# The role of animal decisions in the development of vegetation mosaics

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## Abstract

A model of herbivore foraging in mosaic landscapes, which seeks to explain how individual decisions of foraging herbivores affect the composition and spatial arrangement of that environment, is described. Animals choose where to forage depending on their perception of the scale of information and the degree of determinism in their foraging decisions. The quality of the vegetation, expressed in terms of potential net energy intake rate, is determined by the patterns of vegetation growth, the animals' intake rate and the digestibility of the vegetation. In situations where the net energy intake rate first increases and then declines, a grazing lawn with utilised and non-utilised areas can develop when animals are selective in their foraging behaviour. The results indicate that herbivore behavioural ecology needs to be considered alongside stocking density in the management of vegetation mosaics. The current model can be developed to take into account the details of multi-species interactions with heather-grass mosaics.

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## Introduction

Some systems are characterised by our ability to build comparatively simple models to predict their behaviour. If we know their initial state and what processes are occurring, we will be able to predict their state subsequently. The spread of an inkblot on a piece of chromatography paper is such a system. Our knowledge of the capillary flow of the solvent on the paper and the adhesion of the dyes to the paper enable us to explain mechanistically what is happening, and the process is repeatable and predictable. We can think of these systems as predictable or 'linear'. On the other hand, the formation of snowflakes by sublimation inside clouds is an example of a process, which is not generally predictable (it can be described as non-linear). Although the nature of the processes is generally understood, and some general observations can be made, it is not possible to predict what a single flake will look like.

Vegetation mosaics fall into the same category. We understand the principles of how plant growth and senescence processes control the biomass and nutritional value of a patch of vegetation, and we know what vegetation herbivores prefer. However, optimal foraging theory cannot explain the development of the spatial structure of mosaics: for example the assumption that herbivores always choose the best patch irrespective of location (e.g. Fretwell & Lucas 1969) does not seem valid in a complex mosaic (Moen *et al.* 1997; Farnsworth & Beecham 1999.). Even though we cannot predict the precise effects of foraging on composition and pattern of a mosaic, there are a number of aspects of mosaics about which it would be useful to have knowledge:

a) What is the characteristic scale of the mosaic and what would its variogram be?

b) What is the degree of determinism in how landscapes might evolve?

c) Are changes in the spatial structure of the landscape, resulting from changing the grazing pressure, reversible?

d) How stable are the characteristic features of a landscape with respect to small changes in stocking density?

There are a variety of mosaic landscape types. At one extreme there lies mosaics of different tree species and clear patches within forests, which have been explicitly modelled to take account of growth, succession and tree death caused by wind, fire and disease (Huston 1992, Hendry & McGlade 1995). Forest mosaics often have a fractal structure. In grazed open-ground ecosystems two common mosaics are grass-grass mosaics, such as *Nardus stricta* clumps occurring within non-tussock grasses, such as *Agrostis* and *Festuca* spp. and shrub-grass, such as *Calluna vulgaris* (heather) – grass (*Agrostis* and *Festuca* spp.) mosaics.

However, there are no spatially explicit models of these systems that use animal behaviour models to explain how an initially homogeneous landscape can become a mosaic. However, a hypothesis concerning grazing lawns put forward by McNaughton (1984) states that, when the nutritional quality of vegetation declines with the age of the plant, and there are insufficient animals to fully graze an area before this deterioration occurs, animals will restrict their grazing to only part of the landscape, leaving other parts ungrazed. Without a spatially explicit mechanistic model, however, we cannot answer the kinds of questions asked above.

## The HOOFS system

The HOOFS system (Hierarchical Object Orientated Foraging Simulator) (Beecham & Farnsworth 1998, Farnsworth & Beecham 1999) provides a flexible framework for exploring the theory of how animals forage in heterogeneous environments. The object-orientated design means that it is possible to build up scenarios from a number of alterable and interchangeable elements. The components can be grouped into three main kinds or ‘layers’.

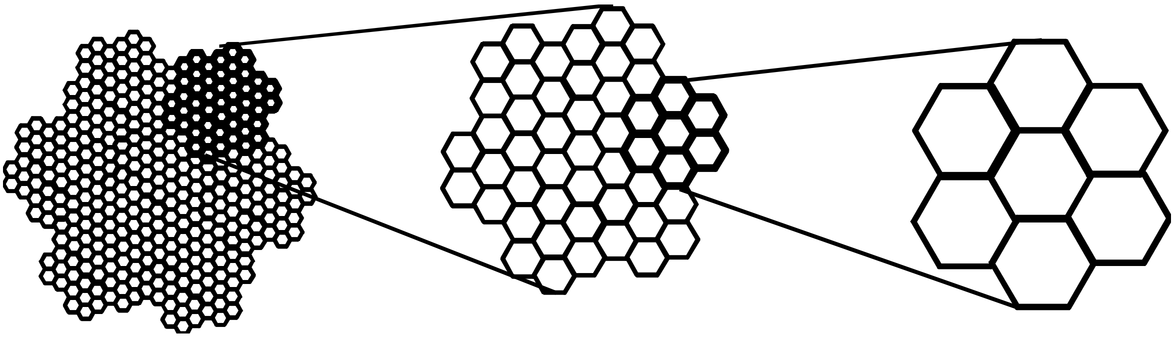

**Figure 1** Hierarchical organisation of groups of seven patches into super-patches and groups of seven super-patches into higher order super-patches.

In the model the landscape has a multi-scale hierarchical structure: the structure consists of a hexagonal array of patches (Fig. 1). The patches are grouped in such a way that seven of these patches form a group of patches known as a first order super-patch. The first order super-patches can themselves be grouped into groups of seven to form a second order super-patch and so on until the desired landscape size is reached. One feature of the model which results from its object-orientated design is the ability for any order of patch or super-patch to be perceived in the same way by an animal, and this allows an animal to perceive a landscape at several levels simultaneously. An animal standing on an arbitrary patch will have a set of 6 patch neighbours with perceived quality, $Q_{0,1}$ to $Q_{0,6}$ respectively, and then 6 super-patch neighbours, $Q_{1,1}$ to $Q_{1,6}$, and so on. The $Q$ values for the individual patches can be calculated from patch-specific state variables. In the following examples $Q$ is taken to be equivalent to the rate of net energy intake, but is more generally the goal for which animals are supposed to be optimising their foraging behaviour, so might also include optimisation for social spacing or for micronutrient intake. In this paper it will be determined by plant growth and herbage consumption as the animals forage.

At the core of the model lies the animal-decision layer. Every animal is modelled as an autonomous agent foraging in the environment. An animal may choose to move to one of the six patch neighbours. The probability of moving to neighbour $i$ is given by Equation 1. The $A_j$ terms are a set of constants which correct for the fact that the patches and successive super-patches have different rotational alignments.

$$p_i = \frac{\sum_{j=0}^{4} 7^{mj/2}\left(A_j Q_{ji} + \left(1 - A_j\right)Q_{j(i+1)}\right)^b}{\sum_{j=0}^{4} 7^{mj/2} \sum_{i=1}^{6}\left(A_j Q_{ji} + \left(1 - A_j\right)Q_{j(i+1)}\right)^b} \qquad \textbf{(1)}$$

The probability of choosing patch $i$ ($p_i$) is dependent on the values of $Q$ for all the patches and super-patches the animal perceives and is modified by exponents $b$ and $m$. $b$ determines the degree of determinism. When $b=0$, patch choice is random. As $b$ approaches infinity, patch choice becomes more deterministic with the animal choosing the best available choice of patch and super-patch. The parameter, $m$, determines the extent to which the choice is weighted towards nearest neighbour patches or towards further away patches. A value of $-\infty$ means that the choice is based only on neighbouring patches, whereas a value of 0 implies that all levels in the hierarchy are given the same weighting of choice. The other decision that animals make is when to leave a patch. Using a marginal value calculation, it is possible to develop a model which describes how intake rate declines with grazing time on the patch in order to predict when animals will leave a patch. This calculation is simplified by assuming that animals graze patches down to a fixed level at a constant rate of intake.

The final layer is the set of functional relationships that describe, amongst other things, the plant biomass production and intake rate. From the point of view of the McNaughton hypothesis the most important relationship is that between plant biomass and the value of $Q$.

Plant growth is governed by a sigmoid function (Birch, in press) (Eq. 2). The curve is similar to the logistic curve. The maximum growth rate is determined by $r$ and the maximum biomass determined by $K$, with a further parameter, $c$, determining the biomass at which maximum growth occurs. Biomass is indicated by $y$. Setting $c=3$, gives the growth curve shown in Fig 2.

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \frac{ry(K - y)}{K - y + cy} \qquad \textbf{(2)}$$

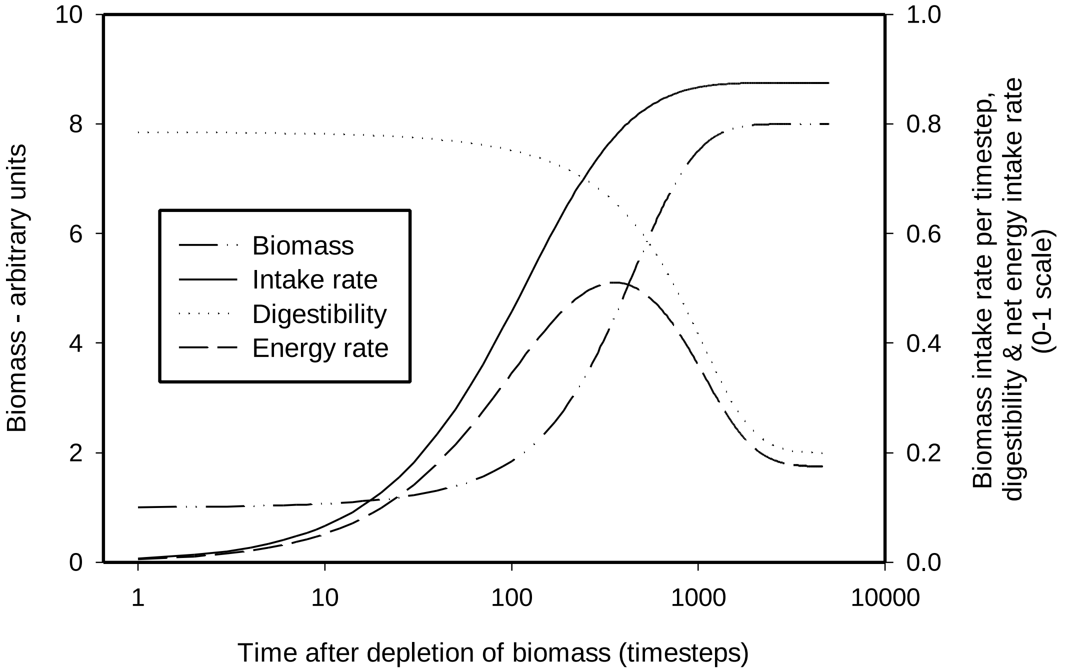

**Figure 2** Derivation of the time since depletion to intake rate of energy relationship from vegetation growth, biomass intake and digestibility relationships.

When a patch is being grazed by an animal, the rate of change of biomass, ignoring growth, is given by Equation 3. Intake rate, of biomass, *I*, is simply – *dy/dt*.

$$I = -\frac{dy}{dt} = \frac{(y-h)}{t_s + (y-h)/i} \qquad \textbf{(3)}$$

This relationship, previously described as a type 2 functional response (Holling 1959), is an asymptotic relationship where there is a fixed time of movement or searching, $t_s$, and a maximum rate of intake, *i*, proportional to the amount of food. The patch is grazed down to biomass *h*.

If we assume that *Q* is proportional to the intake rate of net energy available, *Q* is a function of biomass and digestibility. As a simplification, we will consider digestibility, *D*, to be net energy per unit biomass (Eq. 4). Under the McNaughton hypothesis, digestibility decreases with time. We have used a logistic curve to describe how *D* remains high for a period of time then drops as a result of senescence, lignification or, eventually, succession as invasion by less digestible species occurs (Eq. 5),

$$Q = ID \qquad \textbf{(4)}$$

$$D = 1 - \frac{1-b}{1+e^{(-at+at_m)}} \qquad \textbf{(5)}$$

where *b* is the digestibility of infinitely old vegetation, $t_m$ is the time at which the digestibility is midway between 1 and *b*, and *a* is the decay rate for the digestibility of the vegetation. Figure 3 shows different functions for how *Q* varies over time with different assumptions for *a*, *r* and *b*. These hump-shaped time-energy curves have been shown to lead to two-state stability of grazed ecosystems (Prins 1996; Van de Koppel *et al.* 1996), but no model has examined these in the context of the relationship between spatial organisation of vegetation and the animals' search strategy.

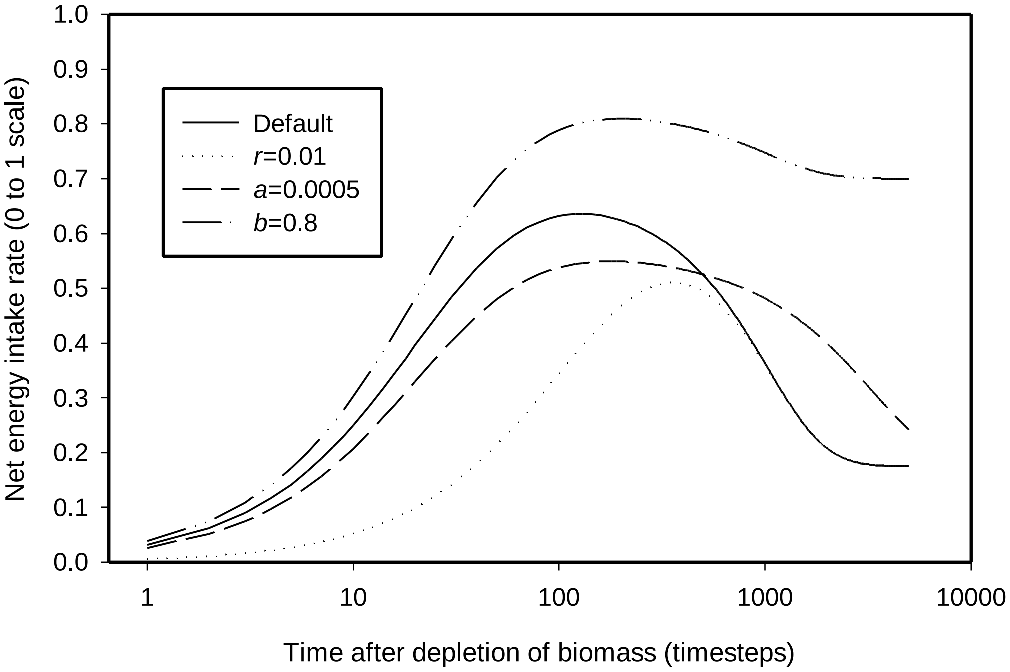

**Figure 3** How net energy intake rate varies with time. Depending on values for rate of growth, *r*, rate of decline of digestibility, *a*, and digestibility of material of age ∞, *b*. In default case *r*=0.06, *a*=0.002 and *b*=0.2.

## Simulation results

Three variables were altered in the simulations. The rate of decay of vegetation quality (*a* in Eq. 5) was varied between 0 (no decline in quality) and 0.002. The degree of determinism, b in Eq. 1, was varied between 0 (random) and 3. The parameter m in Eq. 1 was varied between –2.0 and 0. Other parameters were as follows: *K*=8, *c*=3, *b*=0.2, $t_s$=1, *i*=1, *h*=1, $t_m$=500. There were 10 animals foraging the landscape, made up of 2401 patches, for 15000 timesteps. A timestep is the time an animal needs to forage in a patch of biomass *h*. Three alternative strategies for foraging with *a*=0.002 were examined: 1) Random foraging, b =0 2) Choice of patch biased towards neighbouring patches, b =3 and m =-2.0, 3) Choice of patch uses long-range information, b =3 and m =0. A further scenario (4) was investigated where there was no decline in vegetation quality, *a*=0, b =3, m =-2.0.

It can be seen that the patterns of time since last grazing a patch, resulting from these three strategies are very different (Fig. 4). In scenario 1 there is a random pattern of different ages of vegetation with no clear structure. Paths where animals had recently depleted vegetation can be seen. Only at the edges of the landscape are there patches of vegetation which have not been grazed for a long time and where plant succession could occur. In scenario 2 an irregularly shaped grazing lawn has formed. Because the animal decisions are only determined by the age of neighbouring patches the patch choice is arbitrary, with respect to long-range information. As time increases, parts of the landscape have gradually been lost to older vegetation, but in a way which is non-deterministic. In scenario 3 the avoidance of general areas of older vegetation and the favouring of previously grazed vegetation has resulted in a stable lawn in the centre of the landscape with a very rapid transition from favoured to unfavoured patches. In scenario 4 patches with older vegetation are favoured over patches with vegetation which has been recently grazed, resulting in most of the landscape being grazed fairly frequently.

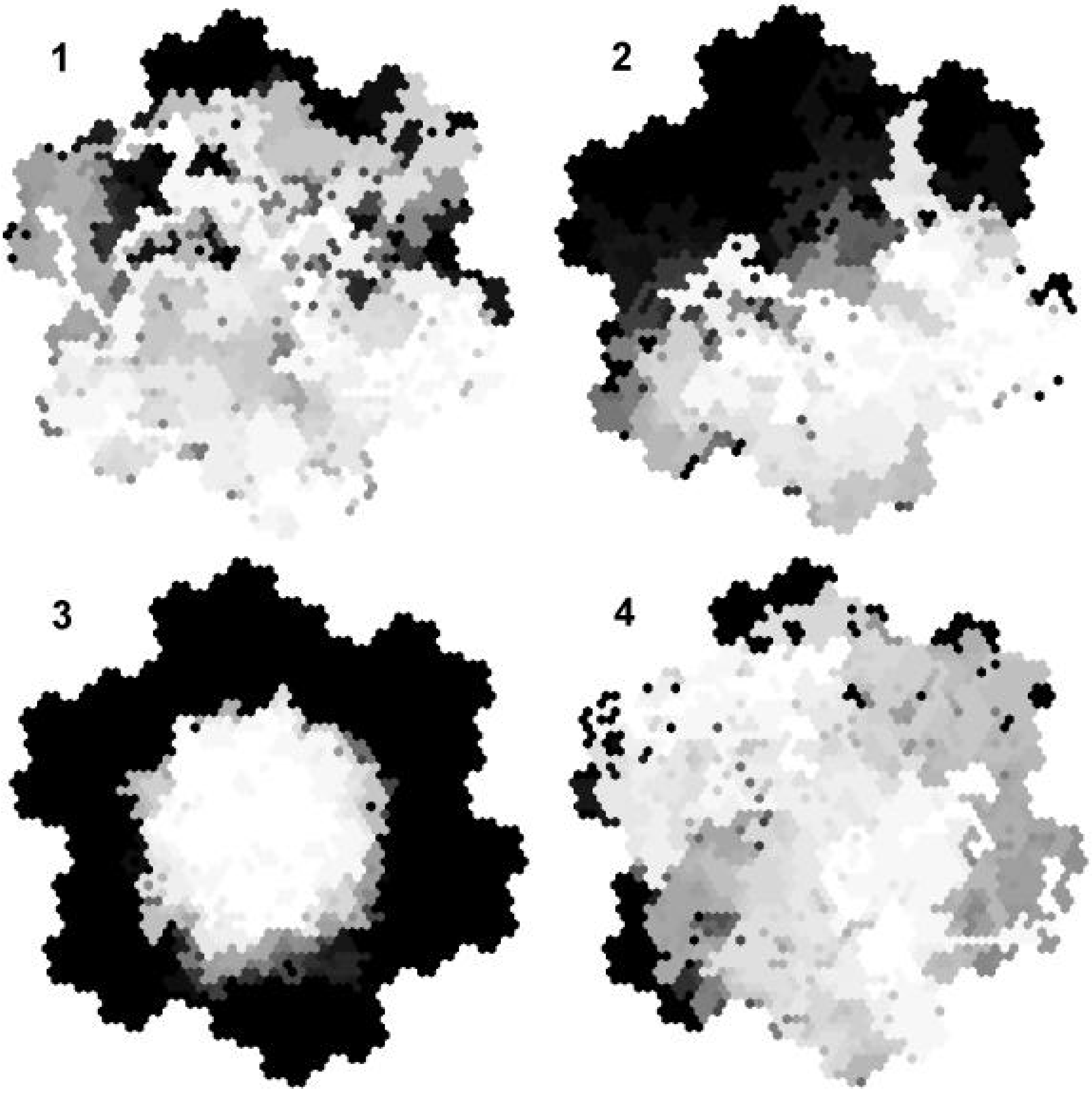

**Figure 4** Patterns of vegetation age (oldest vegetation is darkest) for four landscapes under four scenarios. 1) $b$ =0; 2) $b$ =3, $m$ =-2 & $a$=0.002; 3) $b$ =3,$m$ =0 & $a$=0.002; 4) $b$ =3,$m$ =-2 & $a$=0.

The same effects can be seen in the histogram of age of vegetation (Fig. 5). In scenarios 1 and 4, most of the vegetation is recently grazed. There is less chance of vegetation surviving to be $\geq$10000 units old if the tallest vegetation is actively being sought out and this is reflected in a lower proportion of vegetation in the intermediate age classes in scenario 4. The strong bimodality in vegetation ages resulting from grazing lawn formation is very apparent in scenarios 3 and 4. Because the edge of the lawn is sharper when long range information is used in decision making, the proportion of vegetation in intermediate classes in scenario 3 is particularly low.

The effects of these parameters on the rate of net energy intake by the grazing animals is shown in Table 1. Where vegetation quality is maintained (scenario 4) actively choosing a patch results in a higher overall level of intake than from random patch choice.

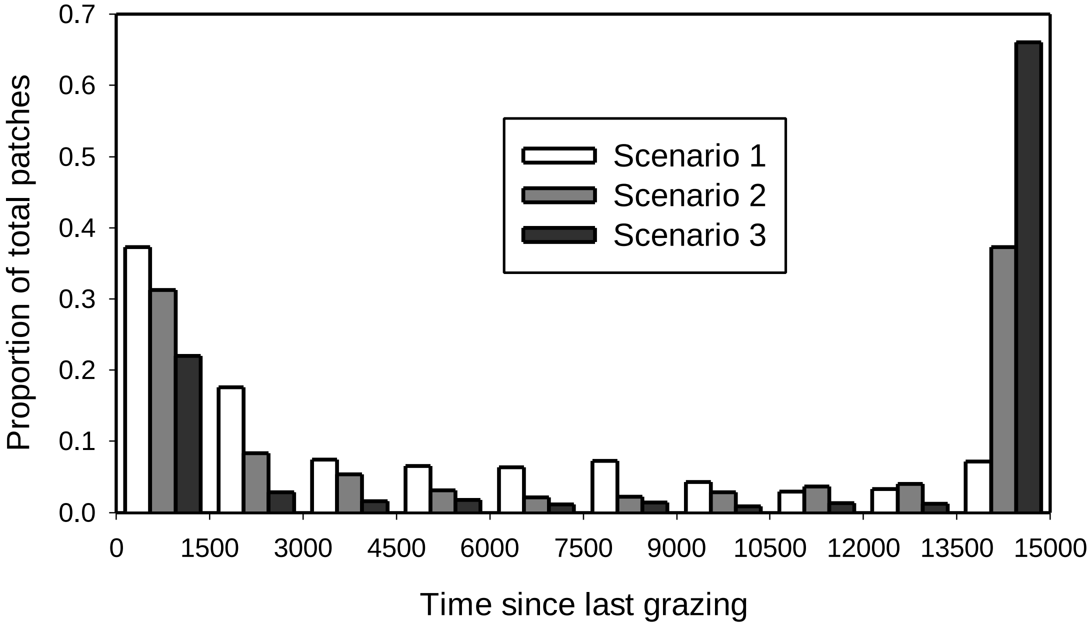

**Figure 5** Histogram of vegetation age (oldest to youngest) for the four scenarios in Figure 4.

On the other hand, if time - net energy intake relationship is hump-shaped (scenarios 2 and 3) the overall net energy intake rate for animals that actively choose patches is lower than in a purely random scenario. This is particularly so for scenario 3 where long range information is used. There is a conflict between the best strategy for the individual and the group. The individual gains a competitive advantage by finding the best patch available. The group may perform better by choosing patches to maintain high digestibility of vegetation in the future.

| Scenario | Parameters | Net energy intake |
|---|---|---|
| 1 | $b$=0 | 0.57 |
| 2 | $b$=3, $m$=-2 & $a$=0.002 | 0.50 |
| 3 | $b$=3, $m$=0 & $a$=0.002 | 0.20 |
| 4 | $b$=3, $m$=-2 & $a$=0 | 0.67 |

**Table 1**: Long term mean net energy intake for 10 animals foraging, comparing four different scenarios for $b$, $m$ and $a$.

## Discussion

If we consider the relationship between net energy intake rate and time (Fig 6) and consider a model where the animal always chooses the best available patch (optimal foraging), there will always be an optimal point of depletion. When stocking density is high, the time taken for all animals to use up the vegetation is less than the time for vegetation to reach its maximum quality: the whole landscape is used, depletion occurs at a constant biomass and fixed time $t_1$, $Q_1$. As stocking density is reduced, the time for an animal to revisit a previously grazed patch, $t$, increases, until it reaches $t_{\mathrm{opt}}$, which is the point at which net energy intake is maximal, defined as $Q_{\mathrm{opt}}$. At lower densities still, animals will prefer more recently depleted vegetation of quality $Q_{\mathrm{opt}}$, to the least recently depleted vegetation. Depletion will still occur at $t_{\mathrm{opt}}$, but a fraction of the vegetation will be left for longer than this, becoming less and less preferred, so that a grazing lawn is formed. Stocking density will determine the proportion of vegetation that is in the grazed part of the landscape.

Now let us consider the more realistic case when stocking density is low, but there is a degree of randomness in patch choice such that $t$ is distributed around $t_{\text{opt}}$. We can describe a probability distribution, shown on Fig. 6 by probability isoclines, around $t_{\text{opt}}$ and $Q_{\text{opt}}$ to indicate this. The probability of being selected declines as a patch ages beyond $t_{\text{opt}}$ so that some patches which are not grazed at or before $t_{\text{opt}}$ will escape grazing altogether. This means that, even when there is exactly enough vegetation in the lawn to sustain the population of animals with depletion at $t_{\text{opt}}$, some vegetation will be lost from the lawn. The average time of depletion will drop below $t_{\text{opt}}$, to $t_a$. If a patch is not grazed, its quality increases and so will its probability of being eaten. As $t_a$ becomes lower through the process of stochastic loss of grazing lawn, the rate at which vegetation becomes older than $t_{\text{opt}}$ decreases. Also, the probability of older vegetation being grazed increases as $Q_a$ becomes closer to $Q_{final}$, the net energy intake rate obtainable from the oldest vegetation. Eventually an equilibrium between loss and gain of lawn will occur, but at a value of $Q$ below $Q_{\text{opt}}$.

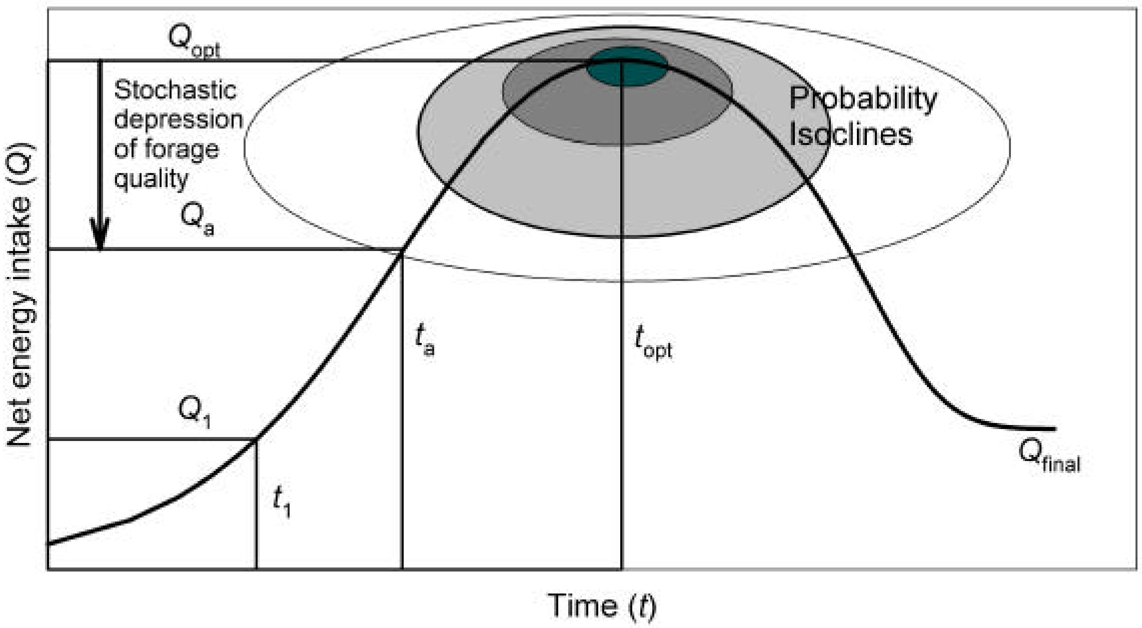

**Figure 6** Energy intake of vegetation obtained from a grazing lawn is depressed by uncertainty of patch choice.

If the distribution of $Q$ around $Q_a$ is wide, i.e. the system is highly stochastic, the chance of a patch being ungrazed is small, and the chance of less preferred vegetation being consumed is higher, so that the equilibrium value of $Q$ tends to be higher than with a small variation of $Q$ around $Q_a$. This is exactly the result observed in the simulations.

We now consider the application of HOOFS to model the dynamics in a heath ecosystem such as that found in the Scottish uplands. The vegetation mosaic typically consists of two main vegetation types (two grasses (*Deschampsia flexuosa*, *Agrostis capillaris)* and a shrub (*Calluna vulgaris*) and two mammalian herbivores (sheep and red deer (*Cervus elaphus*)).

Models of optimal foraging predict diets that contain only one food plant type or the food plants selected by the foragers are ingested in proportion to their relative abundance in the environment, while observed diets consist of a mix of food types that are not in proportion to their relative abundance (Belovsky, 1997). So far, models predicting diet composition have seldom considered the spatial distribution of the food sources. It has been suggested that diet selection by sheep strongly depends on the configuration of the heather/grass mosaic, with an increasing proportion of heather in the diet with increasing fragmentation of grass patches (Clarke *et al.*, 1995; Hester *et al.*, 1999).

Food resources for herbivores are heterogeneous both in space and time. Grassland and dwarf shrub vegetation differ significantly in their seasonal growth. Grass growth and digestibility are high during the growing season (April-September) and low during the winter (Armstrong *et al.*, 1997). Growth and digestibility of the shrub vegetation during the growing season is generally lower than that of grass, but digestibility is more constant throughout the year, making it a more important source of forage during the winter period (Armstrong *et al.*, 1997).

The seasonal changes lead to a change in the spatial pattern of forage availability and diet selection. During the summer the landscape becomes divided into a relatively unpreferred heather matrix with dispersed patches of preferred grass. Because animals spend most of their grazing time on grass patches, any heather foraging will occur near the grass patches. This leads to an increased use of the heather near grass patches (Clarke *et al.*, 1995; Hester & Baillie, 1998). Animal movement between preferentially grazed patches of grass will result in a pattern of paths. This effect will stronger for smaller herbivores, as the height of the shrub vegetation limits their movement through the mosaic. The differential response of animals to the vegetation mosaic leads to differences in the foraging distribution (Hester & Baillie, 1998; Hester *et al.*, 1999; Oom & Hester, 1999). Foraging patterns are also expected to be different during the winter, when utilisation of heather increases.

When relating this to HOOFS, we argue that the development of grass patches in a heather matrix is a special case of emerging grazing lawns. The preferential use of grass patches and the physical limitation of movement will reinforce the effect. Spatially explicit models, such as HOOFS, have been shown in this paper to allow the exploration of the impact of large herbivores on the development of vegetation mosaics. The application of HOOFS can thus lead to a better understanding of the processes and the development of appropriate management strategies in vegetation mosaics including those containing grass and heather.

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