton, Morris & Hardy 1996). The term implies that the grazing system may move discontinuously from a stable state of high productivity to a stable state of low productivity with only a small increase in grazing pressure or with a minor disturbance. This and other harvesting models (Clark 1981) have provided an important paradigm for bioeconomics, namely, that without change in management, a biological resource can become overexploited and fall into a low-productivity state from which it can recover only through dramatic reduction in harvest rate.

Since Noy-Meir’s (1975) analysis, much progress has been made in refining understanding of the grazing process in temperate grassland. Particularly, advances have been made in understanding grazing at the bite scale (Illius & Gordon 1987; Spalinger & Hobbs 1992; Parsons *et al.* 1994). Domestic ruminants remove a relatively fixed proportion (some 40–70%) of standing vegetation with each bite (Ungar, Genizi & Demment 1991; Laca *et al.* 1992). If ruminants harvested 50% of the standing vegetation uniformly across an entire grazeable area each day, this would exceed the ability of the vegetation to recover from defoliation (the estimated sustainable homogeneous removal rate is 2.5% of standing vegetation per day; Parsons & Chapman 1998). Thus, for a grazing system to be sustainable, grazing must take place from only a small portion of the total grazeable area each day (some 5%; Wade 1991; Parsons & Chapman 1998). This simple calculation illustrates that grazed grassland is necessarily heterogeneous, because at any time, different patches will be in different states of recovery from previous defoliations. As has long been recognized, ‘continuous’ grazing is not a continuous process, but involves a succession of discrete defoliations at the bite scale, each followed by a

variable period of regrowth (Hodgson & Ollerenshaw 1969; Morris 1969; Clark *et al.* 1984). Furthermore, it is not a deterministic process: because animals take bites from only a small part of the total area on any day, there is some uncertainty as to exactly where animals choose to take bites. Thus, when considering grazing at the bite scale, we must deviate from Noy-Meir’s assumptions in three ways: we must assume (1) spatial heterogeneity instead of homogeneity, (2) discrete instead of continuous defoliation and (3) stochasticity instead of determinism.

Below we introduce an implicitly spatial model with these characteristics, where we treat a field as a collection of bite-sized patches but ignore their explicit spatial relationships. We use the model to address the following questions: (1) does a consideration of grazing at the bite scale alter our current understanding of the stability and sustainability of grazing systems and (2) how does spatial heterogeneity and variance in defoliation intervals affect the yield of grazing systems?

## Stability of grazing according to Noy-Meir

Noy-Meir’s (1975) analysis demonstrated that a highly simplified representation of a biological process can still produce complex dynamics. In this case, the analysis suggested that continuously grazed ecosystems may be discontinuously stable. The graphical analysis that led to this insight is represented in Fig. 1. High and low stock densities support only one stable equilibrium vegetation state, but at intermediate stock densities the model allows three equilibria (i.e. states of zero net change; the points of intersection of growth and consumption curves). The two outer points of intersection are stable equilibria. Thus, as the arrows indicate, vegetation states near these equilibria approach them more closely. The intermediate equilibrium is unstable and nearby vegetation states are repelled and then attracted by one of the two stable equilibria.

The existence of two alternative stable equilibria at one stock density has also been called ‘dual stability’ which, in Noy-Meir’s analysis, arises under the following conditions: (1) the consumption function must display non-linearity between zero and the vegetation state that supports the maximal instantaneous rate of

vegetation growth and (2) there exists an ungrazeable plant reserve. These conditions are quite realistic in many grazing systems, notably in temperate zone pastures, and so we concentrate our analysis on this case.

### A bite scale model for grazing

We derive a model to describe the dynamics of bite-sized patches. Variables are summarized in Table 1. Patch state is represented by a single state variable,  $b$ , the vegetation biomass per unit ground area. At the

bite scale, grazing is a discrete process with dynamics governed by instantaneous consumption  $c$  and subsequent plant growth  $g$  in the time  $t_{\text{int}}$  between defoliations:

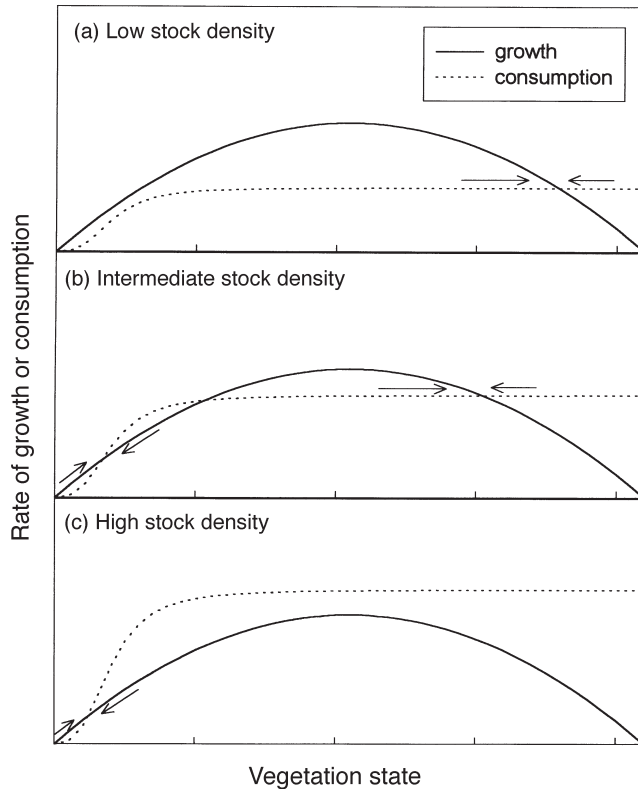
$$b(j+1) = b(j) - c(b(j)) + g(b'(j), t_{\text{int}}), \quad \text{eqn 1}$$

where  $b(j)$  is the biomass *immediately prior* to the  $j$ 'th defoliation and  $b'(j)$  is the biomass *immediately after* the  $j$ 'th defoliation, so:

$$b'(j) = b(j) - c(b(j)). \quad \text{eqn 2}$$

Formulating the grazing process by looking at patch state only once during the interval between defoliations allows us to identify equilibrium conditions, even though it is understood that biomass density in a patch is continually changing. Patch equilibria,  $b^*$ , exist where growth in the interval between defoliations is exactly equal to the amount of biomass removed in each defoliation:

$$g(b^* - c(b^*), t_{\text{int}}) = c(b^*). \quad \text{eqn 3}$$



**Fig. 1.** Stability analysis based on Noy-Meir (1975). Plant growth rates (solid lines) and rates of consumption (dotted lines) as functions of vegetation state. Intersections of the growth and consumption functions mark equilibrium points. The arrows indicate the direction of state change.

**Table 1.** List of variables

Symbol	Meaning	Unit
PATCH-SCALE VARIABLES		
$b$	biomass (dry mass) density just before grazing in patch	$\text{kg m}^{-2}$
$b'$	biomass density just after grazing in a patch	$\text{kg m}^{-2}$
$c$	biomass density removed in one bite	$\text{kg m}^{-2}$
$g$	biomass density increase between defoliations	$\text{kg m}^{-2}$
$m_{\text{bite}}$	biomass per bite	kg
$t_{\text{bite}}$	handling time per bite	s
$t_{\text{int}}$	time in the interval between successive defoliations	days
ANIMAL- OR FIELD-SCALE VARIABLES		
$M_a$	biomass intake per animal per day	kg
$N_a$	number of bites taken per animal per day	—
$T_a$	grazing time per animal per day	s

### DEFOLIATION

The consumption function,  $c$ , describes the biomass that is removed in a single bite. It captures the instantaneous and local functional response of animals to patch state. Herbivores remove variable amounts of foliage in a single bite, but removal tends to be proportional to the amount of standing vegetation (Ungar *et al.* 1991; Laca *et al.* 1992; Edwards *et al.* 1996), although a portion of the biomass may be considered ungrazeable, thus:

$$c = 0 \text{ if } b \leq b_{c,\text{min}} \\ c = f(b - b_{c,\text{min}}) \text{ if } b > b_{c,\text{min}}, \quad \text{eqn 4}$$

where  $b_{c,\text{min}}$  is the ungrazeable portion of the standing biomass (which precludes grazing to extinction). The parameter  $f$  is the fraction of biomass in the grazeable horizon ( $b - b_{c,\text{min}}$ ) that is removed by the grazer in one bite. Default values for all parameters are listed in Table 2 using the example of grazing by young cattle.

### GRAZING INTERVAL (DURATION OF REGROWTH)

In contrast to the consumption function, which captures the instantaneous response of animals to local patch states, the function determining the grazing interval depends on how animals interact with the rest of the pasture. We can envisage the grazing interval as the time taken by animals to repeat the present defoliation of a single patch in all other patches in the pasture, thus, the time taken to return to the first defoliated patch. This return time depends on stock density, intake demand per animal and physical constraints such as handling time per bite. But the relationship is not simple, because animals may encounter patches in variable states and exploit them in variable ways. They may also not graze from

all the other patches before they return and so return times may be variable.

To address this uncertainty, we consider two contrasting alternatives. First we cast grazing at the patch scale as a deterministic process in which all patches are defoliated and when they are in exactly the same state. This case can be seen as equivalent to a systematic, sequential defoliation of a large number of patches. In this way, we can derive equilibrium solutions based on the dynamics of a single patch (equation 3), because by assumption all patches in this case have identical (though time-displaced) dynamics. Second, we assume that animals defoliate patches at random and independent of patch state. To do this we must expand the model to consider many patches simultaneously (we chose 2000). Steady-state solutions for this stochastic model are identified by simulation.

In both the deterministic and stochastic cases, the relationship between handling time per bite,  $t_{\text{bite}}$ , and bite mass,  $m_{\text{bite}}$ , is linear (e.g. Spalinger & Hobbs 1992; Parsons *et al.* 1994):

$$t_{\text{bite}} = t_{\text{preh}} + k_{\text{mast}} m_{\text{bite}}, \quad \text{eqn 5}$$

where  $t_{\text{preh}}$  is the time required to open and close the jaws to prehend a bite and  $k_{\text{mast}}$  is the mastication (chewing) time per unit bite mass. We ignore for now other time-consuming activities associated with foraging.

Bite mass is calculated by multiplying consumption  $c$  from a patch (in units of kg biomass per  $\text{m}^2$ ) with bite (patch) area  $a_{\text{bite}}$ :

$$m_{\text{bite}} = c a_{\text{bite}}. \quad \text{eqn 6}$$

Bite area is considered here to be constant and independent of patch state (Demment, Laca & Greenwood 1987; Ungar & Noy-Meir 1988).

As did Noy-Meir (1975), we assume that animal intake per day is limited either by a maximum grazing time per animal  $T_{\text{a,max}}$  or by the rate of digestion to give a maximum daily intake of mass per animal  $M_{\text{a,max}}$ . Hence, in the *deterministic* case, where all

bites taken are assumed to be of identical size, the number of bites taken per animal per day is:

$$N_{\text{a}} = \frac{M_{\text{a,max}}}{m_{\text{bite}}} \quad \text{if } N_{\text{a}} t_{\text{bite}} < T_{\text{a}}$$

or

$$N_{\text{a}} = \frac{T_{\text{a,max}}}{t_{\text{bite}}} \quad \text{if } N_{\text{a}} m_{\text{bite}} < M_{\text{a}} \quad \text{eqn 7}$$

and the defoliation interval,  $t_{\text{int}}$ , is derived as the time taken for all animals to bite once from all bite-size patches per ha, which is:

$$t_{\text{int}} = \left( N_{\text{a}} \frac{S}{10\,000} a_{\text{bite}} \right)^{-1}, \quad \text{eqn 8}$$

where  $S$  is stock density in animals per ha and 10 000 scales from animals per ha to animals per  $\text{m}^2$ .

In the *stochastic* case,  $m_{\text{bite}}$ ,  $t_{\text{bite}}$  and  $t_{\text{int}}$  are not identical across patches, but depend on random patch selection. We determine their distribution by simulating defoliation in 2000 patches. A daily foraging bout ends when one of two conditions is satisfied:

$$\sum_{j=1}^{N_{\text{a}}} m_{\text{bite},j} \geq M_{\text{a,max}} \frac{S}{10\,000} 2000 a_{\text{bite}}$$

or

$$\sum_{j=1}^{N_{\text{a}}} t_{\text{bite},j} \geq T_{\text{a,max}} \frac{S}{10\,000} 2000 a_{\text{bite}}. \quad \text{eqn 9}$$

#### PLANT GROWTH

We depart from the convention of using a two-parameter logistic equation and use a modified growth function that describes features of growth that have been shown to be important in modelling the response of grass to defoliation (Johnson & Parsons 1985; Parsons, Johnson & Harvey 1988). Briefly, in the logistic equation, the rate of growth is determined solely on the basis of current vegetation biomass. Thus, the function cannot distinguish between a situation where current biomass is the result of a recent lenient defoliation or the result of a severe defoliation that took place some time ago. Yet, observation (Grant *et al.* 1983; Parsons *et al.* 1983, 1988) and leaf-age-structured models (Johnson & Parsons 1985; Parsons *et al.* 1988; Thornley & Johnson 1990) of grass growth suggest that these two situations can produce very different specific growth rates. After lenient defoliation, net growth rate per unit biomass tends to be slow, because much of the standing biomass consists of older leaves, which contribute to a high rate of senescence. After severe defoliation, old and new leaves are almost all removed and so there is a predominance of young leaves in the regrowing vegetation. Thus, when vegetation has recovered to the same biomass as after the lenient defoliation, the rate of senescence is lower and therefore net growth rate per unit biomass is larger.

Leaf-age-structured growth models incorporate the effect of defoliation severity explicitly but here we seek

**Table 2.** List of parameters

Symbol	Meaning	Default value
$a_{\text{bite}}$	bite area	0.004 $\text{m}^2$
$b_{\text{max}}$	maximal biomass density	0.321 $\text{kg m}^{-2}$
$b_{c,\text{min}}$	residual biomass density, animals cannot deplete biomass in patch to less than this	0.0153 $\text{kg m}^{-2}$
$f$	defoliation fraction for grazeable biomass	0.5
$k_{\text{mast}}$	mastication time per unit biomass	2000 $\text{s kg}^{-1}$
$t_{\text{preh}}$	prehension time per bite	0.82 s
$\mu$	maximal relative growth rate	0.1 $\text{day}^{-1}$
$M_{\text{a,max}}$	maximal daily intake per animal	8 kg
$S$	stock density	6 $\text{an ha}^{-1}$
$T_{\text{a,max}}$	maximal daily grazing time per animal	48000 s

Source, Parsons *et al.* (1994); intake parameters set here for young cattle (Penning *et al.* 1997)

a simpler formulation. We introduce a function in which the rate of growth after defoliation depends not only on current patch state  $b$ , but also on the initial condition for regrowth, the patch state  $b'$  just after the last defoliation. The variable  $b'$  modifies the intrinsic rate of growth  $\mu$ :

$$\frac{db}{dt} = \mu b \left(1 - \frac{b'}{b_{\max}}\right) \left(1 - \frac{b}{b_{\max}}\right) \quad \text{eqn 10}$$

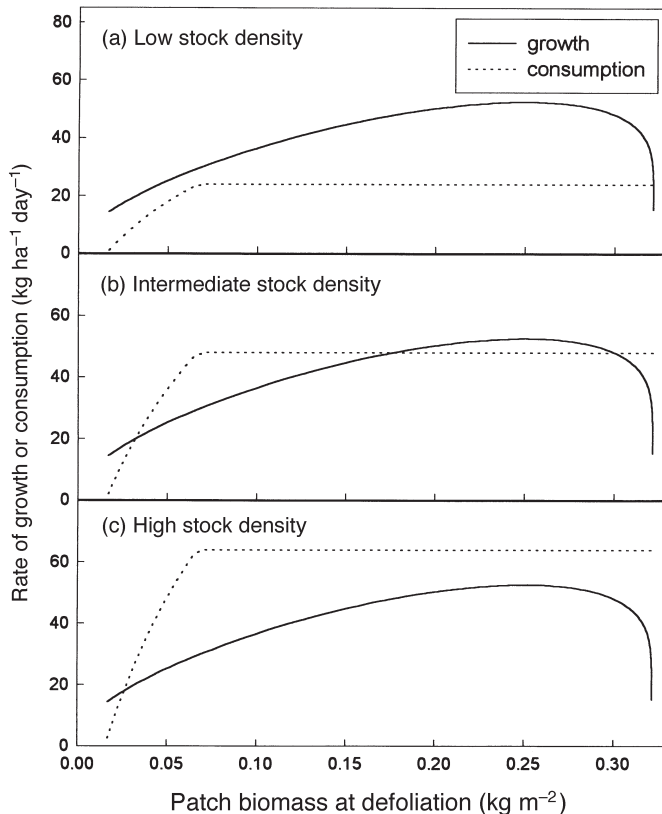
with  $b_{\max}$  as the maximal biomass. When  $b' \ll b_{\max}$  (implying severe defoliation), relative (specific) growth rate is maximal and the function becomes indistinguishable from the logistic equation. Larger values of  $b'$  imply more lenient defoliation and predict lower relative growth rates than the logistic equation.

Because  $b'$  is constant for one growth interval,  $b'$  can be taken to be a parameter and equation 10 can be integrated just like the logistic equation. We can therefore formulate the function for the finite growth increment  $g$  of equation 2:

$$g(b', t_{\text{int}}) = b' \left( \frac{Y}{1 - \frac{b'}{b_{\max}}(1 - Y)} - 1 \right), \quad \text{eqn 11a}$$

where

$$Y = \exp \left( \mu \left(1 - \frac{b'}{b_{\max}}\right) t_{\text{int}} \right). \quad \text{eqn 11b}$$



**Fig. 2.** Stability analysis on the field scale for the discrete patch-based model with deterministic patch selection. Average plant growth rates (solid lines) and average rates of consumption (dotted lines) as functions of patch biomass just prior to defoliation. Intersections mark equilibrium points. The defoliation fraction is set to  $f=1.0$  and stock densities to 3 (a), 6 (b) and 8 (c)  $\text{ha}^{-1}$ . All other parameters are set to default values.

In the stochastic case, defoliation intervals and initial conditions for regrowth vary between patches, so we apply the growth function individually to each of the 2000 patches following each day's defoliations.

## Results

### ANALYSIS OF THE DETERMINISTIC MODEL

We compare the deterministic and stochastic cases to distinguish the effects of discrete patch utilization *per se* from the effects of stochasticity in patch selection. We emphasize, here, that our distinction between determinism and stochasticity applies strictly to the patch scale: at the field scale (on the basis of assuming that a field contains a very large number of patches) both alternatives generate deterministic dynamics.

Figure 2 is the equivalent of Noy-Meir's (1975) graphical analysis (Fig. 1), now based on the deterministic patch model. In the deterministic case we can extrapolate from the patch scale to the field scale, simply by dividing the consumption function  $c$  (equation 4) by the interval  $t_{\text{int}}$  that would allow animals to return to a patch (equation 8) and dividing the growth function  $g$  (equation 11a,b) by the interval that would allow plants to regrow to the biomass just before defoliation. We can do this because, in the deterministic case, any harvested patch is representative of all patches that are harvested at any time. Clearly, the basic phenomena of Noy-Meir's (1975) dual stability model are preserved, in particular, the fact that dual stability arises at intermediate stock densities and when the flat portion of the consumption curve (where the rate of digestion limits intake) intersects the growth curve twice.

Figure 3a shows the patch dynamics corresponding to the region of dual stability in Fig. 2b. The upper equilibrium is characterized by long defoliation intervals (in this example 55 days) and patches that recover to nearly maximum density. The lower equilibrium is characterized by short intervals (8 days) and little recovery. Average biomass densities for the two equilibria are  $0.145 \text{ kg m}^{-2}$  and  $0.023 \text{ kg m}^{-2}$ , respectively. Dual stability implies that, depending on initial conditions, all patches in the field should fall into either one or the other of the two dynamical patterns.

We can now explore parameters of grazing not considered by Noy-Meir (1975). In Fig. 4, we illustrate the effect of the defoliation fraction  $f$  on growth and consumption. In our model, this parameter affects not only consumption but also growth, because our growth function incorporates the effects of grazing severity. In the consumption function, defoliation fraction  $f$  shifts the location of the point, where consumption becomes limited by the rate of digestion (rather than by time) to the right. This 'switch' point is located at the bite mass, where bites are just large enough to satiate animals in the maximal time allotted to grazing. Thus, when bite fractions are smaller,

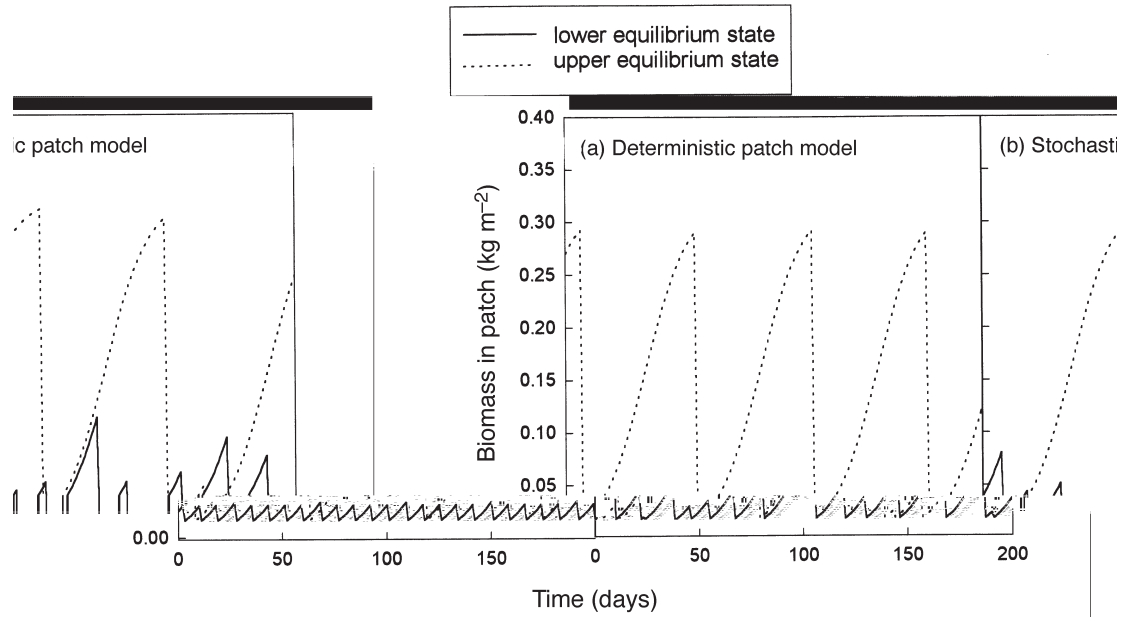


Fig. 3. Examples of patch dynamics in the dual stability domain: (a) for the deterministic patch model with parameter values corresponding to Fig. 2b; (b) for the stochastic patch model with parameter values corresponding to Fig. 5b.

biomass needs to be higher at the switch point. In the growth function, small defoliation fractions move the biomass density that is optimal for regrowth after defoliation to the left. Because  $f$  moves the switch

point of the consumption function and point of optimal growth in opposite directions, conditions for dual stability (i.e. where the flat portion of the consumption function intersects twice with the growth function) become increasingly limited. Indeed, Fig. 4c shows that no dual stability can exist for  $f = 0.2$  at any stock density. One can calculate that dual stability disappears at  $f = 0.4$ , where the optimum of the growth curve coincides with the switch point for animal intake. Thus, while Noy-Meir (1975) noted the significance of this relationship between the growth curve and the consumption curve on stability, we can now associate a mechanism with the phenomenon: dual stability should be impossible if herbivores grazing deterministically take less than about 40% of the standing biomass.

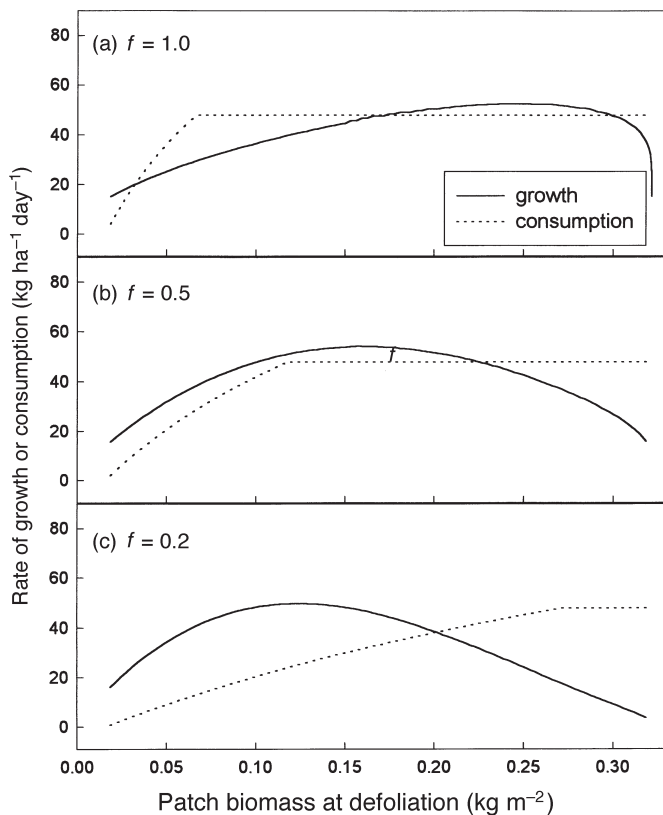


Fig. 4. The effect of defoliation fraction  $f$  on stability. Average plant growth rates (solid lines) and average rates of consumption (dotted lines) as functions of patch biomass just prior to defoliation. Except for  $f$ , all parameters are set to default values

SIMULATION OF RANDOM PATCH SELECTION

Figure 5 is the equivalent of Figs 1 and 2, now for the stochastic case, i.e. assuming random patch selection. The growth curve in this figure was approximated by letting 2000 patches evolve to a steady mean state. Each point on the curve represents a separate simulation with a different number of defoliations per day. The consumption curves are calculated based on the corresponding stationary distributions of patch states.

In the stochastic case, dual stability is found in a much smaller region of parameter space. For example, at  $f = 1.0$ , dual stability exists only for a small range of stock densities between 4.8 and 5.1  $\text{an ha}^{-1}$  and at  $f = 0.5$  it does not exist for any stock density.

The patch scale dynamics associated with dual stability in the stochastic case are illustrated in Fig. 3b. As in the deterministic case, the upper equilibrium

(the average biomass is  $0.130 \text{ kg m}^{-2}$ ) is characterized by longer defoliation intervals (on average, 30 days) and the lower equilibrium ( $0.066 \text{ kg m}^{-2}$ ) by shorter intervals (15 days). Although patch dynamics at these alternative stable states are quite different from one another, total animal intake is actually very similar (see Fig. 5b). In the stochastic case, defoliation intervals at equilibrium have a negative exponential distribution (as they should in a Poisson process) and so a mean to standard-deviation ratio of 1. A negative exponential distribution for defoliation intervals has been observed in sheep-grazed pastures (Edwards 1994), suggesting that it is not unrealistic to assume random patch selection under some conditions.

#### Preference in patch selection

So far, we considered only two extreme forms of patch selection: one where all patches are harvested in exactly the same way and one where patches are selected totally at random. Next, we consider a case where animals exhibit preference for patches of a certain biomass. Preference by large ungulate herbivores for either short (low biomass) or tall (high biomass) grass patches has been observed in experiments

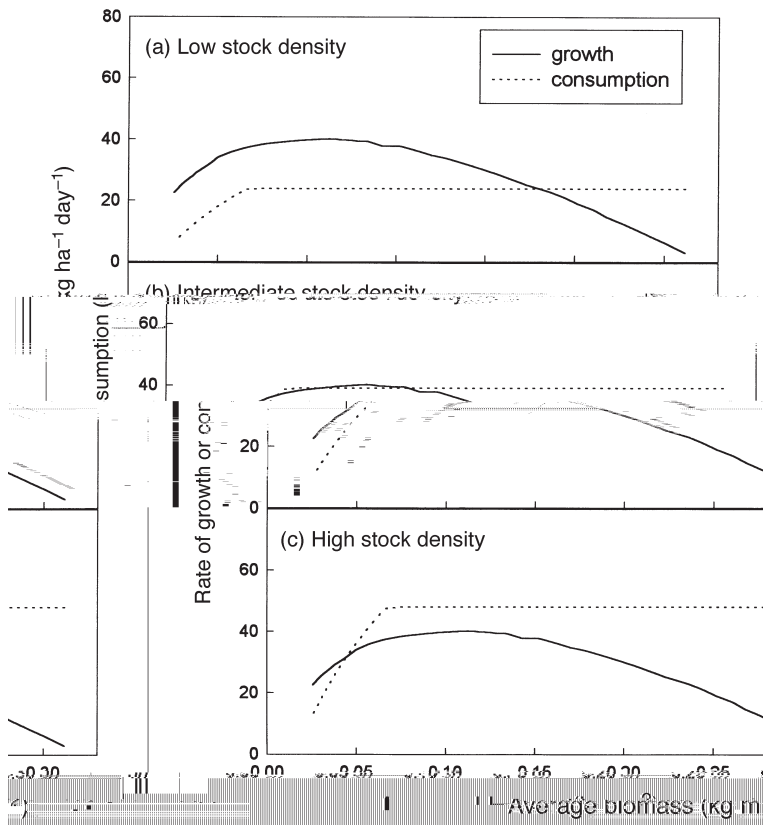
(Harvey & Wadge 1994; Distel *et al.* 1995) and so it is pertinent to consider both possibilities.

To examine the effects of preference, we assume that patch encounter is still random but that patches are rejected with a probability of 80% when they are either above or below a certain biomass threshold. Thus, animals reject patches either if they are above  $0.2 \text{ kg m}^{-2}$  or if they are below  $0.12 \text{ kg m}^{-2}$ . In reality, patch rejection is associated with an additional time cost, one of 'searching' and/or 'lost opportunity' (Spalinger & Hobbs 1992; Parsons *et al.* 1994; Thornley *et al.* 1994). In a model that is not explicitly spatial, we cannot relate search time, for example, with the additional distance travelled by animals. Instead, we associate a fixed time cost with every patch that is encountered and rejected. For the purpose of comparison, we assume that patch rejection is associated either with no additional time cost, or with an additional cost equivalent to  $\frac{1}{2}t_{\text{preh}}$  and  $t_{\text{preh}}$ .

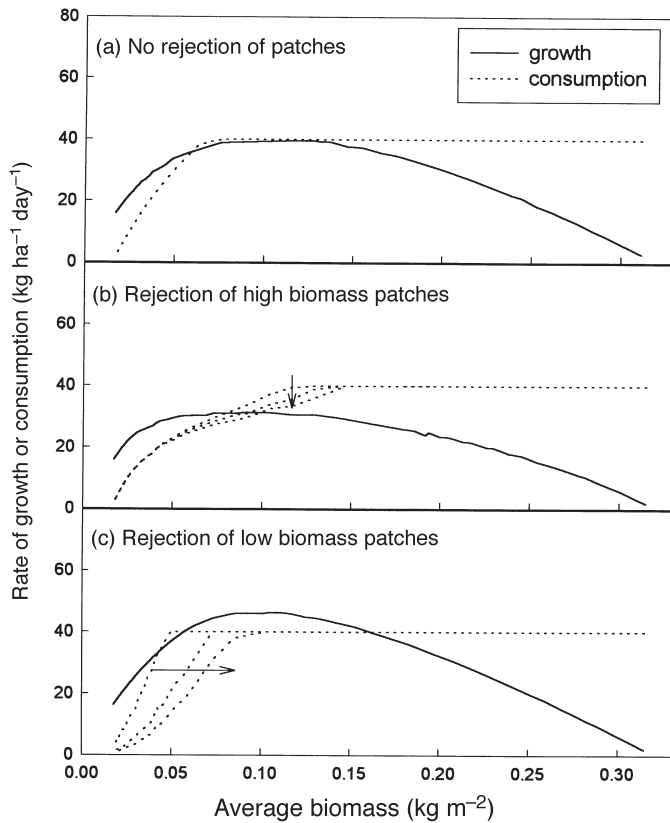
In Fig. 6, we assumed a defoliation fraction of  $f = 1.0$ , to maximize, in this simulation, the amount of biomass variation that animals can respond to. Under these conditions, patch selection has large effects on vegetation growth and animal intake. When animals reject high biomass patches (Fig. 6b), animal intake can be severely reduced compared to a situation when animals do not reject (Fig. 6a). Interestingly, in the steady-state equilibrium, the reduction of animal intake is not so much the result of the additional time cost associated with rejection but owing to the state of the vegetation, which supports less growth. Animals have this negative effect on vegetation growth, because, by rejecting patches above a certain biomass, they (1) allow a larger portion of the field to approach ceiling yield and thus cease to grow and (2) increase the grazing pressure in the remaining portion of the field, which also reduces the rate of regrowth. When animals reject low biomass patches, the effect on the vegetation is opposite (Fig. 6c). The maximal vegetation growth rate is now greater, so that more animals could be supported at a satiating intake level. Compared to animals that do not reject (Fig. 6a), animals also achieve satiation at lower average vegetation biomass, provided the cost of patch rejection is low.

#### DISCONTINUOUS STABILITY REVISITED

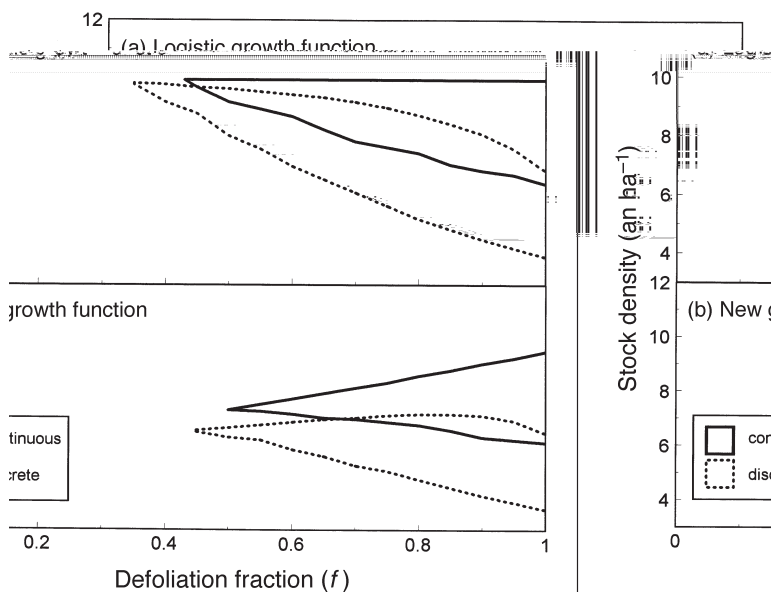
Our analysis of a spatial model suggests that dual (i.e. discontinuous) should not be as common as Noy-Meir's non-spatial analysis suggests. The present model is different from Noy-Meir's model in several aspects: (1) it describes grazing as a discrete (as opposed to continuous) process at the patch scale, (2) it uses a different growth function, which attributes smaller relative growth rates to vegetation after lenient defoliation and (3) it considers stochasticity in patch selection. In Figs 7, 8 and 9 we examine systematically the role of each feature on the dual stability domain.



**Fig. 5.** Stability analysis for the patch-based model with random patch selection. Average plant growth rates (solid lines) and average rates of consumption (dotted lines) are based on steady-state solutions for fixed bite numbers taken at random from 2000 patches and presented as functions of average patch biomass. The defoliation fraction is set to  $f = 1.0$  and stock densities to 3 (a), 4.9 (b) and 6 (c) an  $\text{ha}^{-1}$ . All other parameters are set to default values.



**Fig. 6.** Stability analysis for three cases of preference in patch selection. Average plant growth rates (solid lines) and average rates of consumption (dotted line) are based on steady-state solutions for fixed bite numbers taken from 3000 patches and presented as functions of average patch biomass. The defoliation fraction is set to  $f = 1.0$  and stock density is  $5 \text{ an ha}^{-1}$ . All other parameters are set to default values: (a) no rejection of randomly encountered patches; (b) 80% of all randomly encountered patches above  $0.2 \text{ kg m}^{-2}$  are rejected; (c) 80% of all randomly encountered patches below  $0.12 \text{ kg m}^{-2}$  are rejected. Multiple dotted lines correspond to different costs of rejection and the costs increase in the direction of the arrows (see text for detail).



**Fig. 7.** Dual stability domains for continuous and discrete, deterministic defoliation. The highlighted areas circumscribe parameter domains (in defoliation fraction  $f$  and stock density) that generate dual stability. All other parameters are set to default values.

In Fig. 7, we compare the effect of modelling grazing as a discrete *vs* continuous process *per se* on the dual stability domain. To generate a continuous version of our model, the amount of biomass consumed per day was subtracted uniformly from across all patches, instead of subtracting it only from those patches where bites were taken (this procedure is actually adopted in some grazing models that assume spatial homogeneity, see Woodward 1998). The areas highlighted circumscribe the range of  $f$ -values and stock densities that allow dual stability. Modelling grazing as a discrete process *per se* appears to have little effect on the size of the dual stability domain, but for both growth functions, shifts the dual stability domain towards lower stock densities.

In Fig. 8, we assume defoliation is a discrete process throughout and we now consider the effect of deterministic *vs* stochastic patch selection. For both growth functions, random patch selection greatly reduces the dual stability domain compared to deterministic patch selection and the new growth function has an even smaller dual stability domain than the logistic under random patch selection. Finally, Fig. 9 shows that herbivore selectivity, modelled here as the tendency to reject patches above or below a biomass threshold, can also impact stability. The rejection of high biomass (tall) patches tends to reduce the dual stability domain, while rejection of low biomass (short) patches tends to do the opposite. However, near  $f = 0.5$ , dual stability disappears in all cases.

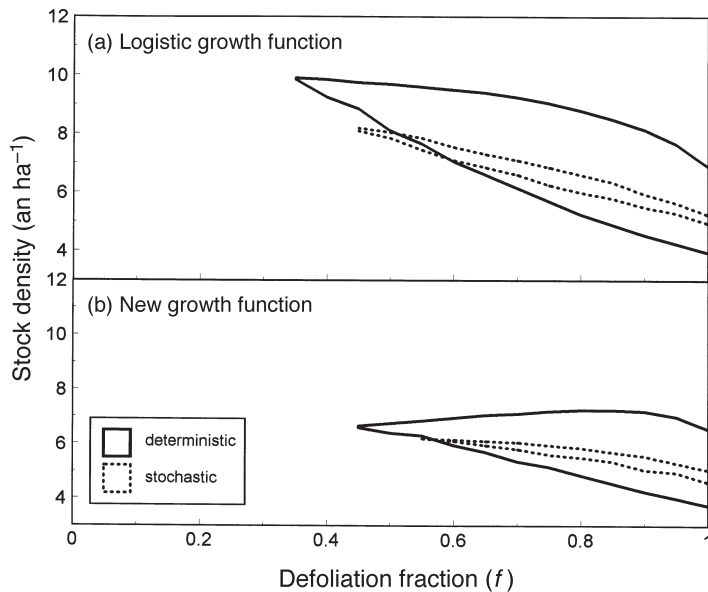
## Discussion

### DUAL STABILITY IN TEMPERATE GRAZED GRASSLANDS

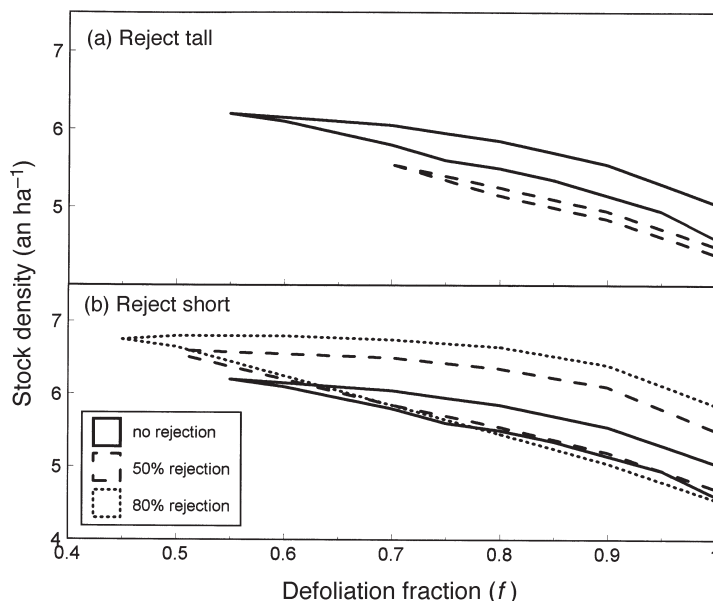
Although both general (Noy-Meir 1975) and more parameterized grazing models for temperate grasslands (e.g. Johnson & Parsons 1985; Parsons, Harvey & Woledge 1991) have supported the expectation that dual stability can arise in grazed systems, empirical evidence for this is sparse and is limited to situations where the cause of the system's discontinuous productivity remains ultimately unexplained (Mott 1960; Paulsen & Ares 1961; Morley 1966; Owen & Ridgman 1968). Seasonal variation in weather means that the grazing system is often in a transient state, i.e. following an equilibrium that shifts with season. This makes it difficult to characterize the stability of a system empirically. However, dual stability remains a serious issue, as it is critical to know whether the system is moving towards a productive or an unproductive state. Variation in weather, like fluctuation in stock density, could precipitate the system's decline towards an unproductive state. As Noy-Meir noted, to recover from an 'overgrazed' state would then require a drastic reduction in stock density across the dual stability region and into the region where there exists only one 'upper equilibrium state'. Production at or near the maximum could be maintained

only 'by very frequent, almost constant, adjustment of stock density in response to fluctuations in vegetation' (Noy-Meir 1975).

We have analysed the dual stability property of a model that was very similar to previous models in its basic assumptions and parameter settings, but that



**Fig. 8.** Dual stability domains for deterministic and random patch selection with discrete defoliation. The highlighted areas circumscribe parameter domains (in defoliation fraction  $f$  and stock density) that support dual stability. All other parameters are set to default values.



**Fig. 9.** Dual stability domains for different cases of preference in patch selection. Patch encounter is random and there is no additional cost associated with patch rejection. The highlighted areas circumscribe parameter domains (in defoliation fraction  $f$  and stock density) that generate dual stability. All other parameters are set to default values: (a) patches above  $0.2 \text{ kg m}^{-2}$  are rejected with probability 0 (no rejection) or 50%. A rejection probability of 80% does not give dual stability; (b) patches below  $0.12 \text{ kg m}^{-2}$  are rejected with probability 0 (no rejection), 50% or 80%.

described grazing as a discrete process at the bite scale. When we made no further assumption about the animal's ability to forage, i.e. when we assumed that animals eat from any patch they encountered and encounter was random with respect to patch condition, we found that dual stability was much less likely (there was a far smaller domain for dual stability) than previous models predicted. This was true whether we used a traditional logistic or the new growth function. Defoliation fractions per bite had to be in excess of 50% of the grazeable biomass for dual stability to occur and even then, it occurred over a much smaller range of stock densities. In addition, the potential effects of dual stability were minor, because the productivity of the two stable equilibria was very similar. Thus, the two equilibria would be virtually indistinguishable in a field situation.

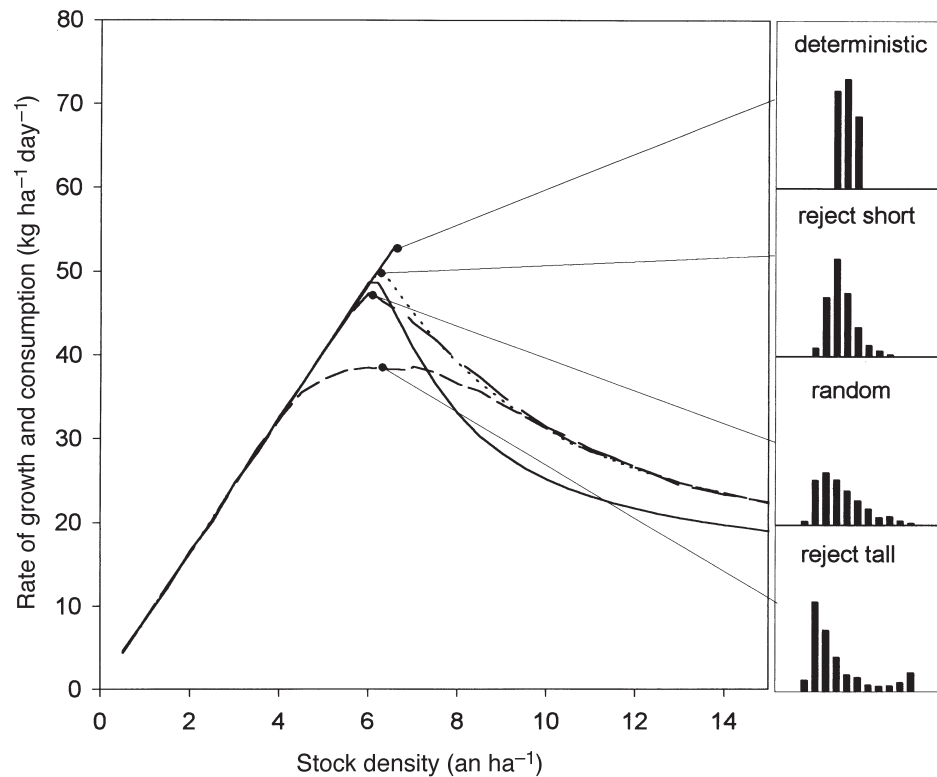
When we assumed that animals exhibit preferences for patches of given states, the result was somewhat different (Fig. 9). Dual stability was *less* likely when animals rejected patches of large biomass, but *more* likely when they rejected patches of low biomass (showed a preference for large biomass areas), provided the time costs of making such choices were low. However, as for random patch selection, dual stability was impossible when the defoliation fraction was 50% or lower. Actual defoliation fractions for large ungulate herbivores have been reported to be in that same region of about 50% (Ungar *et al.* 1991; Laca *et al.* 1992), where, according to our model, dual stability should only be a marginal phenomenon. Thus, we suggest that earlier models, in part by ignoring the stochastic and spatial nature of grazing, over-emphasized the importance of dual stability.

#### THE ROLE OF HETEROGENEITY IN YIELD

We have seen that grazing is fundamentally linked to the generation and maintenance of spatial heterogeneity in pasture. There is a widely held perception that spatial heterogeneity is always deleterious to productivity and this is used to justify a management that maintains spatial homogeneity at all times (e.g. cutting instead of grazing). However, spatial heterogeneity, *per se*, is not deleterious. Consider the case where grazing at the patch scale is deterministic with constant defoliation interval. We can imagine such a grazing process to be replaced by a cutting regime, so that patches, instead of being grazed sequentially, are cut simultaneously at that same defoliation interval. Under grazing, pasture state would be spatially heterogeneous, under cutting it would be spatially homogeneous, but the productivity of the two systems would be exactly equal, because the resulting initial patch states and defoliation intervals were the same.

In Fig. 10, we compare the equilibrium yields (as animal intake) that can be expected under a wide range of stock densities. We also show the biomass





**Fig. 10.** The rates of growth and consumption in the equilibrium as a function of stock density for four selection scenarios: deterministic (solid line), random (long-dashes), 80% rejection of high biomass (tall) patches (dotted line) and 80% rejection probability for low biomass (short) patches (short dashes). The cost of rejection is  $\frac{1}{2}t_{\text{preh}}$ . All other parameters are set to default values.

frequency distributions for patches at optimal stock density, where yield is maximal. In comparing deterministic and random patch selection, we see that random patch selection introduces additional heterogeneity in patch state. Maximal attainable yield is reduced from  $53 \text{ kg ha}^{-1} \text{ day}^{-1}$  under deterministic grazing to  $48 \text{ kg ha}^{-1} \text{ day}^{-1}$  under random patch selection. Part of this loss of yield can be recovered, when animals exhibit a preference for high biomass patches (or reject low biomass patches), possibly by narrowing the variation in patch states around a more productive mean. The theoretical maximal growth rate for the vegetation growth function is  $58 \text{ kg ha}^{-1} \text{ day}^{-1}$  (it occurs when  $b' = 0.049 \text{ kg m}^{-2}$  and  $t_{\text{int}} = 28.2$  days). This comparison illustrates that mechanistic intake constraints, which are the only factors restricting yield in the deterministic case, have as much to do with removing yield from its theoretical optimum as has additional patch heterogeneity imposed by random patch selection. On the other hand, it should also be noted that for most stock densities, random patch selection allows either equal or greater yield than deterministic grazing. Thus, in practice, the uncontrollable and stochastic elements of herbivore grazing should not impose a serious limitation to yield.

Far more deleterious to the maximal attainable yield than random grazing, is a patch selection process that favours patches with low biomass (or, the

rejection of high biomass patches). Although there is a reduced tendency for such a system to have dual stability (two alternative stable states, realized at different times) the system instead has a tendency to generate bimodal frequency distributions and so gives the impression of maintaining two distinct patch populations side by side. This phenomenon has indeed been observed repeatedly in practice in cattle-grazed systems (e.g. Laca *et al.* 1992; Gibb *et al.* 1997; and see 'grazing lawns' phenomenon in rangeland Coughenour 1991). Although preference for low biomass patches is arguably of merit, that is, it may increase the quality of the ingested food, it is also widely recognized as reducing production per ha, because the animals persist on only a fraction of the total grassland resource. The mechanism we propose as being responsible for this phenomenon (rejection of large biomass patches) has not been validated empirically but our model predicts that cattle may in this way divide the pasture into distinct areas, both far removed from optimal conditions. In Gibb *et al.*'s (1997) experiments, increasing cattle stock density increased the size of the frequently grazed area and decreased the size of less frequently grazed area (this was also the case in our simulation). However, populations of 'tall' and 'short' patches were aggregated to form 'tall' and 'short' lawns. This clearly requires that some elements of preference act at scales larger than that of individual bites.

Noy-Meir's analysis of a continuous, non-spatial grazing model posed an important hypothesis for managing grazing systems. His analysis suggested that, to maximize yield (i.e. animal intake per ha) in grazing systems, stock density has to be set to the highest value that still supports the upper equilibrium state (all animals are satiated, or nearly so). However, this strategy was also seen to be associated with a large risk of 'falling off' the upper equilibrium state and onto the lower equilibrium state by passing (possibly after slight decline in vegetation growth) through the boundary of the two respective basins of attraction. Thus, the optimal way to manage a grazing system appeared to be a compromise between maximizing yield and minimizing the risk of overgrazing.

Our analysis comes to a different conclusion. For any stock density, when the defoliation fraction is at or less than 50%, there is only one stable mean pasture state (i.e. the stationary spatial average of continuously changing patches), and therefore, any marginal change in stock density leads to a corresponding marginal change in yield. Thus, there should not be any apparently spontaneous transition to overgrazed conditions or failure to recover from an overgrazed state without stock reduction, and a strategy to avoid overgrazing by operating below the optimum for vegetation growth would no longer be a priority.

What remains to be a management concern is the optimization of pasture growth itself. We did not find evidence from our study that any particular defoliation fraction optimizes intake. However, we did find a close interaction between foraging behaviour and vegetation growth. In all aspects of foraging behaviour that we considered here, we found a notable effect on pasture state and growth. There are many detailed and spatial analyses of foraging (Stephens & Krebs 1986; Farnsworth & Illius 1998; Grunbaum 1998), which take the costs of different foraging strategies into account, but these include less detailed descriptions of the effects of foraging strategy on resource regeneration. Progress now requires a spatially *explicit* account of grazing that combines the principles established in this paper with developments in optimal foraging theory.

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