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How herbivores optimise diet quality and intake in heterogeneous pastures, and the consequences for vegetation dynamics

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Abstract

Understanding the interplay between foraging behaviour and vegetation dynamics in heterogeneous pasture is an essential requirement for evaluating the value of the resource for large herbivores and for managing that resource. The orientation of selective grazing behaviour between intake and diet quality depends on the spatial and temporal scales considered. In the short-term scale of a grazing sequence, there is evidence that large herbivores tend to optimise the intake rate of digestible materials by adaptation of their biting behaviour and by patch choice. On a day-to-day scale, there is evidence that large herbivores tend to prioritise the quality of the diet to minimise digestive constraints within the time that they can spend grazing. On a pasture scale, the search for areas giving the best trade-off between quantity and quality of intake leads to the optimisation of their foraging paths, in particular by modulating their sinuosity in response to heterogeneity. Repeated grazing of preferred patches creates a positive feedback on forage quality and enhances heterogeneity. Long-term consequences on vegetation dynamics, botanic composition and grassland quality are less understood.

Keywords: ruminant, heterogeneous pastures, grazing behaviour, intake, vegetation dynamics

Introduction

Grazing management aims to provide herbage in quantity and of sufficient quality to satisfy animal needs while sustaining the grassland. On grassland of high productivity, extensive management for environmental purposes, such as reducing pollution and enhancing biodiversity, can be achieved by lowering grazing pressure, resulting in the development of pasture heterogeneity. Marginal environments, such as semi-arid areas, wetlands or uplands, are characterized by a low productivity and do not suffer high grazing pressures. When grazing pressure is low, the larger area offered to large herbivores makes the actual grazing pressure vary spatially and temporally, as they can make their own choices on what to eat. The uneven use of the grassland by large herbivores will lead to enhanced heterogeneity in biomass availability and quality due to edaphic factors. Understanding the interplay between foraging behaviour and vegetation dynamics is therefore an essential requirement for evaluating the resource value for the animals and for managing that resource.

The interaction between grazer and vegetation is dynamic and bidirectional. The structure, quality and distribution of plant material affect the quantity and quality of the grazed diet, while grazing affects the structure and composition of the vegetation. Frequently grazed plants and areas will diverge from the less frequently and ungrazed plants and areas, creating spatial patterns at different scales (Marriott & Carrère, 1998). Based on the Optimal Foraging Theory (Stephens & Krebs, 1986), it can be postulated that animals try to maximise the intake of energy and minimise the related costs. To achieve this, foraging behaviour consists of a series of discrete decisions at the successive spatio-temporal scales of bite prehension through

to patch choice and plot utilisation. All the decisions represent trade-offs, in particular between diet quantity and quality, since in heterogeneous grasslands, areas of low biomass and high quality coexist with areas of high biomass but poor quality (Wallis de Vries & Daleboudt, 1994). In the present review, we will focus on the trade-offs at the main relevant temporal scales of plant/animal interactions: the short-term scale of bite prehension and patch choice within a grazing sequence, and the longer-term scale of intake over a day and beyond. Large herbivores integrate into their decisions the knowledge they have gained on the nutritional consequences of their diet choices (Provenza, 1995) and on the resource availability and spatial distribution (Dumont & Petit, 1998). We will then examine how foraging behaviour affects how animals use pastures and the consequences on vegetation dynamics.

Optimising biting behaviour and patch choices during grazing sequences

A functional way to represent a heterogeneous pasture is as a mosaic of patches. A patch can be defined as an area over which intake rate is relatively constant (Illius & Hodgson, 1996) which implies a relative homogeneity in the structure and composition of the vegetation. When grazing a patch, what does the animal try to achieve? It is often postulated that grazing behaviour aims to maximise intake rate.

In order to explain how sward characteristics within a patch affect intake rate, many authors have used an analytical breakdown that splits intake rate into bite mass and time per bite, then bite mass into bite volume and bulk density of the sward, and then bite volume into bite area and bite depth (for reviews, see Prache & Peyraud (2001) and Penning & Rutter (2004)). Bite depth tends to be a constant proportion of sward height slightly modulated by sward density. Bite area is dependent on the size of the animal's dental arcade and on sward height and density. Time per bite can be split into the sum of the time required to collect and sever a bite, which is considered independent from bite mass, and the time required to masticate a bite, which is dependent on its mass and its resistance to chewing (Parsons *et al.*, 1994). Finally, intake rate increases with bite mass which in turn increases with both sward height and density.

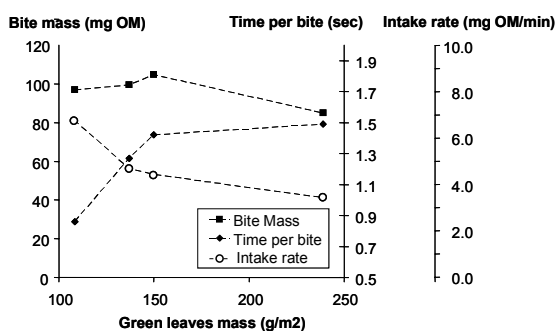


Figure 1 Bite characteristics and intake rate in sheep grazing a maturing and accumulating cocksfoot sward at low stocking rate (5 ewes on 3000 m²) from April to September (from Garcia *et al.*, 2003a)

The geometry of the biting process combined with a representation of the vertical distribution of sward biomass supports the mechanistic modelling of intake rate (Parsons *et al.*, 1994; Baumont *et al.*, 2004) and gives satisfactory predictions on vegetative swards. Based on this approach, it can be predicted that intake rate could be maximised by increasing bite mass. However, bite mass may be limited by the pseudostem, which has been suggested to constitute a physical barrier to bite depth due to the greater resistance to defoliation related to its layered structure and higher fibre content (Illius *et al.*, 1995). Even for large ruminants that have enough strength to sever pseudostems (Griffiths *et al.*, 2003), deeper biting should also decrease the quality of the plant material ingested, as the nutritive value of the grass generally decreases from the top to the bottom of the sward (Delagarde *et al.*, 2000). When the composition of the sward is more complex, as is the case on maturing swards containing reproductive material, sheep have been shown to significantly increase time per bite in relation to selective behaviour for green leaves (Prache *et al.*, 1998; Garcia *et al.*, 2003a). Bite mass remained stable throughout the course of the season, although biomass strongly accumulated in the sward (Garcia *et al.*, 2003a, Figure 1). This behaviour in favour of bite quality decreases intake rate, indicating that sheep did not adopt a strategy of intake rate maximisation only. Rather, they would try at the bite level to optimize both the quality of the plant material ingested and the intake rate.

During a grazing sequence, animals frequently face a choice between patches differing in vegetation structure and/or quality. When patches differ only by their sward height, cattle have been shown to select the feed that provided the highest food intake rate (Distel *et al.*, 1995). Similar results have been reported for sheep (Kenney & Black, 1984) and goats (Illius *et al.*, 1999) presented with a choice of different forages or plant species, when the forages giving higher intake rate also had a higher quality and energy intake rate. In contrast, preferences of sheep between forages providing similar intake rates were in accordance with differences in nutritive value (Baumont *et al.*, 1999). However in these experiments, animals did not really face a trade-off between quality and quantity, unlike when they have a choice between frequently and infrequently grazed patches.

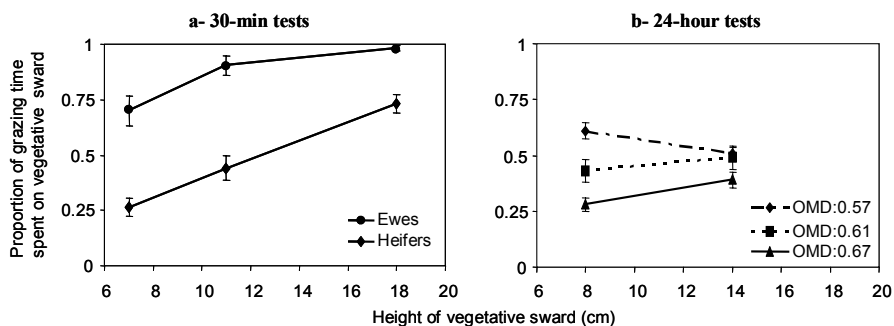


Figure 2 Diet choice between a reproductive and a vegetative sward according to height: a- effects of species (sheep and cattle) during a short-term test (from Dumont *et al.*, 1995 a; b); b- effects of the decreasing quality of the reproductive sward (OMD = organic matter digestibility) on heifer's choices on a day-to-day scale (from Ginane *et al.*, 2003)

Frequently grazed patches remain of high quality (digestibility) but low availability, and provide a low intake rate. Conversely, available biomass accumulates on infrequently grazed

patches that can allow a high intake rate of lower quality plant material. To simulate this situation, Dumont *et al.* (1995a; b) offered sheep and cattle a choice between a reproductive sward of high height/low quality and vegetative swards of low height/high quality. These experiments revealed that differences in quality were important, and sheep clearly preferred the vegetative swards except at the lowest height. Heifers, which are disadvantaged on short swards where bite depth is limited (Illius & Gordon, 1987), showed an overall lower preference for vegetative swards than sheep, and their switch to the reproductive sward was more pronounced (Figure 2a). Garcia *et al.* (2003b) investigated in sheep how short-term preferences between more or less intensively grazed swards evolve during the grazing season. During spring and early summer, differences in quality were low or absent and animals preferred the less grazed and tall patches that allowed easier selection of green leaves. In late summer, their preference switched to the more intensively grazed patches that were of higher quality due to vegetative regrowth. Criteria characterizing relative quality, such as relative abundance of green leaves or relative digestibility, were able to explain the observed choices during the grazing season. This suggests that animals integrate both intake rate and quality at the patch choice stage, and should therefore act as energy intake rate maximisers (Tolkamp *et al.*, 2002).

This should particularly apply when the preferred patches are dispersed spatially, implying moving costs for the grazing animal in terms of time and energy. Short-term tests have shown that sheep and cattle are able to integrate these costs and modify their choices accordingly. They decreased their preference for a good-quality hay, either when the amount offered (reward) per distance walked decreased (Dumont *et al.*, 1998) or when the difference in quality between the reward and another lower quality hay available without moving decreased (Ginane *et al.*, 2002a). In both experiments, the ewes and heifers selected the food option that maximised their rate of energy intake, as predicted by the optimal patch choice model. However, the choices were suboptimal and conformed to an overmatching pattern in favour of the good-quality forage (Senft *et al.*, 1987).

Balancing digestive and time constraints to optimise intake and diet choice

At the day-to-day scale grazing animals have to satisfy various nutritional needs in the time that they can spend grazing. Optimal trade-offs between quantity and quality may vary with the time scale, i.e. between short-term rate of food intake and long-term rate of nutrient assimilation (Wallis de Vries & Daleboudt, 1994; Newman *et al.*, 1995; Wilmshurst *et al.*, 1995). The regulation of diet choice and intake integrates digestive and nutritional feedbacks which govern the balance between motivation to eat and satiety, and which modulate feed preferences (Baumont *et al.*, 2000). The longer time scale also integrates behavioural compensatory mechanisms incorporating walk speed between patches (Roguet *et al.*, 1998), biting rate and grazing time (Taweel *et al.*, 2004).

Herbivores faced with a quantity-quality trade-off on a long-term scale were shown to selectively graze high quality patches of low to intermediate height or biomass (Wallis de Vries & Daleboudt, 1994; Wilmshurst *et al.*, 1995; Ginane *et al.*, 2003). This behaviour does not maximise short-term intake rate but would allow the animals to maximise their energy intake on a daily basis (Fryxell, 1991). Indeed, digestible organic matter intake probably has to be considered as the currency the animals want to maximise on a daily basis and beyond. Digestible organic matter intake integrates both the quality and the total quantity of food ingested, and a given level may result from a wide range of theoretically possible strategies from maximising quality to maximising quantity. Maximising quality implies high selective

behaviour for parts of plants or patches of high digestibility that are often of low accessibility. This option reduces intake rate and increases the time spent grazing. Maximising quantity implies less selective behaviour and the processing of less digestible material through the digestive tract. The trade-off between quantity and quality has to take into account the link between behavioural and digestive constraints (Baumont *et al.*, 1990). Progress in integrating intake and digestion has been achieved by mechanistic modelling (Illius & Gordon, 1991; Sauvant *et al.*, 1996). The latter proposed a self-regulated intake model in which the decision whether to eat or not is taken every minute by comparing a motivation-to-eat function with a satiation function based on digestion and a metabolic sub-model. Time spent eating is governed by the balance between motivation to eat, which depends primarily on energy demand, and satiation which integrates the energy supply and the fill effect of the ingested forage, based on its digestion kinetics in the rumen (Baumont *et al.*, 1997). This model has recently been extended to grazing integrating the intake rate response to sward characteristics (Baumont *et al.*, 2004). A simulation, using this model of how intake is regulated from short sward of high quality to tall sward of lower quality, is illustrated in Figure 3. If dry matter intake increases with sward height, despite the decrease in sward quality, digestible organic matter intake is maximised for the combination of highest quality and height. When the sward is shorter, the increase in grazing time does not fully compensate for the decrease in intake rate. When the sward is higher and of lower quality, intake rate and dry matter intake increase but digestible organic matter intake decreases. The higher satiation effect of ingesting lower quality plant material limits the time spent grazing. Predictions made using this model are in favour of prioritising quality, in accordance with the model developed by Hutchings & Gordon (2001) stating that the 'digestibility' strategy is the most efficient.

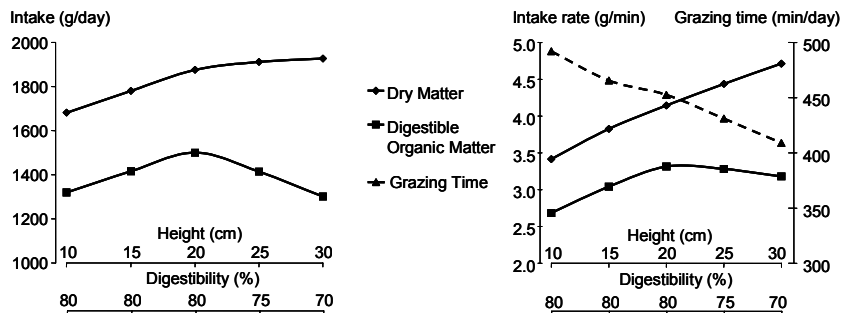


Figure 3 Prediction of intake rate, grazing time and daily intake in sheep with concurrent variations in sward height and digestibility. Data simulated using the model developed by Baumont *et al.* (2004).

In the field, grazing time is widely used by ruminants as a way of adapting to a decrease in availability of the feeding resource (Allden & Whittaker, 1970; Penning *et al.*, 1991; Rook *et al.*, 1994; Gekara *et al.*, 2001). In choice situations too, cattle and sheep have been shown to increase their grazing time on the preferred sward as its accessibility decreased while a lower quality alternative was simultaneously offered (Hester *et al.*, 1999; Rook *et al.*, 2002; Ginane *et al.*, 2003). By experimentally investigating animal choices as the pressure of constraints increases, it may be possible to estimate which factor in the quantity-quality trade-off is first prioritised. An experiment conducted throughout the grazing season with sheep at different

stocking rates showed that they constantly maximised the quality of their diet in conditions of either low quantity-high quality (high stocking rate) or high quantity-low quality (low stocking rate) (Garcia *et al.*, 2003a). In choice experiments with a vegetative sward height constraint, heifers have been shown to maintain or lengthen the proportion of their grazing time spent on short vegetative swards compared to reproductive swards, thereby revealing their priority for diet quality (Ginane *et al.*, 2003, Figure 2b). When the daily time available for grazing was strongly limited, heifers maintained their choice for the vegetative sward at the expense of total intake (Ginane & Petit, 2005).

However, since grazing time is not indefinitely increasable, especially for producing animals with high nutritional requirements that need a long basal grazing time (Gibb *et al.*, 1999) and, since digestive regulation limits the large intake of rapidly ingestible material, animals are unlikely to behave in an all-or-nothing way, and the optimal trade-off would be to ingest both alternatives in relative proportions depending on the nature and intensity of the harvesting and food-processing constraints. Furthermore, mixed diets are the general rule in choice situations (Duncan *et al.*, 2003) and the nutritional hypotheses put forward in the literature vary greatly according to the choice situation. For example, sheep have been shown to eat straw (Cooper *et al.*, 1995) or 10-mm polyethylene fibres (Campion & Leek, 1997) to prevent rumen disorders and restore normal rumination activity when fed a high concentrate diet. The partial preference of heifers for clover *versus* grass may be due to a prevention of sub-clinical bloat status (Rutter *et al.*, 2004). Finally, goats at turn out appear to seek herbage species that are relatively low in protein and rich in fibre in order to reduce the variation in ingesta composition as far as possible given the large seasonal variations in vegetation composition (Fedele *et al.*, 1993). An underlying mechanism would be the ability of animals to learn the post-ingestive consequences of their previous choices. Faced with trade-offs between food concentrations of energy and protein (Wang & Provenza, 1996) or energy and toxin (Ginane *et al.*, 2005), herbivores showed they were able to perceive these characteristics and to adapt their diet choices accordingly. As post-ingestive stimuli need to be periodically reinforced, the animal regularly has to re-evaluate the benefits and costs of the different choices.

Optimising spatial utilisation of a pasture

The search for areas that allow the best trade-off between intake quantity and quality induces repeated grazing on such areas. It can be hypothesised that when animals perceive sward heterogeneity, their foraging walks are no longer random but structured to respond efficiently to the sward structure (Parsons & Dumont, 2003). Three behavioural mechanisms are involved in optimising the spatial utilisation of the resource: the modulation of foraging velocity (Shipley *et al.*, 1996), the use of spatial memory and visual cues (Edwards *et al.*, 1996; Dumont & Petit, 1998), and the modulation of foraging path sinuosity (Ward & Saltz, 1994). These behavioural mechanisms concur to modulate spatial utilisation through resource abundance or resource heterogeneity and complexity (Dumont *et al.*, 2002).

A persistent issue is to identify the spatial scales at which the animals perceive the heterogeneity of the pasture, and to characterise how animals modulate their foraging paths through resource abundance and heterogeneity. Garcia *et al.* (2005) have used fractal analysis to analyse the foraging paths of ewes grazing a continuously-distributed and spatially-limited resource. This method, which investigates the functional heterogeneity of a habitat (Marell *et al.*, 2002), can identify the heterogeneity at which the animal responds. It also provides insight into the hierarchical levels of foraging behaviour (Nams, 2005). In this study, the vegetation did not exhibit any spatial distribution before the experiment and ewes adopted a

random walk at the beginning of the grazing season. This corresponds to the absence of any optimal searching scale, and remains the most advantageous as it reduces the costs of searching in homogeneous non-patchy environments (Foccardi *et al.*, 1996). The vegetation structure became more complex after a few weeks of grazing, and the sheep modulated their foraging paths through resource abundance and/or sward structure. A breakpoint was identified at 5 metres, for which the fractal dimension is always low, meaning that the animal's path is straighter at that scale (Figure 4). Within a scale of 0-5 metres, the modulation of sinuosity was not linked to sward abundance and structure, and sheep mainly developed behavioural adaptations at bite and feeding station scales (Garcia *et al.*, 2003a). Within a scale of 5-12 metres, the behavioural mechanisms involved the modulation of foraging path sinuosity, which implies an adaptation of spatial utilisation in relation to the perception of the environment. Grazing paths were tortuous on tall swards in summer (higher fractal dimension), and straighter on heterogeneous, well-structured swards showing visual cues in the autumn. The breakpoint for fractal dimension across spatial scales may thus indicate the hierarchical threshold in spatial adaptation of the foraging behaviour of grazing herbivores (Garcia *et al.*, 2005). This experiment suggests that the determinants of sward heterogeneity organisation, described in Adler *et al.* (2001), are rather more complex in grassland systems than in moorlands or forests, where the distribution of the resource is discrete and more easily perceptible by the foraging animal. Fractal dimensioning proved to be a useful synthetic tool for identifying the scales of inter-patch and intra-patch movements.

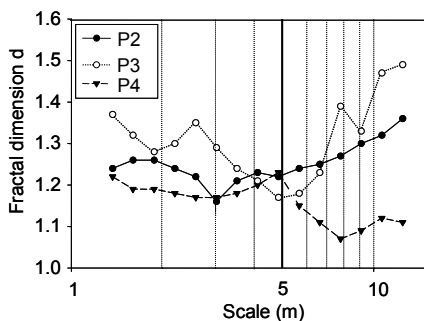


Figure 4 Evolution of the fractal dimension of foraging paths across spatial scales between 1 to 12 m in ewes grazing a cocksfoot sward managed at a low stocking rate (5 ewes on 3000 m²) in May (P2), July (P2) and September (P4) (from Garcia *et al.*, 2005).

Consequences on vegetation dynamics

Few studies have documented the effects of large herbivores on the spatial heterogeneity of the grazed vegetation (Adler & Lauenroth, 2000) and the consequences on vegetation dynamics at different spatial and temporal scales (Parsons *et al.*, 2000). Repeated grazing of preferred patches and partial rejection of others leads to a bimodal frequency distribution of patch states in the plot (Parsons & Dumont, 2003). When grazing pressure is low, this means that large herbivores focus their grazing activity, only on a part of a pasture. A macro-heterogeneity, characterised by the coexistence of well grazed areas (low quantity, high quality) and partially-rejected areas (high quantity, low quality), will emerge. The spatial organisation of these areas could be influenced by the localisation of several attractive points such as water and sleeping areas.

Foraging behaviour determines the severity and frequency of defoliation on patches and thus the quality and quantity of the biomass resulting from the post-grazing regrowth. When animals regraze previously defoliated areas, they maintain the sward in a more juvenile and more digestible state (Donkor *et al.*, 2003). This, together with other possible mechanisms including a reduction of senescent material and an increase in below-ground available nitrogen, creates a positive feedback between grazing and forage quality (Adler *et al.*, 2001). This positive feedback promotes the continued use of previously grazed patches.

In many cases the reduction of growth is less than expected from the proportion of biomass removed, which means that the vegetation is able to develop a compensatory response to defoliation (Ferraro & Oestersheld, 2002). The different mechanisms involved in this compensatory response may be linked to plant environment (the decrease of self-shading), plant physiology (an increase of photosynthetic rate, the reallocation of growth from other parts of the plants, reduction of leaf senescence and greater light use efficiency) and morphogenetic adaptation (an activation and proliferation of axillary meristems: tillering and clonal development). The compensatory response increases with defoliation intensity, and a longer recuperation time after defoliation favours the occurrence of a compensatory response (Ferraro & Oestersheld, 2002). Garcia *et al.* (2003b) have shown that sheep graze patches at relatively low frequency but high severity, rather than the reverse.

While patch grazing may produce short-term positive feedbacks, changes in composition may cause negative feedbacks. Pastor *et al.* (1997) suggested that when the short-term increases in forage quality caused by grazing are outweighed by the compositional shift towards unpalatable or low nitrogen plant species, patch grazing cannot persist. This is more likely to occur in ecosystems where very distinct functional plant groups compete (i.e. grasses *vs.* shrubs). While there is evidence that grazing may influence plant diversity, it is not clear whether changes in spatial pattern drive this effect. At the patch scale, grazing may affect plant diversity by reducing local competition between species (Collins *et al.* 1998), but also through selective defoliation which creates an asymmetric competition for the preferred species. At a larger scale, these modifications may be caused by the uneven use of the grassland by grazing animals, an uneven distribution of excreta from grazing animals or an uneven dispersal of plant seeds through the faeces across a grassland (Shiyomi *et al.*, 1998).

A more functional approach which describes species from a functional rather than a taxonomic perspective should help to capture the long-term evolution of the grazed ecosystem (Lavorel *et al.*, 1997). The use of quantitative traits (measurable characteristics on individuals), to which continuous numeric values can be assigned, has recently been advocated (Lavorel & Garnier, 2002). In a pasture managed for the long-term with a gradient of grazing intensity, Louault *et al.* (2005) identified three important functional groups based on four significant traits: lamina dry matter ratio, specific leaf area, elongated plant height and the start of flowering. The first group corresponds to competitive species that are tolerant to grazing, the second to small-sized conservative species, which avoid being grazed, and the third to large conservative species. The first two groups coexist in well-grazed pasture, whereas the third is present in tall non-defoliated areas. This leads to the hypothesis that the structural heterogeneity created by grazing could modify the community process, and induce some persistent divergence in pasture diversity.

Conclusion

Over the last two decades, investigations of biting behaviour, diet selection and intake at pasture have led to great advances in the understanding of plant-animal relationships. Selective grazing tends to optimise diet quality at the different levels of feeding behaviour. However, most of the studies were conducted in simple experimental conditions – mono or bi-specific, vegetative or reproductive swards – and often on a short-term basis. In more complex situations like natural grassland of high diversity, predictions of diet selection, intake and the large herbivores' impact on the vegetation remain hazardous. The nutritive value – and thus animal performance – of a diet containing a high number of various plants is difficult to predict, as the digestive effects of forage associations are poorly understood. Forage diversity should stimulate intake (Ginane *et al.*, 2002b), but the respective roles of digestive and behavioural factors have yet to be established. As plant diversity increases, the ability of large herbivores to discriminate and make appropriate associations between plant characteristics and nutritional consequences should decline. Further studies need to be conducted to increase our understanding of the relative importance of pre- and post-ingestive cues in diet selection in complex situations. Integrative modelling linking intake and digestion should be further developed to improve the prediction of animal response to various types of pastures.

The development of a predictive understanding of diet selection in complex situations should allow a more effective use of herbivores as “landscape engineers”. This implies extending our current knowledge to wider temporal and spatial scales, and integrating the related complexity. Modern techniques, for example associating GPS localisation and marker techniques to estimate diet composition, as proposed by Milne (2002), should provide deeper analysis of the relationship between plant diversity, vegetation heterogeneity and diet selection. Progress in modelling and computer science should allow the development of long-term and spatially-explicit models that can be usefully applied to simulate the effects of plants, animals and management characteristics (Baumont *et al.*, 2002).

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