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How do sheep exploit pastures?
An overview of their grazing behaviour from homogeneous swards to complex grasslands

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SUMMARY – A better knowledge of the interactions between plants and herbivores is needed to define appropriate management strategies for animals and grasslands within the context of sustainable grazing systems. Small ruminants exploit a wide range of resources from homogeneous swards and grass-clover associations to highly biodiverse grasslands and shrubby rangelands. In this paper, we first analyse how sheep graze homogeneous swards or simple plant associations, which requires considering prehension and digestive constraints. In spatially heterogeneous environments, herbivores need to gather information about vegetation distribution and quality, and use that information to forage efficiently. We therefore then provide an overview of what we propose are some of the key cognitive and social processes that determine the use of vegetation mosaics by sheep. Finally, we identify the lack of knowledge in how herbivores exploit diverse and complex grasslands, and we consider discrimination and generalisation behaviours as well as animals' response to environmental uncertainties. The impact of sheep on the evolution of complex grasslands is illustrated by two medium-term surveys of sward biodiversity outcomes. We conclude on shrubland utilization by sheep and goats, and on research needs in order to extrapolate the knowledge from studies on grazing sheep to the management of shrublands by small ruminants.

Keywords: Biodiversity, foraging costs, grazing, sheep, social behaviour, uncertainties, vegetation mosaics.

***RESUME –** "Comment les ovins exploitent-ils les pâturages ? Aperçu de leur comportement de pâture, à partir de prés homogènes jusqu'aux herbages complexes". La connaissance des relations entre les herbivores domestiques et les végétations qu'ils exploitent est essentielle pour définir des modes de conduite des troupeaux répondant à un objectif de durabilité des systèmes d'élevage. Les petits ruminants exploitent une large gamme de ressources allant des couverts monospécifiques et des associations graminées légumineuses jusqu'aux prairies naturelles diversifiées et aux landes associant strates herbacée et ligneuse. Dans cette revue, nous commençons par expliquer comment les ovins exploitent des couverts mono- ou bispécifiques, ce qui nécessite de prendre en compte les contraintes de prélèvement et les contraintes digestives. Dans les végétations en mosaïque, les herbivores apprennent la distribution et la qualité des sites alimentaires, et utilisent cette information pour augmenter leur efficacité de recherche alimentaire. Ceci nous amène à discuter les mécanismes de mémorisation, ainsi que les coûts et les bénéfices de la sociabilité sur les choix individuels. Enfin, nous identifions un manque de connaissance sur les choix alimentaires des herbivores en milieu complexe, et la nécessité de mieux appréhender les processus de discrimination et de catégorisation des aliments par les animaux, ainsi que les tactiques comportementales qu'ils mettent en œuvre pour s'adapter aux variations imprévisibles de leur environnement alimentaire. L'impact du pâturage ovin est illustré grâce à deux suivis à moyen terme de la biodiversité de couverts herbacés exploités selon différents modes de conduite. Nous concluons sur les spécificités des milieux associant herbacées et ligneux, et sur les connaissances déjà acquises sur caprins, dont la poursuite est nécessaire afin de mieux gérer ces différents types de couverts.*

***Mots-clés :** Biodiversité, comportement social, coût de recherche, imprévisibilité, ovins, pâturage, végétation en mosaïque.*

Introduction

A better knowledge of the interactions between plants and herbivores is needed to define appropriate management strategies for animals and grasslands within the context of sustainable grazing systems. Sustainability focuses on the maintenance of productivity and stability in the soil, plant and animal components of pastoral systems, and further considers the economic and social impact of management practices. Small ruminants exploit a wide range of resources from homogeneous swards and simple associations, such as grass-clover swards, to highly biodiverse grasslands and shrubby rangelands. They differ from large ruminants for their nutrient requirements relative to gut capacity, their ability to feed selectively and to graze short swards, and to a lesser extent their capacity to digest low quality foods. Consequently, behavioural adjustments of small ruminants in response to low food availability are chiefly geared to maintaining the nutrient value of the diet, whereas large ruminants first aim to maintain their rate of dry matter intake (Demment and Greenwood, 1988; Hodgson *et al*., 1991; Dumont *et al*., 1995). In addition to inter-individual variations in selectivity (Prache *et al.*, 1998b), the foraging behaviour of sheep has also been shown to vary with physiological stage (Newman *et al*., 1995), feeding motivation (Dumont *et al*., 1995), previous grazing experiences (Arnold and Maller, 1977; Nolte *et al*., 1990; Ramos and Tennessen, 1992), body weight (Prache *et al.*, 1998b), and consequently with breed (Newborn *et al*., 1993; Du Toit, 1998; Osoro *et al*., 1999).

Compared to animals fed indoor on dry forages, grazing animals face prehension and research challenges. Initial work on the grazing behaviour of herbivores largely focused on prehension and mastication constraints onto homogeneous swards, according to their height and density. Bite dimensions and jaw movements of the animals have been exhaustively described, and intake indirectly estimated as the product of bite mass, biting rate and grazing time (Penning *et al*., 1991; Ungar *et al*., 1991; Laca *et al*., 1992; Flores *et al*., 1993; Penning *et al*., 1994). This approach reached its limit as soon as swards were heterogeneous in height, so that it rapidly became obvious to describe (Gibb and Ridout, 1988) and take account of the spatial distribution of sward height in vegetation dynamics and foraging models (Schwinning and Parsons, 1999; Parsons *et al*., 2001). A radical change of paradigm resulted from the integration of mechanisms across spatial and temporal scales within a hierarchical model of foraging: Foraging from bites, through feeding stations, patches and feeding sites up to the long-term habitat is functionally defined by the herbivore's attributes and perception (Senft *et al*., 1987; Bailey *et al*., 1996). The response of herbivores to higher levels in the hierarchy constrain the operation of foraging behaviour at lower levels, whereas behaviour at lower levels can be used to explain higher level behaviour. This approach leads to consider the animal point of view about where and when to place their bites, and the patch as the crucial scale that constrains the efficient exploitation of resources. Beyond the idea that young herbivores learn from social models (Nolte *et al*., 1990; Thorhallsdottir *et al*., 1990), more emphasis has also been put recently onto the understanding of how social forces can directly alter feeding behaviour and plot exploitation due to the social grouping tendencies of domestic herbivores (Lawrence and Wood-Gush, 1988; Scott *et al*., 1995; Dumont and Boissy 2000; Sibbald *et al*., 2005a). This approach should be further favoured by the development of Agent-Based Models, which enable to simulate group behaviour from the local interaction between individuals (Dumont and Hill, 2004).

Although the dynamic of grazed systems depends on the interaction between plants, herbivores and environmental conditions over many generations and at spatial scales greater than the range of influence of any single organism, many specific features of the heterogeneity are induced by decisions made by herbivores about where and when to place their bites (Parsons and Dumont, 2003). In this review, we focus on how sheep graze pastures within an increasing gradient of complexity: The understanding of how they graze simple swards requires considering prehension and digestive constraints. Then, we discuss some of the key processes that determine the use of vegetation mosaics by sheep, which requires to integrate constraints relative to the search for food, and social interactions. Finally, we identify the lack of knowledge in how herbivores exploit diverse grasslands and we consider discrimination and generalization behaviours as well as the animals' response to environmental uncertainties. We illustrate our current thinking framework with two examples of medium-term surveys of vegetation dynamics in pastures grazed by sheep.

Grazing simple swards

The lowest level of decisions for an herbivore is the selection of bites within patches. Great progresses have been made in understanding the physical limitations arising from sward structure, that determine the bite characteristics and instantaneous intake rate (IIR) within a homogeneous patch (Prache and Peyraud, 1997). On the patch, IIR is represented as the ratio of bite mass to the time required to harvest and masticate it. These variables mainly depend on the ease with which herbage is gathered into the mouth, the resistance of herbage to fracture and mastication, as well as the presence of barrier components. On vegetative patches, intake rate is mostly determined by bite mass, and by the functional relationship relating time per bite to bite mass. Height of herbage and bulk density are the major determinants of bite mass (Laca *et al*., 1992). Time per bite is the sum of prehension time, which is considered to be independent of bite mass, and mastication time, which linearly increases with bite mass. The slope of this regression varies with herbage fibre content, and is for example lesser for legumes than for grasses (Newman *et al*., 1994). On reproductive patches, stems form physical barriers to defoliation that greatly affect bite mass, especially for selective herbivores such as sheep. Instantaneous IR is further impaired by an increased time required to prehend and masticate bites (Prache *et al*., 1998a). Green leaf mass per unit area has been shown to be the best predictor of bite mass and IIR across sward phenological stages (Prache, 1997; Prache *et al*., 1998b) and managements (Penning *et al*., 1994).

A higher level of decision is the choice of a new patch where to graze. When searching costs are negligible, herbivores generally prefer patches where they can eat at the faster rate (Roguet *et al*., 1998a). However, preference is not absolute and IIR is usually lesser than predicted by optimal patch choice models. For example, on adjacent monocultures of ryegrass (*Lolium perenne*) and clover (*Trifolium repens*) at the same height, the proportion of clover in the diet is generally around 70%, even though herbivores graze clover faster than grass (Parsons *et al*., 1994). Likewise, ewes offered a choice between adjacent monocultures of ryegrass and tall fescue (*Festuca arundinaceae*) at the same height included around 70% of ryegrass in their diet (Prache *et al*., 2002). The preference for a plant species is also sensitive to variations in sward height: On grass-clover associations, the proportion of clover in sheep diet decreases to 50% when clover was at 3 cm and grass at 9 cm (Harvey and Orr, 1996). We studied the relationships between intake rate and choices of sheep between vegetative and reproductive cocksfoot (*Dactylis glomerata*) patches (Prache *et al*., 1998b). The functional responses on vegetative and reproductive patches lead to the prediction that, according to an IIR maximization hypothesis, sheep should spend most time feeding on vegetative patches when these are high. They should partly switch to reproductive patches when the green leaf mass on vegetative patches goes below to 0.3 t DM/ha, which was equivalent to a 9 cm-high sward in this study (Prache *et al*., 1998a). This prediction is in good agreement with the preference measurements made by Dumont *et al.* (1995).

Additionally, a trade-off exists in grazed environments between staying in one patch (the cost of missed opportunity to feed in a higher quality patch) and moving to exploit a new patch (the cost of walking and searching for patches). Patch residence time is therefore a key variable linking both within and between temporal and spatial scales, and depends on the average profitability of the environment. The Marginal Value Theorem (Charnov, 1976) predicts that the optimal residence time on a patch should increase with both patch value and distance between patches. In general, tests of the model have shown good qualitative fit, but grazing herbivores usually achieve lower IIR than predicted by the model, by spending longer at any patch (Bazely, 1988; Roguet, 1997). Roguet *et al.* (1998b) found that during the grazing down phase of a vegetative and a reproductive cocksfoot sward, sheep adjusted their behaviour to resource depletion similarly on both swards, by decreasing the time spent grazing and the number of bites per feeding station. The initial tactic of foraging search was gradually abandoned in favour of a "lawn-mower" tactic, with few steps taken between feeding stations, and a higher walking speed.

The integrating of ingestion and digestion has progressed with the use of modelling techniques (Sauvant *et al*., 1996). The integration of short-term foraging decisions to daily intake necessitates linking IIR with satiation processes and with the animal's motivation to eat, but factors controlling feeding motivation remain poorly understood. Postingestive signals coming from the feed contribute to the satiation process. Ingestion and digestion are linked by the nutritive value and the fill effect of the ingested forages. The main factors influencing herbage intake are firstly the quality and the nature of the herbage, secondly the availability of the herbage and its architecture. The OM digestibility of herbage consumed determines its filling effect and *ad libitum* intake. During the first vegetation cycle, the digestibility of the forage and the voluntary intake of animals fed fresh forages indoor decrease sharply with the age of the forage (Demarquilly *et al*., 1981). Maintaining a leafy sward is therefore essential for providing high levels of intake in high producing animals. For legume species, the decrease in digestibility with the age of the plant has less effect on intake, due to lower cell wall content. Likewise, it is well known that intake is generally higher on legume and mixed grass/legume swards than on pure grass. Recent findings have demonstrated that offering a choice to animals may further enhance its motivation to eat. Champion *et al*. (1998) observed that lactating ewes offered adjacent grass and clover monocultures had greater daily intakes (+13%) than ewes fed on either pure grass or pure clover. Recently, Cortes *et al*. (2005) recorded the ingestive behaviour and intake of dry ewes fed on either pure ryegrass, pure tall fescue swards, or adjacent ryegrass-fescue monocultures, all swards being maintained at 9 cm. In order to test a management practice allowing to limit the risk of overgrazing the preferred sward and undergrazing of the less-preferred one, the effect of grazing two monocultures successively was tested, fescue from 09:00 to 16:00 h and ryegrass from 16:00 to 9:00 h. This study demonstrated that offering a choice to the animals led to a significant increase in intake (+14% compared to pure swards) whether the monocultures were offered simultaneously or successively. This was mediated by a significant increase in grazing time rather than in intake rate.

Modelling intake has been attempted either by using empirical equations based on animal and sward characteristics (Delagarde *et al*., 2001), or by a mechanistic approach based on the integration of processes occurring at a finer scale (Baumont *et al*., 2004). The first models consider swards as a homogeneous patch. In continuously grazed swards, the animals graze the upper stratum which is mainly composed of green leaves, and a maximum intake is reached for a sward height of about 6 cm in sheep (Penning *et al*., 1991). Under this threshold, the animal is no longer able to compensate the decrease in IIR by a proportional increase in grazing time. Under rotational or strip grazing, animals can be forced to graze into the lower strata that contain more pseudostem and dead material. Under slow rotational grazing, it has been shown that the intake of lactating ewes is better related to green leaf mass per hectare than to sward height (Penning *et al*., 1994). Animals also increased their daily grazing time in order to respond to a decrease in IIR (Prache *et al.,* 1998b). In the latter stages of sward defoliation, grazing time decreased, because the animals no longer spent a lot of time and energy on selecting only a small quantity of green leaves among stems and dead material, or because they anticipated a change of plot. The ewes gave-up later on the reproductive sward, which in relation to their lower instantaneous intake rate onto this sward, could be related to a will to maintain a minimum daily intake. This was confirmed by García *et al.* (2003), who directly measured daily intake and organic matter (OM) digestibility of the diet selected by sheep over the year in two cocksfoot plots at different stocking rates. In spring, when grass was abundant, the ewes reached levels of intake of digestible OM between 1000 and 1250 g/day. From summer, the higher stocking rate resulted in a decrease in resource biomass, whereas the lower stocking rate resulted in the accumulation of low quality material. In both plots, sheep foraged selectively on green leaves. Consequently, intake of digestible OM decreased to 800 g/day, mainly due to a decrease in bite mass at the high stocking rate, and a decrease in diet digestibility and in bite mass at the low stocking rate. On both plots, the ewes increased their grazing time to cover their needs, but did not increase it enough to maximize daily intake, due to the costs of harvesting the best sward components. In the case of intensive rotational or strip grazing, herbage mass declines significantly during the day and herbage availability is then generally described in terms of herbage allowance, i.e. in kg OM/kg liveweight/day. Under these conditions, intake increases curvilinearly with herbage allowance, and green leaf allowance is a better predictor of herbage intake than total herbage allowance (Delagarde *et al*., 2001).

An example of a more mechanistic model is given by Baumont *et al*. (2004) who developed a model of intake rate integrating sward structure and foraging decisions, based on the nutritional requirements and digestive processes of an animal. The initial model simulating intake of animals fed indoor (Sauvant *et al*., 1996) was made of a ruminal digestion sub model in interaction with a feeding motivation sub model, the decision to feed being mediated by the comparison of the outputs of the two sub models. Two new sub models were added in order to deal with pasture conditions: (i) a sward-horizon sub model describing the sward as vertically-distributed horizons, each characterized by its nutritive value and potential IIR; and (ii) a foraging decision sub model describing preferences between horizons, which is based upon their relative abundance and potential IIR. In this way, interactions between vegetation characteristics and the animal's internal state are dynamically integrated from short-term decisions at the bite scale, to dry matter intake over several days. Satisfactory validations were obtained on data sets recorded under either rotational or continuous grazing (Penning *et al*., 1994; Prache *et al*., 1998b). A further development would be to simulate behaviour and intake on swards associating several plant species, by using a general framework based on preferences rules.

Grazing in a mosaic

Until now, we have considered how herbivores place their bites in space and time, where search costs are less than handling costs and these can overlap, so there are no additional search costs for foraging. Grazing selectively can however substantially increase searching costs and reduce daily intake (Champion *et al.*, 1998). In a fine-grained mixture of two food items, costs increase substantially with the degree of selectivity of the animal (Prache *et al.*, 1998b) and if the preferred food becomes less abundant (Thornley *et al.*, 1994). Optimizing the desire for a mixed diet and the cost/benefit ratios of foraging predicts complex selective foraging phenomena. Thornley's model suggests that if searching costs are very high, the animal would be expected to eat whatever is in front of it. With intermediate costs, the animal would be expected to select their preferred diet when the composition of the vegetation is close to that mixture, but in situations were the abundance of the preferred food in the vegetation is lower, animals would be expected to progressively forgo preference (Fig. 1a).

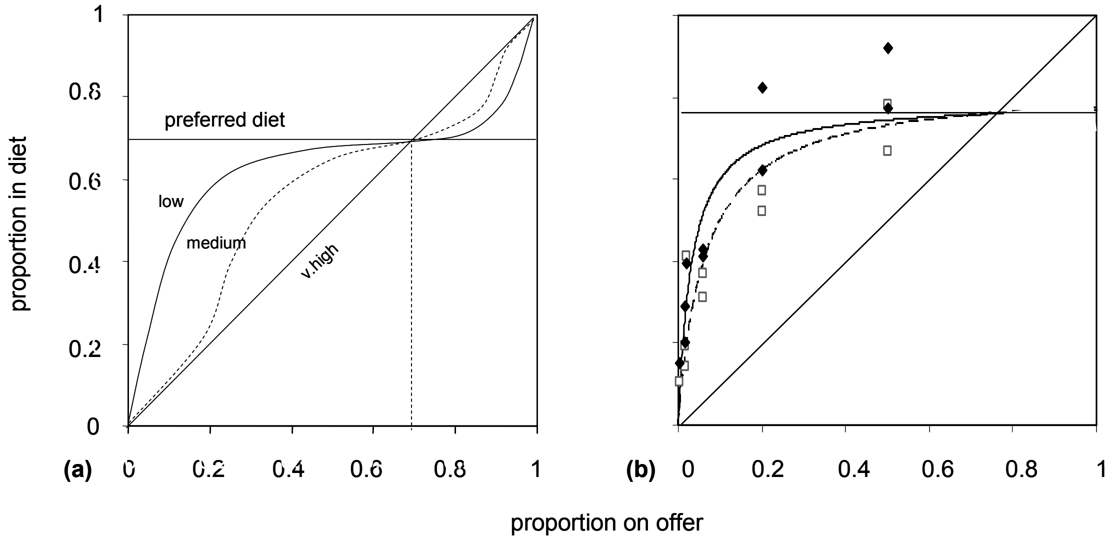


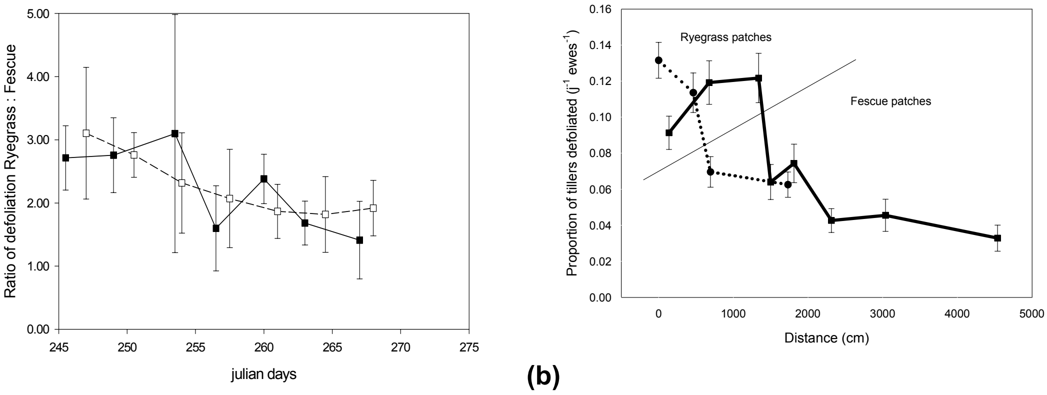
Fig. 1. (a) The effects of partial preference, and of low, medium, and very high foraging costs on the proportion of preferred food in the diet, in relation to its abundance in the vegetation, as predicted by a model that seeks the optimal trade-off between the benefits and costs of foraging selectively (Thornley *et al.*, 1994). (b) Data from a range of sources show the effect of aggregated (solid symbol) and dispersed (open symbols) spatial distribution of food are consistent with differences in foraging costs (Dumont *et al.*, 2002).

The foraging environment of an herbivore is often composed of a mosaic of preferred vegetation patches distributed within a lower quality background. Where the distribution of preferred patches is not detectable at a distance, the use of spatial memory allows animals to walk directly to the patches offering high food rewards, and consequently decreases searching costs. Sheep can quickly learn the distribution of a preferred food offered in bowls in an arena (Edwards *et al.*, 1996) or hidden within a pasture (Dumont and Petit, 1998), or grass species planted in patches mown to look like surrounding vegetation (Dumont *et al.*, 2000). Sheep also learn the amount of food found in the patches and better exploit those offering a higher reward (Dumont and Petit, 1998; Dumont *et al.*, 2000). Dumont and Hill (2001) have modelled that the memory capacity of sheep mostly affect their searching success when the density of preferred patches in the environment is intermediate. We can now return to the issue of heterogeneity and the prospects offered by memory capacity to reduce foraging costs. Data from a range of studies, in which preferred patches were distributed in different ways and at different abundances, are plotted together in Figure 1b, which shows that herbivores are more successful in selecting preferred patches where they are more aggregated (Dumont *et al.*, 2002). Relating this to the theoretical responses to different overall costs of foraging (Thornley *et al.*, 1994), the data are consistent with the aggregated food leading to lower foraging costs.

However, when Dumont *et al.* (2002) compared the exploitation of preferred ryegrass patches covering 6% of the plot area according to their distribution within a tall fescue background, they observed that sheep no longer increased their use of ryegrass when it was aggregated into a single large (24 x 24-m) patch rather than into eight medium-sized (8 x 9-m) patches. Within the highly aggregated pattern, an animal wanting to graze ryegrass while its social peers were on fescue would often have to separate from the group. Indeed social behaviour can be both beneficial and detrimental to individual foraging success. Herbivores gather information from their peers about vegetation distribution and quality, but conspecific attraction and competition for food can also alter their foraging behaviour and distribution within plots (Arnold, 1985; Dumont and Hill, 2001). In stable groups, social behaviour can impose motivation conflicts for animals that are reluctant to graze away from their peers. Under range conditions, social cohesiveness affects the distribution patterns of sheep together with fluctuations in food availability (Arnold, 1985). At pasture, we observed how sheep foraged within a narrow grass field that contained an area of preferred food (a tall grass patch) at a distance of either 15 or 50 m from where, at the end of the field, there was a sealed pen containing a group of their social peers (Dumont and Boissy, 2000). At 15 m, the usage of the preferred patch was unaffected by whether the sheep grazed alone or in a group. Conversely, sheep were reluctant to graze away from their parked peers to use the preferred patch if it was located at 50 m, especially when they grazed alone or in a group of two. The ewes were always more vigilant within a small group.

In addition to group size, the strength of social links within the group affects diet and habitat selection in grazing herbivores. Affinity relationships between pairs of animals are one of the most striking features of social organisation in groups of herbivores, and are more particularly responsible for the cohesion of groups (Arnold, 1985; Boissy *et al*., 2001; Fisher and Matthews, 2001). The degree of affinity with social partners modulates the foraging behaviour of individual animals in different ways. Feeding preferences are partly learned from social models and the degree of affinity of lambs with these social models affects their acceptance of a new food (Thorhallsdottir *et al*., 1990). Social group also modulates the exploitation of feeding sites for their discovery, utilization and leaving decisions (Dumont and Boissy, 1999). In a stable group of lambs, with animals conditioned to prefer either wheat or milo, the feeding choices and foraging location of individuals were largely determined by the behaviour of the other animals of the group, whereas in newly constituted groups where affinities had not developed yet, lambs always expressed their own preferences (Scott *et al*., 1995). Under free ranging conditions, social interactions vary in importance, according to the affinity between individuals. When sheep from different flocks are mixed together, they avoid animals from the other flocks (Lawrence and Wood-Gush, 1988; Warren and Mysterud, 1993). Social affinities can however have a positive effect on the ability of animals to express their feeding preferences. Boissy and Dumont (2002) used the motivation conflict test described above, with 35 m between the feeding and social attractants, and ewes tested with either familiar or non familiar conspecifics. Ewes tested with familiar conspecifics more easily left the group of parked peers to reach the preferred feeding site located away, grazed it longer, vocalised less and were less vigilant compared to ewes grazed with unfamiliar animals. Inter-individual distances were also reduced when ewes grazed with familiar conspecifics. Sibbald *et al*. (2005a) recorded within-group sociability indices at pasture as the tendency to stay close to the other animals of the group. Then, they observed that sheep with higher sociability indices were more reluctant to leave a group of parked peers to feed in bowls of pellets located at a distance, had lower maximum and average distances from the parked peers, hesitated longer before starting to feed in the bowls and were more vigilant (Sibbald *et al*., 2005b). When vegetation is heterogeneous and the preferred items are distributed in small, widely-spaced patches, it is likely that individuals who move away from their peers will more readily exploit these patches. We made a first comparison of the use of such patches within a mosaic by groups of four ewes being either unfamiliar, familiar with low sociability indices or familiar with high sociability indices. We concluded that unfamiliar ewes were more successful grazers than the other types: they spent 73% of grazing time feeding on preferred patches *vs* 62.5 and 65.5% for the familiar ewes with low and high sociability indices (Erhard *et al*., unpublished data). The use of vegetation mosaics by sheep is thus partly determined by social relationships between animals, such as their general sociability and their attraction for some particular peers. The recent development of Agent-Based Models, which enable to simulate group behaviour from the local interaction between individuals, should promote the inclusion of social-oriented cognition in foraging models. Such models can perfectly integrate the experimentally-demonstrated laws, processes and theoretical frameworks developed in herbivore foraging, and should therefore offer opportunities to improve our knowledge of mosaic exploitation by herbivores (Dumont and Hill, 2004).

Grazing within a mosaic requires not only considering patch use, but also the dynamics of sward consumption across patch boundaries. It has indeed been assumed that preferred patches should attract herbivore groups, and that the exploitation of background vegetation should therefore be higher around the preferred patches. Carrère *et al*. (unpublished data) compared the defoliation activity of sheep in 1-ha tall fescue plots, in which ryegrass was either aggregated into a single 24 x 24-m patch or eight 8 x 9-m patches. The two plots were continuously grazed by a flock of 13 ewes during one month. Either at a daily or a monthly scale, and whatever the aggregation pattern, ryegrass patches exhibited a greater probability of defoliation than the tall fescue background (0.117 *vs* 0.059 d^{-1} ewe^{-1}). Consequently, the ryegrass patches were maintained at a lower sward height than fescue (4.73 *vs* 6.73 cm), without any difference between the two aggregation levels (Dumont *et al.*, 2002). Ewes defoliated ryegrass with a very variable time pattern along the grazing period, with the alternation of periods of high defoliation probability (preference expression) and periods of low defoliation probability (rejection of very short patches). Variations were sharper in the 24 x 24-m pattern (Fig. 2a). For the tall fescue background, the further away from a ryegrass patch, the lesser the probability of being defoliated (Fig. 2b). The defoliation probability of fescue tillers was around 0.065 d^{-1} ewe^{-1} in the 1 m crown around a ryegrass patch, 0.043 d^{-1} ewe^{-1} in the 5-25 m crown and fell to 0.033 d^{-1} ewe^{-1} at 45m. The association between spatial and temporal variability in the utilisation of vegetation mosaics combined with a highly selective foraging behaviour of grazing sheep will determine long-term vegetation dynamics.



(a) **(b)**

Fig. 2. (a) Evolution of the ryegrass to tall fescue defoliation ratio according to ryegrass distribution: a single 24 x 24-m patch (solid line) or eight 8 x 9-m patches (dotted line). (b) Evolution of the proportion of defoliated tillers (d/ewe) according to ryegrass distribution: a single 24 x 24-m patch (solid line) or eight 8 x 9-m patches (dotted line). The distance axis represents the distance between measured quadrat and the middle of the nearest ryegrass patch. The first three points of the solid line and the first two points of the dotted line are situated in the ryegrass patch (Carrère *et al.*, unpublished data).

Grazing diverse grasslands

The ability of herbivores to learn the post-ingestive consequences of previous choices has been largely demonstrated in "simple" experimental trials, in which a few feeds were offered simultaneously or successively to the animals (Provenza, 1995). When grazing diverse and complex grasslands, herbivores simultaneously exploit a large number of food plants, which results in the individual effect of the consumption of each plant species being difficult to assess. Understanding choice regulation within complex grasslands thus necessitates to better characterize the discrimination abilities of herbivores between plant species (which are necessary to learn the quality of foods), and how herbivores can generalize appropriate food preferences amongst similar food items (which requires that animals can categorize food items) within a new environment. The ability of sheep to visually distinguish between ryegrass and clover has been demonstrated by Edwards *et al*. (1997), and it can be assumed from the repeatability of preference measurements between grass species, sward heights and sward densities that herbivores can also easily distinguish between such plant characteristics. Recent findings have demonstrated that horses are capable of solving problems based on relative size concepts, since they correctly choose the larger of two stimuli associated with a food reward (Hanggi, 2003). This supports the idea that herbivores could categorize certain stimuli, but this has not been demonstrated yet for small ruminant species.

In complex environments, herbivores also face changes in the spatial and temporal distribution of resources, some of them being predictable such as grass growth patterns, other being less predictable, for example feeding site depletion by competing animals. In order to assess how sheep maintain their foraging efficiency in less predictable environments, Hewitson *et al*. (2005) recorded how groups of three ewes searched for patchily distributed bowls containing pellets, hidden within a grass plot, the provisioning of the bowls and the weight of pellets therein being altered to create differences in within- and between-patch variability. Where bowl position was predictable, the ewes showed increased foraging efficiency by reducing the time devoted to pellet foraging in relation to the total mass of pellets consumed and by visiting fewer empty bowls while searching within a site. Where bowl position became less predictable, the ewes increased sampling within sites, visiting more empty bowls before leaving a site, and starting to graze later. This ability to switch between foraging tactics may allow sheep to maintain foraging success under variable conditions. In another experiment, Hewitson (2002) showed that the way sheep adapt to less predictable environments is also modulated by the social status of the animals. Pairs of ewes of known dominance status were offered a choice between a stable patch containing unlimited hay accessible to both animals, and a high quality but variable patch containing variable amounts of preferred pellets only accessible by one sheep at any time. The dominant ewes behaved as "scroungers" (Barnard and Sibly, 1981), following more than the subordinates, which they consistently displaced at the variable patch. The subordinate ewes responded more than the dominants to environmental conditions, being more likely to follow when previous information suggested a high reward at the variable patch, and when the relative difference between pairs in the hierarchy decreased.

As a consequence of their foraging selectivity, which results in an uneven use of the herbage resource, herbivores have a great impact on vegetation structure and diversity in extensive grazing systems (Marriott and Carrère, 1998; Parsons and Dumont, 2003). Coran *et al*. (2005) compared the impact of rotationally grazed sheep in a semi-natural grassland, according to stocking rate (moderate *vs* low) and sheep breed: commercial (Finnish) *vs* traditional (Karst). After three years of grazing, it was concluded that the traditional breed at a low stocking rate could favour vegetation diversity (richness, entropy and dominance), with an average of four new species recorded per plot *vs* only two and one for the commercial breed grazed at a low or a moderate stocking rate. Louault *et al.* (2005) reported that for a permanent fertile grassland managed during 15 years at three contrasting levels of herbage use: high (H, 1 cut + 4 sheep grazing periods), medium (M, 4 sheep grazing periods) and low (L, 1 sheep grazing period), total species number reached 19, 20 and 27 in H, M, and L, respectively, with dicotyledonous species accounting for 37, 30 and 52% of the number of species. Among the most abundant species, there were only five grasses common to the three treatments (*Holcus lanatus, Poa trivialis, Elytrigia repens, Agrostis capilaris* and *Poa pratensis*), and there were 6, 2 and 10 treatment specific species in H, M and L, respectively. A functional analysis of vegetation dynamics, based on the recording of plant morphological and functional traits was developed in order to understand the mechanisms of these changes. It can be hypothesized that plant species selected in response to a given factor (e.g. herbage use) exhibit some converging traits that condition their performance in the community (Diaz *et al.*, 2001). For example, a decline in herbage use reduces individual leaf mass, specific leaf area and shoot digestibility, but increases leaf C and dry matter content (Lavorel and Garnier, 2002). Louault *et al.* (2005) identified different plant functional types based on the value of plant functional traits. The high herbage use level resulted in two short and early flowering types being co-dominant, a competitive grazing-tolerant and moderately grazing-avoiding type, and a grazing-avoiding non-tolerant type. The low herbage use level was dominated by a third type, neither grazing-avoiding nor grazing-tolerant, but strongly competitive for light.

In this review, we focused on the behavioural mechanisms underlying sheep foraging and on their grazing impact. Herbivores also have a potential impact on vegetation dynamics as agents of seed dispersion at the landscape scale (Marriott *et al.*, 2004). They can introduce new species into plant communities, either via dung deposition (Malo and Suarez, 1995; Mitlacher *et al.*, 2002) or seed transport on their fleeces (Fischer *et al*., 1996). The fleeces of transhumant sheep held propagules of up to 85 vascular plant species, i.e. nearly 50% of the total calcareous grassland species. By this way, transhumant sheep can play a key role in the restoration of abandoned grasslands.

Conclusion

In this review, we analysed how sheep graze pastures within an increasing gradient of complexity, with a focus on the underlying behavioural mechanisms and some illustrations of their impact on sward botanical composition. The foraging behaviour of sheep and goats has been directly compared in different environments (e.g., Gong *et al*., 1996; Papachristou, 1997). Studies have demonstrated the ability of goats to learn food characteristics in their young age (Distel and Provenza, 1991) and from social partners (Biquand and Biquand-Guyot, 1992). When offered a simple choice between two patches of different plant species, goats have also been shown to select the patch allowing the higher intake rate (Illius *et al*., 1999). When IIR ratio was close to one, bites were equally allocated between the two patches, which is in agreement with the predictions of optimal choice models. In more complex environments, goats have been tested for their ability to learn the postingestive consequences of antagonist stimuli (Ginane *et al*., 2005), and to increase their daily intake as the result of the diversity of plant species (Meuret and Bruchou, 1994). Conversely, we lack studies to quantify their cognitive abilities and the influence of social partners on the way goats use vegetation mosaics. Even if the processes that have been demonstrated on grazing sheep are likely to also operate in goats, it would be highly valuable to obtain similar (and sometimes comparative) information in order to improve the management of shrublands by small ruminants. Shrublands are necessarily heterogeneous vegetation mosaics, characterized by a greater stability in the spatial distribution of the shrubby and herbaceous layers. Herbivores select bites among a wide spectrum of bite mass and structures (Agreil *et al*., 2005), including young or older shoots, flowers and pods, but they also have to deal with the physical and chemical plant defences against herbivores (Papachristou *et al*., 2003), and with the vertical structure of vegetation, which can result in some preferred (and regeneration) organs being no longer accessible to the animals. Trampling and the usually high impact of animals on shrubs at grass patch boundaries (Hester *et al*., 1999) have been shown to affect the dynamics of *Calluna vulgaris* (Palmer *et al*., 2003) and *Buxus sempervirens* (Rousset and Lepart, 2003). Studies of the vegetation dynamics of shrublands will also require integrating the natural life cycle of shrub species, for example for *Cytisus scoparius*, and the risk of shrub invasion, which can limit the animal movements (Carrère *et al*., 1999).

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