CHAPTER 5A

FORAGING IN A HETEROGENEOUS ENVIRONMENT

Intake and diet choice

EMILIO A. LACA

Department of Plant Sciences, University of California, Davis, One Shields Ave,
Davis, CA 95616, USA
E-mail: ealaca@ucdavis.edu

Abstract. Resource heterogeneity and its effects on consumers are crucial in the dynamics of landscapes with large herbivores. Although all elements necessary for a general quantitative theory of resource heterogeneity and foraging behaviour across spatial scales are available, such a theory has not been put forth yet. We need to learn what scales, what resources and what types of heterogeneity are relevant to conserve and manage landscapes with large herbivores. More specifically, what scales, variables and heterogeneity are important in determining intake and diet selection by large herbivores? Large herbivores interact with their resources through a series of nested processes such as ingestion, searching, digestion and resting, which define relevant scales. Empirical relationships between animal performance and average resource abundance are scale-specific. Extrapolations should be based on explicit models to change scale, and will benefit by using concepts and techniques from geostatistics. Heterogeneity and average herbage mass are frequently related, so that measured effects on intake cannot be unequivocally attributed to total herbage mass. Resource heterogeneity can affect intake and behaviour through non-linearity of responses to local conditions, selectivity and changes of local functional response due to global conditions. In general, coarser resolution of heterogeneity allows a greater selectivity. These points are illustrated with examples from the literature and reinterpretation of published and unpublished data.

Keywords. spatial scale; resource distribution; grazing; patchiness; functional response

INTRODUCTION

Integration of what we know about herbivores in conceptual and quantitative models immediately results in the realisation that “spatial patterns of resources may regulate resource uptake and depletion rates within the landscape, with potential implications for demographics, intraspecific competition, and community assembly” (Milne et al. 1992). Heterogeneity is a rich and multidimensional concept (Skidmore and Ferwerda, Chapter 4). Thus, it is useful for making general assertions, but it is too

Herbert H.T. Prins, Frank van Langevelde (eds.), Resource Ecology: Spatial and Temporal Dynamics of Foraging, 81-100.

general to describe well-defined quantitative relationships. Heterogeneity is necessary for life and physical events to happen. The living and the physical worlds are flows and changes that are possible because of, and fuelled by, heterogeneity. The concept is so central to the way we understand and study the world that its study cuts straight across disciplinary and hierarchical organisations of science. In the context of herbivore foraging, a relevant issue is whether there is a general conceptual framework to interpret past research and plan future studies to improve management and conservation of ungulates based on resource heterogeneity (Box 5.1).

Resource heterogeneity is a key factor in ecology; there is room for a synthetic theory to interpret empirical results and to derive hypotheses for conservation

How one operationally defines, measures and thinks of heterogeneity has a major impact on our ability to understand and manage landscapes where large herbivores are an important component (landscapes with large herbivores, LLH). Evidence and quantification of effects of heterogeneity on LLH are abundant in the literature; but is there a synthetic theory available to put empirical results into perspective, and to derive hypotheses of practical relevance for management or conservation? Has vegetation heterogeneity been defined and measured in the most meaningful way to increase our ability to predict animal and landscape responses?

Heterogeneity of an LLH is multidimensional because it simultaneously has values for all scales (heterogeneity is scale-dependent) of time and space, and for all variables or functions of variables considered. Once again, this argues for the need to move beyond statements invoking ‘heterogeneity’ in general into more specific questions that are organised by a conceptual framework: what scales, what variables and what types of heterogeneity are relevant to understand and manage LLH? More specifically, what scales, variables and heterogeneity are important in determining intake and diet selection by large herbivores? How and how much do they determine diets and intake?

This chapter uses examples from the recent literature to address some of the foregoing questions. Literature sources are, by the most part, restricted to the last 12 years. However, when no new articles explaining important concepts were found, older references are included. This is not a review, but an attempt to present the some relevant concepts and theories in a coherent structure and with some support from the literature, and additional references to guide the reader into the subject. The goal is not to give the reader a prescription, but to pose explicitly the questions and issues that the information brings up.

Box 5.1. *Components of resource heterogeneity*

Perhaps the simplest way to quantify heterogeneity involves a measure of variance and one of spatial pattern. Consider the heterogeneity of herbage abundance in a 10,000-ha grassland, as measured with a resolution of 0.25 m^2. Imagine that the centre of the quadrat is placed in all points of the grassland and that the mass within it (x = herbage mass within each quadrat) is measured non-destructively. The variance of x would represent the degree of difference among quadrats, regardless of their spatial arrangement. A histogram of the frequency of values of x would be more informative, but less parsimonious. A compromise can be achieved if the distribution of x can be modelled with few parameters. For example, Shiyomi et al. (1991, 1998) modelled the distribution with a gamma function, which requires only two parameters.

Spatial pattern can be summarised into one number: the fractal dimension of the pattern. If herbage mass changed smoothly over space, following a gradient, the fractal dimension would be 2.0. In this case, the amount of herbage in any quadrat could be predicted with certainty using information from surrounding quadrats. On the other extreme, if herbage mass changed completely randomly, taking any value from the distribution regardless of its position relative to other quadrats, the fractal dimension would be 3.0. In this second extreme case, it would be impossible to predict the herbage mass in a quadrat based on the values of adjacent ones. Fractal dimensions between 2.0 and 3.0 would reflect intermediate cases such as a patchy distribution of herbage mass.

Variance and fractal dimension of spatial heterogeneous resources can be used as proxies of variables that are potentially crucial for foragers, particularly for herbivores that depend on sessile resources and have to explore large areas to gather sufficient nourishment every day. Variance of herbage mass and or quality determines the probability of randomly finding a bite of a certain quality and mass. Assuming a unimodal distribution, large variance means that very good and very poor bites are relatively abundant, whereas small variance means that most bites are about the same. A fractal dimension of 2.0 means that all good bites can be found easily and predictably in a gradient towards the best area of the grassland; a fractal dimension of 2.5 means that there are patches of good bites that can be found and exploited by specialised adaptive search mechanisms, whereas a fractal dimension of 3.0 means that bites of all types are finely interspersed, so a systematic search would be the best strategy.

Although variance and fractal dimension can summarise heterogeneity efficiently, this is not always the case, and a more complete and complex set of descriptors may be necessary. The fractal dimension of a given grassland might change as a function of the resolution at which herbivores interact with it. Imagine our 10,000-ha grassland as having a clear W-E gradient over a distance of 10 km, from 10 g 0.25 m^{-2} on a dry hilltop to 100 g 0.25 m^{-2} in a humid valley. Further, consider that due to randomly distributed micro-topography and disturbances, the coefficient of variation of herbage mass at any distance from the hilltop and as measured with the 0.25-m^2 quadrat, is constant and equal to 1.0. A rabbit whose home range is at any point in the gradient would perceive its resource as almost homogeneous with a fractal dimension close to 2.0. The rabbit would search for the randomly distributed good patches, and would not perceive the gradient within its home range because it would be swamped by the random variance. A bison, whose daily movement range could easily span most of the 10 km, would perceive a clear resource gradient with a fractal dimension close to 1.0 over its daily range. The bison can choose where in the gradient to forage, and within that area it can search and select bites.

HETEROGENEITY EVERYWHERE

Spatial heterogeneity has two components (Palmer 1992), i.e., variance (or more generally, probability density function) and spatial pattern or arrangement. For example, a shrub land with a total aboveground mass of 2000 kg ha^{-1} can have 20% of the area covered by shrubs with 10^4 kg ha^{-1} of canopy cover, or it can have 40% cover by shrubs with 5000 kg ha^{-1} of canopy cover. In turn, each one of them can have any spatial pattern imaginable from one block with all shrubs and another empty, to patches to a perfectly regular distribution, as in a plantation. In all cases the average is the same, and within the small or large shrubs, the probability density function is constant across spatial patterns.

Past interpretations of relationships between resource abundance and animal performance may need to be revised with the novel emphasis on heterogeneity

Variance among sample units increases with increasing extent (e.g., area of pasture or region) and decreases with increasing size of the sampling unit (e.g., quadrat area). This appears to be a general property of most regionalised variables (O'Neill et al. 1991) and was described for grazed pastures by Shiyomi (1987). The rate of decrease in variance with increasing quadrat size can be used as a summary characteristic of the spatial distribution of forages. The variance among sampling units is both the degree of heterogeneity and the variety of choices an ungulate has when sampling or perceiving the landscape with a certain resolution. Thus, the evaluation of a given area as habitat for ungulates may strongly depend on the resolution of measurements. On the other hand, the average and extremes of forage quality and mass per unit area will depend on the extent available for animals to choose from. Mobile herbivores can buffer temporal changes in the average availability of forage when grazing large extensions, but are unable to do it in smaller paddocks, even if all average characteristics are the same in both situations (see also Bailey and Provenza, Chapter 2). As a consequence, empirical relationships between animal performance and average resource abundance are scale-specific, and should be used only for the scale at which they were developed, unless some model and theory are used to perform the change of scale. The field of geostatisics provides such models and theories (Wackernagel 1995).

Is it appropriate even to consider heterogeneity as a low-dimensional characteristic of the landscape? In other words, how few independent numbers are necessary and sufficient to characterise completely the heterogeneity that is relevant for large herbivores? This could pose a serious challenge for three main reasons. First, heterogeneity must be considered scale-dependent, and thus it could theoretically be infinitely dimensional. Second, heterogeneity can be defined on any set or function of landscape variables. Third, heterogeneity, like any other landscape variable, can and typically does take different values at different positions in space. This last concept is represented by the idea of ‘texture’, commonly used in image analysis. However, the continuity of scale dependence can be operationally partitioned into a small number of domains of scale (Bailey et al. 1996; Bailey and Provenza, Chapter 2) without significant loss of precision or generality. Ungulates interact with their forages through a series of nested processes such as ingestion and chewing, searching and walking, digestion and rumination, resting, etc. These processes and the associated behaviours define potential scales of interest. The main variables of interest are likely to be abundance of main plant species, topography, cover and water availability; just a few of the myriad of landscape variables. Finally, there are statistical, modelling and measurement methods to detect and correct for spatial variability in heterogeneity itself. Following one paradigm of spatial statistics, spatial variability can be partitioned into trends and residuals. Responses to large-scale trends or gradients have long been the subject of ecology in general and grazing behaviour in particular, and relatively well-established concepts and facts are available. The novel issues are in the spatial correlations of the residuals, and how herbivores might exploit them.

Heterogeneity is indeed everywhere. The fact that heterogeneity is a constant feature of most herbivore–vegetation systems, even those once thought of as homogeneous, questions the validity of experimental relationships between resource abundance and intake. As shown in Figure 5.1, even if the true response to herbage mass were a ramp function, the observed response to the natural covariance between average and heterogeneity of herbage mass would lead to the observation of a concave-down functional response as a result of the selectivity effect. The exact shape of the functional response in the absence of heterogeneity is not that important for this argument. The main point is that in the presence of heterogeneity, animals can select temporal or spatial patches that are better than the average, thus achieving a higher intake rate than in homogeneous resources of equal average value. Heterogeneity and average herbage mass are frequently related, so that measured effects on intake cannot be unequivocally attributed to total herbage mass, unless heterogeneity is controlled or accounted for through statistical methods. For example, heterogeneity of herbage mass per unit area in pasture composed of *Festuca arundinacea*, *Dactylis glomerata*, *Poa pratensis*, *Agrostis alba*, *Trifolium repens* and other minor species depended on herbage mass and whether the level of biomass had been reached by recent growth or grazing (Shiyomi et al. 1998). Components of resource heterogeneity are discussed in Box 5.1. Shiyomi and colleagues have shown in several studies that the frequency distribution of herbage mass per unit area measured with a grain size of 0.25 m^2 can be described by a gamma distribution (Shiyomi et al. 1983, 1984, 1991). The gamma distribution is a common statistical distribution that describes the intervals between random events that follow a Poisson distribution. Shiyomi and colleagues found that the reciprocal of the square root of the coefficient of variation is strongly dependent on the total or average herbage mass per unit area (Figure 5.2). Within the range of herbage mass they studied, heterogeneity increased with decreasing mass, due to both grazing and growth. Thus, generic functional and production responses, particularly those measured in ‘realistic’ field conditions should be reconsidered or at least explicitly state that the response measured is likely not caused only by the change in overall resource abundance, but also by changes in heterogeneity.

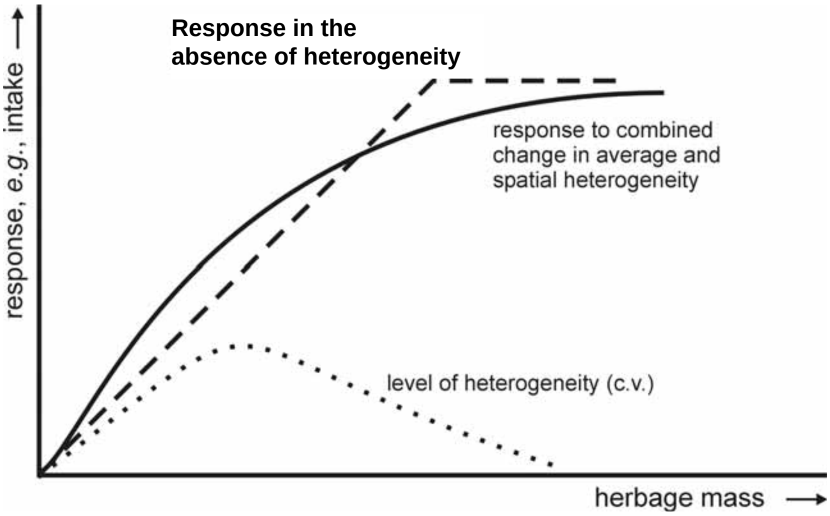

Figure 5.1. *Hypothetical effects of heterogeneity on measured responses to change in herbage mass. The continuous thick line represents the typically observed response. The dashed line represents the hypothetical response to herbage mass in perfectly homogeneous swards. The thin line represents the changes in spatial variance in herbage mass associated with changes in average*

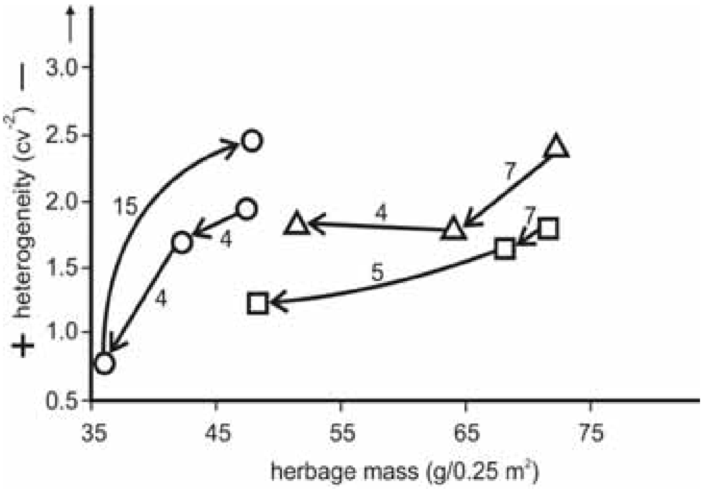

Figure 5.2. *Relationship between sward heterogeneity in mass per unit area measured with 0.25-m^2 quadrats (resolution) and average mass in the whole pasture (extent). Each set of symbols represents a sequence of measurements on sets of parallel transects. Numbers on the lines represent the number of days of grazing (herbage mass declines) or regrowth (herbage mass increases). Based on Shiyomi et al. (1998). Note that heterogeneity increases as the value of the abscissa decreases*

HOW HETEROGENEITY AFFECTS INTAKE AND DIET SELECTION

Heterogeneity is an inherently complex concept, and as indicated above, it cannot be characterised with a single dimension in a quantitatively meaningful and general way. Nevertheless, the concept can be used heuristically as lack of homogeneity, and it can be practically quantified with a few values. Murwira (2003) successfully used two parameters, intensity and dominant scale of vegetation, to determine the relationship between elephant distribution and vegetation heterogeneity. Intensity was defined as the maximum variance in the cover by certain species, and dominant scale was the scale at which the intensity was manifested.

Functional response is affected by forage heterogeneity through selectivity, non-linearity of local effects and integration of information

Regardless of kind and degree, heterogeneity can affect intake and behaviour through three mechanisms: non-linearity of responses to local and instantaneous conditions, selectivity, and change of functional form of local responses due to global conditions. These mechanisms are represented for a hypothetical functional response in Figure 5.3, and are illustrated with examples.

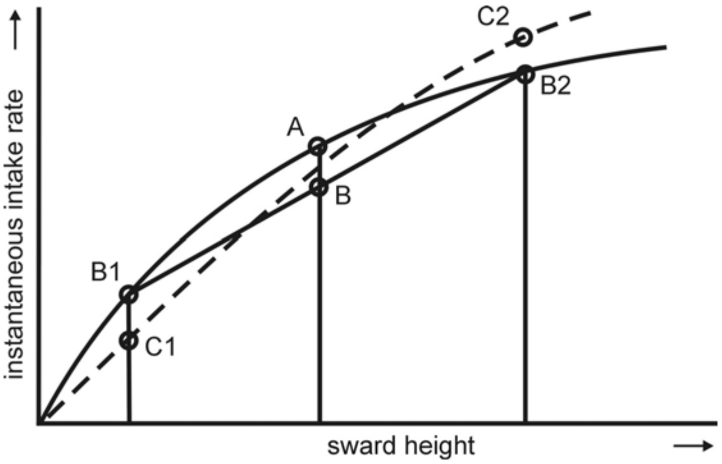

Figure 5.3. *Hypothetical effects of heterogeneity of sward height on intake rate measured at a scale of 10^2 to 10^3 seconds. The continuous thick line represents intake rate in each area of homogeneous sward height. The dashed line represents intake rate within homogeneous patches in a heterogeneous sward. See text for further explanation*

Consider a functional response of instantaneous intake rate to sward height in a leafy pasture. Because of the effects of sward height on bite mass and handling time, this is a concave-down nonlinear response. Point A represents the expected instantaneous intake rate for an intermediate height. Point B represents the expected instantaneous intake rate in a sward that has 50% of the area covered by a short sward (B1) and the rest by a tall sward (B2), such that all average characteristics are the same as for the sward yielding A. The difference between A and B is the effect of the nonlinearity in the absence of selective grazing, i.e., the animal takes 50% of the bites from each sward type. If selectivity is factored in, the response can be any instantaneous intake rate on the continuous curve between B1 and B2, depending on degree and direction of selectivity, and assuming no additional costs for searching due to selective grazing. When searching costs increase due to selectivity, the effect of selectivity is attenuated. Finally, the functional response to the characteristics of each patch in the heterogeneous sward can deviate from what is observed in homogeneous swards. For example, faced with alternating tall and short patches, the animal may take deeper bites in tall patches and shallower bites in short patches than expected on the basis of the 'homogeneous' functional response. The dashed line represents this effect on the functional response. The resulting instantaneous intake rate can vary between C1 and C2, depending on degree and direction of selectivity.

Heterogeneity can affect intake through effects on bite formation and bite dimensions, and effects at larger areas, such as patches, feeding sites and home range (see Fryxell, Chapter 6). Effects at the bite level are probably less responsive to changes in strategy or shape of the functional response, because the constraints on bite dimensions seem to be less subjected to changes in the motivation and behaviour of the forager than to the spatial distribution of forage in the grazed areas. Conversely, heterogeneity has stronger impacts on selection of feeding areas, feeding time and diet selection.

Quality–quantity bivariate heterogeneity

One of the main themes in plant–animal interactions is the trade-off between quantity and quality. In most natural grasslands, the quality of the forage declines as the amount of forage increases due to growth over the season (Prins and Olff 1998). However, patches that are grazed remain in a vegetative stage characterised by low herbage mass of higher quality than patches with more herbage (Fryxell 1991; Wilmshurst et al. 1995). Because ruminants have a limited passage and digestion rate, they choose diets or patches for which cropping rate equals digestion rate (Figure 5.4). The area under the two curves represents feasible combinations of diet quality and intake. This principle explains why grazers prefer short patches in grasslands, why herbivores aggregate to form 'grazing lawns', and patterns of patch selection and body size (Wilmshurst et al. 2000). Heterogeneity over areas that are smaller than the areas visited within a meal interacts with the quality–quantity trade-off by moving up the line of ingestive constraint to the dotted line in Figure 5.4. Herbivores appear to be able to select the preferred patches more easily when the patches are larger (Clarke et al. 1995; Wallis deVries et al. 1999).

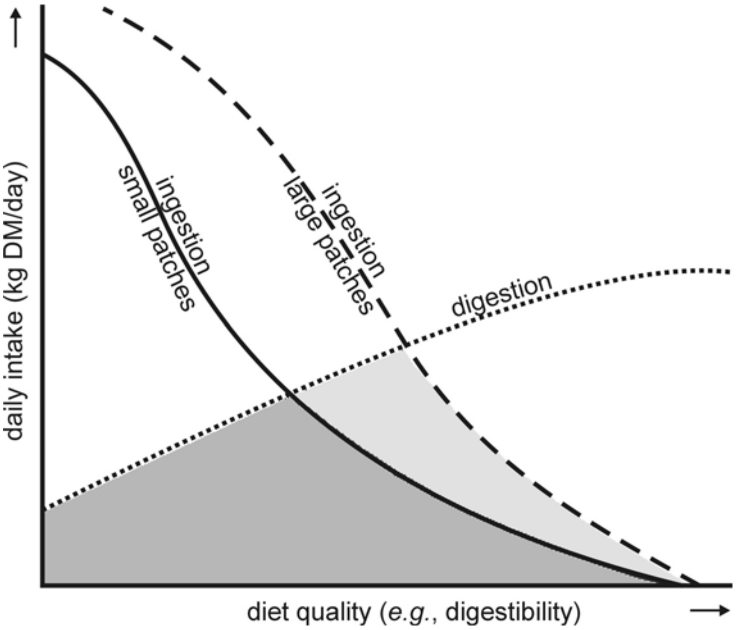

Figure 5.4. *Constraints on daily intake of digestible matter by ruminants. The ingestion curves depend on intake rate and grazing time. Two ingestion curves show the hypothetical effects of spatial distribution of patches of different digestibility. Larger patches make it easier for herbivores to select the preferred choice*

However, the negative relationship between patch quantity and quality observed in natural pastures is not universal (Figure 5.5). Ogura et al. (2002) found a positive correlation ($r = 0.48$) between herbage mass and quality (nitrogen concentration and *in vitro* dry-matter digestibility) and between defoliation rate and herbage mass of patches (r ranged between 0.6 and 0.8) in *Paspalum notatum* pastures early in the season. As the season progressed, the correlations reversed to the more typical pattern where tall, previously ungrazed patches have lower quality and more herbage mass than shorter ones, and animals prefer the shorter patches. Late in the season, the correlation between defoliation and pre-grazing herbage mass declined to about -0.5.

The study of herbivore foraging should encompass situations where quality and quantity have any correlation, not just those where quantity and quality have a negative correlation. Although the positive correlation between herbage mass and quality may have been the exception to the norm in places where herbivores evolved, we need to manage herbivores in disturbed and managed landscapes where conditions are novel. We need to extend our understanding of the spatial and temporal patterns of landscape–ungulate interactions to situations that may escape completely the typical habitats or interactions, because management, local disturbances and global change will likely expose herbivores to novel foraging environments.

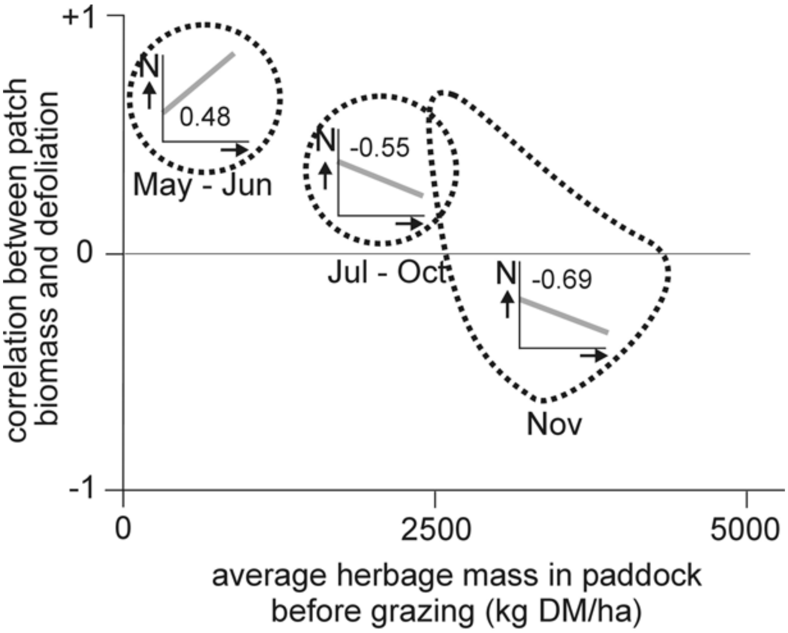

Figure 5.5. *Seasonal patterns of correlation between patch quality, herbage mass and defoliation rate by cattle. Areas encircled by lines represent the scatter of points. Inset graphs are the correlations between nitrogen concentrations and forage mass across patches during each of the three different seasons. Based on Ogura et al. (2002)*

Functional response

Spatial heterogeneity of vegetation determines the functional response of grazers and other ungulates (Drescher 2003). Gross et al. (1993) demonstrated that intake rate by herbivores across a wide range of body sizes is determined by bite mass. Bite mass is determined by the spatial arrangement of the vegetation at a local and very small scale, commensurate with the area of a few bites. Herbaceous swards are described by the proportion of total area covered by canopy, height of canopy, and plant mass per unit canopy volume, called ‘bulk density’. For any given average herbage mass available over an area, tall swards yield larger bites and greater intake rate (Laca et al. 1994a). Therefore, the response of intake to herbage mass should be steeper for swards that increase in height than for those that increase in cover or bulk density (Figure 5.6). If spatial heterogeneity changed with herbage mass, the observed functional response could have unexpected shapes. For example, consider a grassland composed of 20% short patches and 80% tall patches of equal quality, where herbivores select only the tall patches and are limited by intake rate. An increase of herbage mass due to an increase of height of the short patches would not result in any change in intake. In more general terms, the functional response depends on the kind and degree of heterogeneity present in the vegetation.

Considering that simple rules and restrictions can result in extremely complex patterns of response, it should be no news that the functional response can have a variety of shapes, and that at any given level of resource abundance, intake rate is strictly dependent on the spatial distribution of the resource (Drescher 2003), particularly on the relationship between scale of measurement and spatial variance in resource abundance.

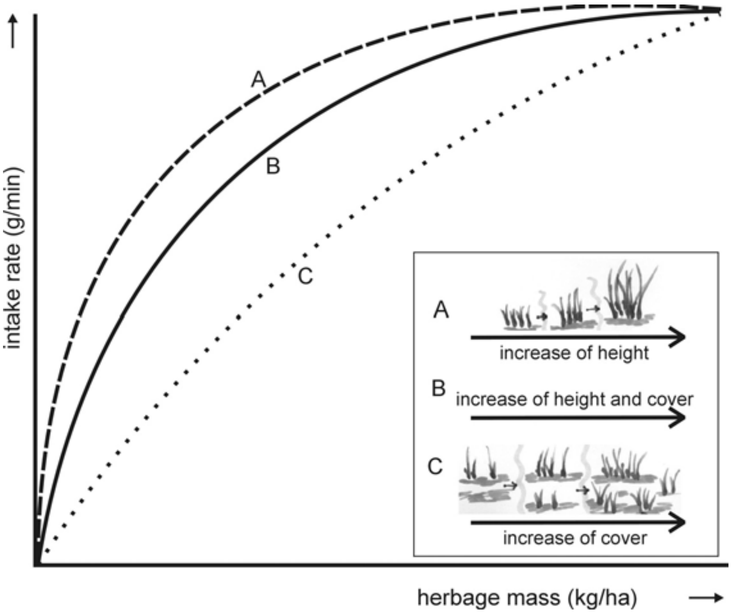

Figure 5.6. Hypothesised effects of heterogeneity of herbage spatial distribution on the functional response that relates intake rate to herbage mass available

INTAKE RATE AND SPATIAL HETEROGENEITY OF FORAGES

Intake rate and bite dimensions of large ruminants respond to heterogeneity at resolutions as fine as 20 cm

Intake rate of grazers over periods of 10^2 to 10^3 s is strongly influenced by bite mass over a wide range of values. In turn, spatial arrangement of plant parts in the volume occupied by the sward determines bite mass. The response of bite mass to sward height is typically linear with a slope directly proportional to sward bulk density, whereas intake rate responds to bite mass with diminishing slope. These relationships have been developed mostly on homogeneous micro-swards, where an artificial canopy is created by manually attaching plant parts to a wooden frame. How well do these relationships describe what happens in heterogeneous swards? Is the response of animals grazing a collection of patches of different characteristics equal to the weighted sum of the responses exhibited when they graze homogeneous areas with characteristics equal to each of the patches in the heterogeneous collection?

Figure 5.7 (Laca unpublished data) shows that the relationship between microsward (Ungar 1996) structure and bite mass changes depending on heterogeneity; a result that weakens the use of functions derived in homogeneous swards (Laca et al. 1992). The largest difference was observed between the bite depth in swards with heterogeneity at a fine scale and the one predicted based on responses to homogeneous swards. In this experiment, cattle exhibited selectivity for tall patches but not for density. When patches were at the level of one bite (10 cm), bite depth reflected grazing to the constant residual height (small cross in Figure 5.7) that

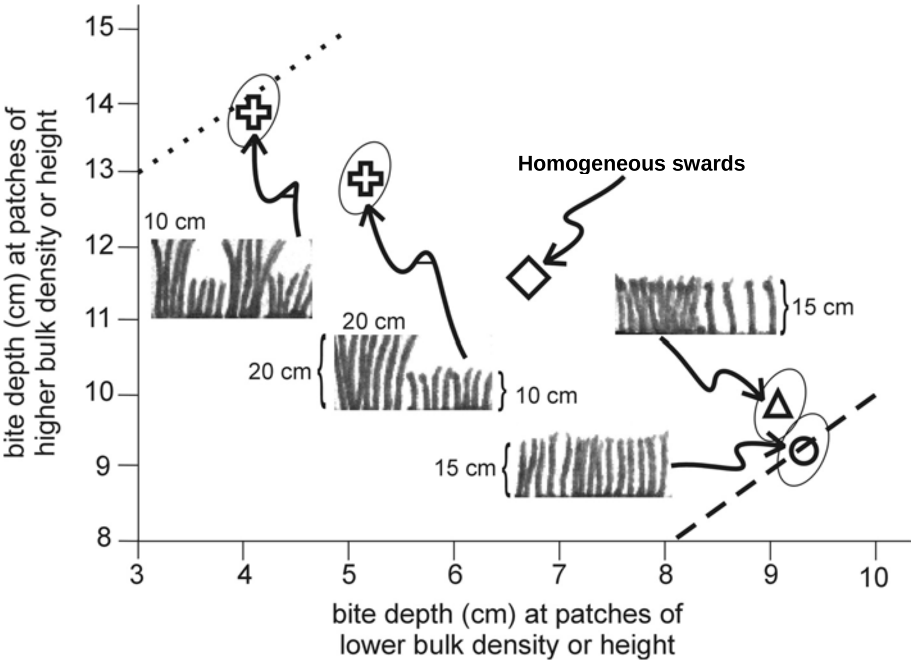

Figure 5.7 *Effects of small-scale heterogeneity of sward height and density on bite dimensions of cattle. The two crosses represent swards with heterogeneity in height in patches of 10 or 20 cm. The triangle represents swards with heterogeneity in density in patches of both 10 and 20 cm. The circle is the homogeneous 15-cm-tall control. The diamond is the calculated bite depth for homogeneous swards of 10 and 20 cm of height. All swards had exactly the same average mass, height and density of grass. Ellipses represent approximately one standard error. Dotted line: expected relationship between bite depth in tall and short patches if animals grazed both patches to a constant residual height. Dashed line is the line where bite depth at patches of lower bulk density (x-axis) equals bite depth at patches of higher bulk density (y-axis).*

would be expected in a homogeneous sward of equal average height (residual height was ca. 6 cm, as in the sward represented by the circle). As the area of patches increased from 10 to 20 cm, bite-depth combination approached the prediction based on homogeneous swards with height equal to each of the patches present. Overall, the results make intuitive sense: small-scale heterogeneity was integrated or smoothed over by the animal prior to the response resulting in a 'response to the spatial average'. As scale of heterogeneity increased, the response became closer to what would happen in separate homogeneous swards.

Ginnett et al. (1999) determined that bite depth responds to vertical heterogeneity in bulk density by comparing grazing behaviour of steers in swards with structures as depicted in Figure 5.8. The vertically heterogeneous sward used can be considered the smallest resolution of heterogeneity in sward height possible.

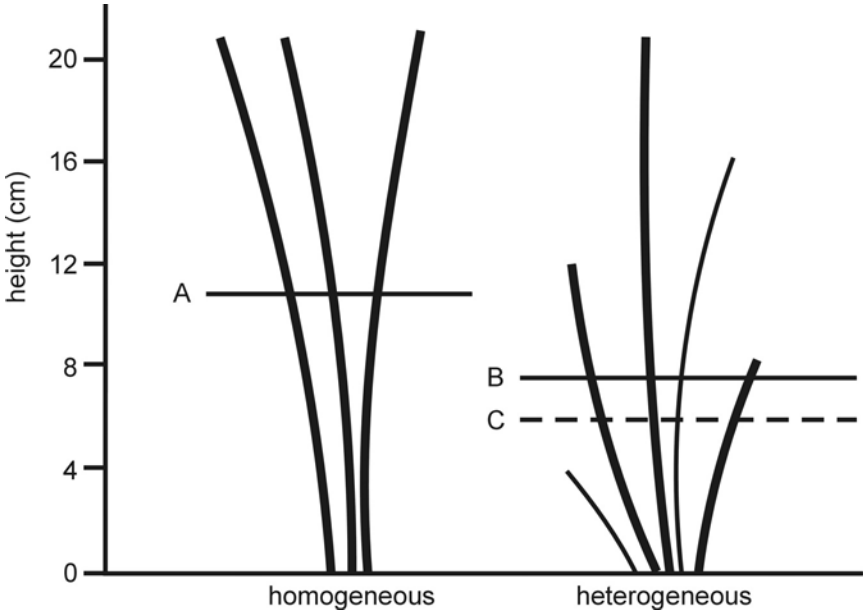

Figure 5.8. *Effect of sward heterogeneity on bite depth by cattle. Both swards have the same mass per unit area and the same maximum height. The continuous horizontal lines A and B show the observed bite depth. Line C shows the expected bite depth in the heterogeneous sward if animals had responded to its average height of 12 cm*

It is interesting to note that the description of heterogeneity becomes hard as the scale of heterogeneity approaches the grain of the forage (one leaf). Ginnett et al. (1999) refer to the treatment consisting of leaves of several lengths in each tiller both as 'variable height' and 'variable bulk density'. In their experiment, bite depth in the heterogeneous swards was 63.7% of the total sward height, leaving a residual height of 7.3 cm. Bite depth in the heterogeneous swards was significantly greater than in the homogeneous sward of equal total height, but not as deep as expected on the basis of average sward height. The consequence of these responses was that the heterogeneous swards resulted in a sigmoid instead of a concave-down depletion curve. This difference in heterogeneity generated significant differences in the expected residence time and depletion at the patch level. In the heterogeneous sward, animals exhibited local, instantaneous behaviour that was intermediate between responses in the homogeneous sward and what was expected if they responded to the average of the heterogeneous one.

DIET SELECTION AND SPATIAL DISTRIBUTION OF PLANTS

Diet composition changes as a function of spatial distribution of dietary options: coarser resolution of heterogeneity allows a greater degree of selectivity

Studies of diet selection by herbivores have focused on the changes in diets as a function of changes in the relative proportion of forage components (for example, leaf and stem, or grass and clover), largely ignoring the spatial arrangement of the components and its potential correlation with their relative abundances. Obviously, these studies assumed that at least at some relevant scale, components of forage are separate in space. Otherwise, diets would always be identical to herbage composition. Some studies, however, provided a basis to assess the role of heterogeneity on diet selection.

Clarke et al. (1995) studied the response of sheep and red deer to the spatial distribution of grass in a heather matrix, keeping the proportion of area covered by each vegetation type the same across treatments. The three treatments were 1 large, 4 medium or 12 small patches of grass covering 1/6 of the total area. Sheep spent more time grazing on grass than on heather, but the degree of selection decreased as patch size decreased. Deer also spent more time grazing on grass than on heather, but they always spent more time on heather than sheep, and their selectivity did not change as a function of grass patch size. These results agree with those obtained by Wallis de Vries et al. (1999) with cattle grazing patches of grass that differed in quality and quantity of forage. It appears that in general, coarser resolution of heterogeneity, or separation of forage options over larger units, allows a greater degree of selectivity.

Hester et al. (1999) conducted a similar experiment with sheep and red deer grazing mosaics of grass and heather, but size of patches was not controlled. Sheep, deer or both grazed 1-ha plots of a semi-natural mosaic containing about 15% of the area covered by grass patches. Grass patches were classified as small (1-6 m^2), medium (6-30 m^2) or large (> 30 m^2). Sheep selected small grass patches, whereas deer showed no consistent selectivity. The greater amount of edge in the small patches resulted in less impact by sheep in the small patches than in the large ones. Given that sheep have greater difficulty moving through heather than through grass, and that they were able to select more grass when patch size was larger (Clarke et al. 1995), it is not clear why they selected the smaller patches in this study.

Selection for a particular dietary component that is preferred (e.g., clover vs. grass) increases with increasing spatial separation between alternatives. Spatial separation of grass and clover resulted in much greater selectivity than mixed swards across a range of relative abundances of grass and clover (Clark and Harris 1985; Ridout and Robson 1991). Even in mixed swards, sheep diets had more clover than in the pastures (Figure 5.9).

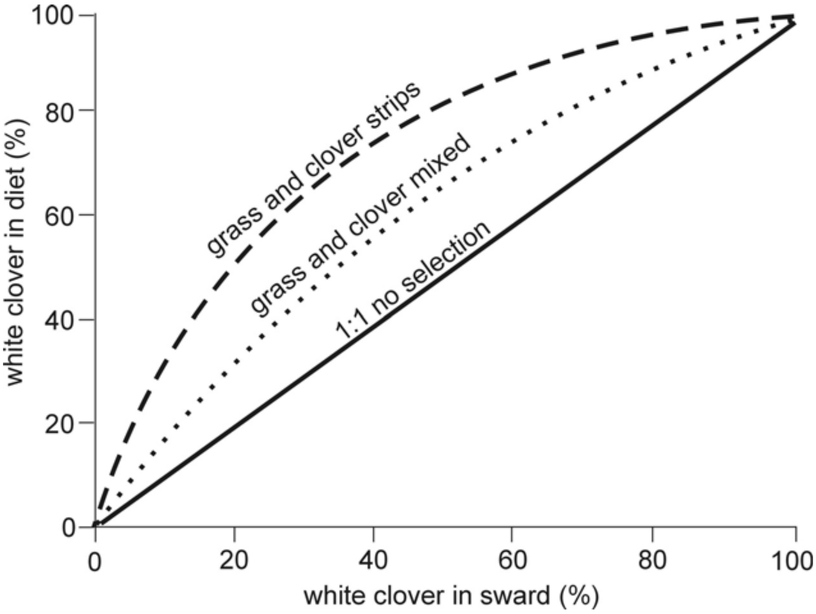

Figure 5.9. *Effect of relative abundance of white clover on diet selection by sheep grazing in paddocks with strips of pure grass and clover or mixed swards. Based on Clark and Harris (1985) and Ridout and Robson (1991).*

Marotti et al. (2002) tested the effects of spatial segregation between forages on diet selection and the mechanisms involved (Figure 5.10). Sheep grazed paddocks with a mixed ryegrass–white clover sward (‘mixture’), ryegrass alone, clover alone, or clover and grass side-by-side (‘choice’). This design allows comparisons to determine the effect of separation and the mechanisms by which these effects take place. As indicated above, the mechanisms can be selectivity for one of the options, changes of response to local conditions based on global conditions, and non-linearity of responses to local conditions. The design allows comparisons to detect selectivity and changes of response, but in order to detect non-linearity effects it would have to be extended to include more than one level of clover content in the treatments.

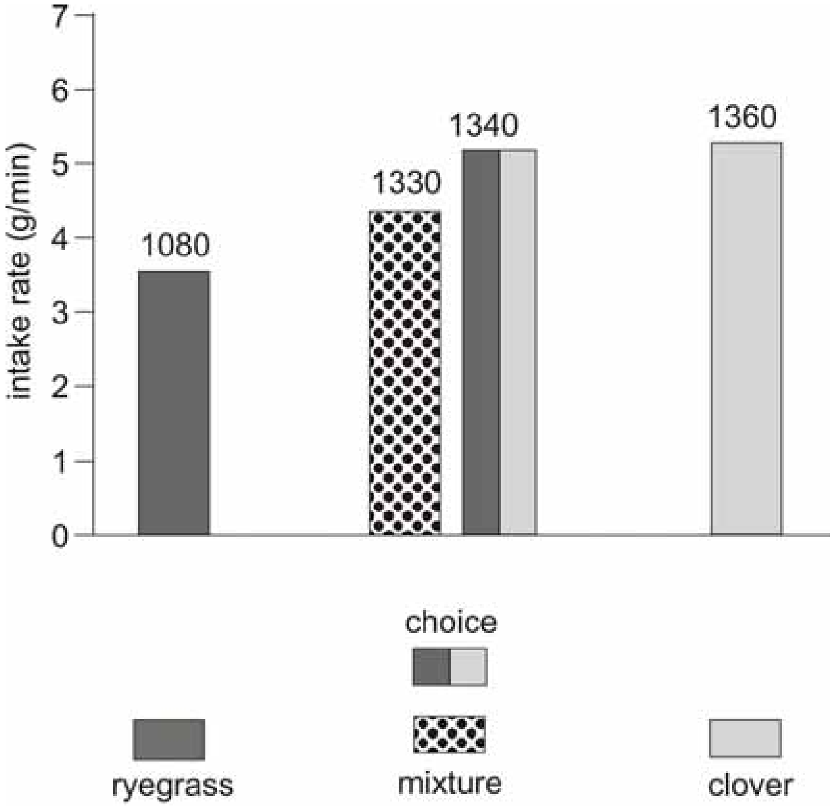

Figure 5.10 *Effect of spatial separation of clover and grass on selectivity and intake rate by sheep (based on Marotti et al. 2002). Sheep grazed paddocks with pure grass (dark bar), pure clover (light grey bar), finely mixed grass and clover (spotted bar), or half of the paddock covered with grass and half with clover (dark and light grey bar)*

Intake rate and bite mass were significantly smaller in pure grass than in pure clover swards. Intake rate in mixed swards was intermediate between pure swards, but in the choice treatment values were very similar to those observed in the pure clover sward. Sheep grazing a paddock with grass and clover in different areas achieved greater daily intake and intake rate than when grazing swards where similar amounts of grass and clover were interspersed (Marotti et al. 2002).

The study by Parsons et al. (1994) included several levels of clover content in the treatments, but only the 'choice' treatment was explored. This was partly compensated for by combining the results from Parsons et al. (1994) with those from Milne et al. (1982), which consist of responses of sheep grazing behaviour to changes in clover–grass proportions in mixed swards (Figure 5.11).

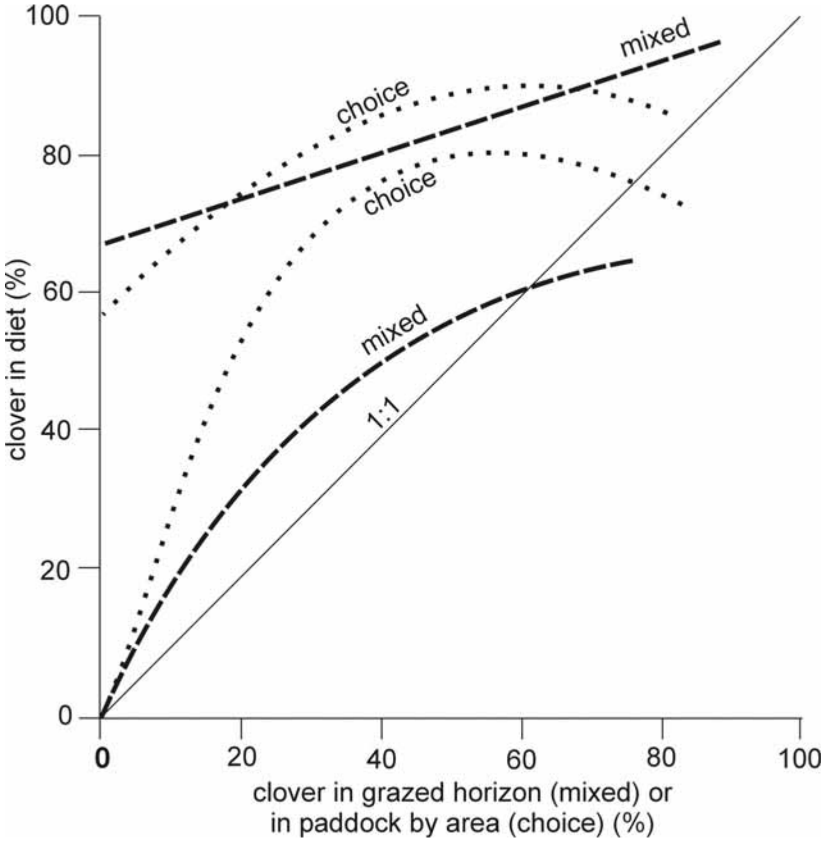

Figure 5.11. *Effects of clover content of the grazed horizon of mixed swards (Milne et al. 1982) or in paddocks containing adjacent areas (choice) of pure clover and pure grass (Parsons et al. 1994) on grazing behaviour of sheep. Full lines are proportion of clover in the diet. Dashed line: bite mass of sheep grazing mixed swards as a percentage of bite mass projected for swards with 100% clover. Dotted line: bite mass of sheep grazing-choice swards as a percentage of bite mass in the pure clover sward*

Several points are remarkable about the responses depicted in Figure 5.11. First, sheep apparently selected a mixed diet (see Prins and Van Langevelde, Chapter 7); and proportion of clover in the diet increased with increasing proportion in the pasture. Arguably, sheep in the choice treatment could have selected any desired diet composition without additional costs for a wide range of proportion of area covered by each species. Why did they not select their favourite diet composition in all treatments that offered at least a minimum area of each species? Parsons et al. (1994) discussed several possible explanations for the changing proportion of clover in the diet, including maximisation of intake rate, novelty, balancing of nutritional needs, preference for rarity and sampling. No single mechanism explains the observed pattern. Second, sheep selected more clover in the choice than in the mixed swards. Considering that mixed and choice treatments are extremes of a continuum, it is interesting to consider how the curves would change from the 'mixed' to the 'choice' as spatial separation and pattern change from completely uniform at all scales (perfectly mixed) to heterogeneous at all scales to completely to adjacent areas of pure grass or clover. I know of no experimental studies that have addressed these distributions and animal responses in manipulative fashion. Note that degree of heterogeneity at the smallest scales perceived by sheep is constrained by the size of plants or plant parts. In other words, under a magnifying glass the pasture always looks like a mosaic of pure clover or pure grass patches. Third, it is likely that the mixed treatment was not completely mixed, but showed some degree of natural patchiness. As indicated in the section on pervasiveness of heterogeneity, although we know that in the 'mixed' treatment grass and clover were more mixed than in the choice treatment, we do not know exactly how patchy the mixed pastures were. More importantly, we do not know if patchiness changed in a structured way as clover content increased. Covariance between clover content and spatial distribution would make it impossible to determine whether the response seen in the mixed curve is due to the change in clover content or to the change in pattern. Finally, the dotted and dashed lines (Figure 5.11), representing bite mass as a percentage of the value on pure clover, are more similar between treatments than diet compositions. The dotted line for the choice treatment was derived assuming that bite mass on the clover and grass parts of the pasture remain constant, regardless of the proportion of clover. The continuous line for the mixed treatment, derived by regression of the measured bite mass on sward composition, is consistent with the assumption that regardless of sward composition, bite mass on clover and grass was constant.

But, can animals gauge the mixing of their diets? Apparently, yes. Not only do ruminants respond to the mixing of dietary components, they also respond to it in a spatial fashion. Animals are able to select diets and spatial location for grazing not only based on positive diet characteristics, but also on amelioration of negative post-ingestive consequences (see also Bailey and Provenza, Chapter 2). Villalba and Provenza (2002) found that lambs preferred foraging locations where tannin-containing food was near food boxes with polyethylene glycol (PEG). Tannins are known to produce negative post-ingestive consequences and constitute an anti-quality factor, but PEG binds to tannins and reduces their negative effects. The implications of this finding are far-reaching in relation to impacts of heterogeneity because it demonstrates that sheep were able to integrate the consequences of mixing spatially separate foods.

Animals can gauge the mixing of their diets

Presumably, ruminants also integrate positive consequences of mixing complementary forages, such as grasses and clover, at temporal scales that allow better rumen functioning than if the same daily diet were split into meals of pure grass or pure clover. Rumen fermentation and microbial growth depend on an almost simultaneous supply of labile, slowly fermentable and N-rich compounds. For optimal rumen function, the mixing has to be at the scale of minutes, definitely shorter than meals. If energy- and protein-rich forages are segregated at large scales, mixing them at the appropriate scale will be more difficult than if they are interspersed at some intermediate level. Thus, the preference to have mixed diets within meals imposes a scale on foraging behaviour that is commensurate with the area grazed in 15-30 minutes. If complementary forages are in patches segregated at large scales, animals should prefer to forage on edges or they would forego the benefits of mixed diets in the short term. As scale of patchiness increases, separation of dietary options eventually has to result in negative effect on the diet, by making it impossible for animals to get a diet mixed within meals (see Prins and Van Langevelde, Chapter 7).

Box 5.2. *Testable hypotheses for future research*

Hypothesis 1. Functional and production responses are likely not only related to the change in overall resource abundance, but also to resource heterogeneity.
Hypothesis 2. Faced with alternating tall and short patches, herbivores take deeper bites in tall patches and shallower bites in short patches than expected on the basis of the functional response measured in 'homogeneous' resources.
Hypothesis 3. In heterogeneous resources, consumers exhibited local, instantaneous behaviour that is intermediate between responses in homogeneous resources and what is expected if they responded to the average of the heterogeneous one.

SYNTHESIS

Heterogeneity of forage resources is the norm, and it should be expected to have implications for intake and diet selection by herbivores. Herbivores respond to heterogeneity by selecting a subset of the options available and by potentially responding in ways that cannot be predicted on the basis to responses derived in homogeneous vegetation, even if developed for each and all of the options. This happens because animals are able to integrate the characteristics of the forage and respond in non-linear fashion to the integrated values. The integration can happen from the perceptual level to cognitive and to physiological levels. Some hypotheses for future research are formulated in Box 5.2.

Modelling and geostatistics help to develop theory of foraging in heterogeneous resources, but it will be impossible to extrapolate to scales not studied

Although in practical terms heterogeneity impacts will not produce responses that are significantly different from predictions based on the study of homogeneous vegetation, the theoretical development of the field will require models that dwell on the variety of scales at which animals integrate information and forage inputs. The fact that heterogeneity is a complex and multidimensional characteristic of the food environment effectively burdens our ability to determine experimentally the responses that are necessary to make management plans or impact assessments. We should borrow and re-cast concepts used in geostatistics and related fields to guide the development of practical principles for the management of herbivores in fragmented landscapes (see also Stein and Georgiadis, Chapter 3, and Skidmore and Ferwerda, Chapter 4).