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How forage characteristics influence behaviour and intake in small ruminants: A review

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SUMMARY – Small ruminant production systems vary widely, from high producing dairy goats to suckling ewes on rangelands. However, in all environments feed characteristics influence animals' motivation to eat, dietary choices and ultimately nutrient intake. This review highlights the common feed factors that influence feeding behaviour and intake, although their expression and consequences depend on the environment. The main characteristics of feeding behaviour are described in terms of the satiation process and motivation to eat. The main feed factors that influence intake are then reviewed. The relationship between the nutritive value of forages and their voluntary intake is well established. The relationship between nutritive value and palatability of feeds is discussed in the light of recent work on how feed characteristics are learned. In grazing situations ease of prehension of the sward influences rate of intake and dietary choices. On heterogeneous resources, animals graze selectively and choose a diet of better quality than that on offer. Recently more effort has been made to model intake and foraging decisions. Management of the grazing circuit has become an important factor in a heterogeneous environment. To conclude, the prediction of intake for small ruminants in different environments is briefly discussed.

Key words: Intake, feeding behaviour, forage, grazing, sheep, goats.

***RESUME –** "Comment les caractéristiques des fourrages influencent le comportement et l'ingestion des petits ruminants : Une revue". Les systèmes de production de petits ruminants présentent une grande diversité depuis des chèvres laitières à haut niveau de production jusqu'à des brebis allaitantes sur parcours. Dans tous les systèmes, les caractéristiques de l'aliment agissent sur la motivation à ingérer, les choix alimentaires et en définitive sur la quantité de nutriments ingérés. Cette revue met en lumière les facteurs alimentaires communs qui influencent le comportement alimentaire et l'ingestion, quel que soit l'environnement. Les principales caractéristiques du comportement alimentaire sont décrites en termes de processus de rassasiement et de motivation à ingérer. La relation entre la valeur nutritive des fourrages et leur ingestibilité est bien établie. La relation entre la valeur nutritive et la palatabilité des aliments est discutée à la lumière de travaux récents sur l'apprentissage des caractéristiques de l'aliment. Au pâturage, la préhensibilité du couvert végétal influence la vitesse d'ingestion et les choix alimentaires. Sur des ressources hétérogènes, les animaux pâturent sélectivement et choisissent une ration de meilleure qualité que la ressource. La modélisation de l'ingestion et du comportement alimentaire a fait l'objet de travaux récents. Dans un environnement hétérogène, la conduite du circuit de pâturage est un élément important. Pour conclure, la prévision de l'ingestion pour les petits ruminants est discutée brièvement dans différentes situations.*

***Mots-clés :** Ingestion, comportement alimentaire, fourrage, pâturage, mouton, chèvre.*

Introduction

Small ruminant production systems vary widely, from intensive feeding with zero-grazing to the utilisation of rangelands in arid areas. In all production systems, it is generally economically sensible to maximise the proportion of forage in the diet to minimise feeding costs. Furthermore, as people are becoming more and more sensitive to the image of animal products, maximising forage utilisation is an increasingly important tool in animal production. In extensive systems, grazing also contributes to resource preservation. However, efficient utilisation of forage resources and control of animal impact on vegetation need thorough knowledge of what determines feeding behaviour and dietary choices.

This paper reviews feed factors that influence feeding behaviour, dietary choices and ultimately nutrient intake in sheep and goats. First, the main characteristics of feeding behaviour are described in terms of the satiation process and motivation to eat. Then, the ways in which vegetation characteristics influence ingestion of forage, feeding behaviour and foraging decisions are reviewed. At grazing, two different situations are considered: (i) situations where animals are free to develop their own foraging strategy; and (ii) situations where shepherds' and animals' strategies interact. To conclude, the prediction of intake for small ruminants in different environments is briefly discussed.

Feeding behaviour and control of intake

Intake is influenced primarily by hunger, which is distressing, and by satiety, which is generally pleasurable. Recently, Forbes (1995) postulated that "ruminants eat that amount of food which leaves them with the most comfortable feelings". Regulation of feed intake and dietary choices combines short-term control of feeding behaviour related to the body homeostatic regulation, and long-term control that depends on nutritional requirements and body reserves (Faverdin *et al.*, 1995). Feed factors act mainly on the short-term control.

Main characteristics of feeding behaviour

Since the 50's the feeding behaviour of ruminants fed indoors or at pasture has been extensively studied (see review by Jarrige *et al.*, 1995; Ungar, 1996). Ruminants fed forages ad libitum eat for 5 to 10 hours per day and spend a similar time ruminating. When fed indoors feeding behaviour is scheduled by the feed distribution, usually two per day. Sixty to eighty percent of daily intake is eaten during two main meals following distributions. Thus daily forage intake is closely related to the amount eaten during main meals (Jarrige *et al.*, 1995).

During a main meal, the rate of intake is highest at the beginning and then decreases continuously as satiation proceeds until satiety. Simple exponential models accurately fit cumulative intake during meals in both cows (Faverdin, 1985) and sheep (Baumont *et al.*, 1989). Initial rate of intake represents the motivation to eat, and the constant of deceleration of the exponential function the satiation process. Kinetics of intake were also modelled on fresh leafy branches offered indoors to goats (Meuret, 1989). Rate of intake, especially at the beginning of the meal, seems to be a key factor for understanding variations in voluntary intake between forages (Moseley and Antuna-Manendez, 1989). At the beginning of the meal, motivation to eat a given forage expresses sensory and nutritive properties of the feed that were learned from previous experience.

At pasture, the feeding pattern of ruminants is determined by the grazing periods that occur essentially during daylight. In a temperate climate grazing time is organised into 6 to 8 periods with two main periods at sunrise and sunset. Rumination time is also divided into periods between meals during the day, and forms the principal activity during the night. At high temperatures (>25°C), animals adapt their activity to avoid grazing at the hottest times: they start grazing earlier in the morning, prolong the evening meal and may also graze at night.

The satiation process

Post-ingestive signals coming from feed contribute to the satiation process. These feedback signals are mainly integrated in the control of intake to prevent excess.

Role of rumen fill

When fed indoors with two distributions and free access to forage, rumen fill, measured as the amount of digesta in the rumen, reaches a first maximum after the morning main meal and the daily maximum after the evening main meal (Baumont *et al.*, 1988). In grazing sheep, Thomson *et al.* (1985) also observed a first maximum in the morning at 9 a.m. and the daily maximum at 8 p.m. in the evening after the main grazing period. That the capacity of the rumen is involved in the control of intake is supported by two types of physiological evidence: (i) stretch-and mechano-receptors are present in the rumen wall (Leek, 1977); and (ii) increasing rumen fill with indigestible material by the equivalent of 1 kg dry digesta decreases intake by 0.6 kg dry matter on average (review by Faverdin *et al.*, 1995). When rumen fill is increased with indigestible material, animals increase the number of meals and the time spent ruminating per kg ingested (Baumont *et al.*, 1990a). This stimulation of rumination behaviour, related to increased stimulation of tactile receptors in the rumen wall, speed up digesta outflow and tends to reduce rumen fill.

Role of nutrients

During the main meals rapid fermentation of the soluble fraction of feed increases osmotic pressure and volatile fatty acid (VFA) concentration of rumen fluid and lowers pH (Rémond *et al.*, 1995). VFA infusion in the rumen decreases feed intake in the short term, more so as the molecular weight of the infused VFA is low (Faverdin *et al.*, 1995). The influence of molecular weight indicates involvement of osmotic pressure (Carter and Grovum, 1990). Signals sensed by chemoreceptors in the rumen wall and/or in the liver enable the animal to avoid excess and nutritional disorders. This may explain the low duration of main meals with grass silages that contain large amounts of organic acids and ammonia, especially when they are poorly preserved (Van Os *et al.*, 1995). In this case, satiation occurs before rumen fill reaches a maximum. The same kind of adaptive phenomena may explain the choice of the feeds lowest in salt when goats were given a diet rich in sodium chloride (Morand-Fehr *et al.*, 1996). During a meal, the signals that contribute to the satiation process act simultaneously and probably additively as indicated by the effects of an increase of rumen fill and an acetate infusion, performed separately or at the same time (Adams and Forbes, 1981). The different signals that are sensed in the digestive tract and the liver are integrated in the central nervous system and balanced with other stimuli (Forbes, 1996).

Motivation to eat and feed preferences

Satiation factors, mainly those related to rumen fill, have been favoured to explain forage intake. Because of prior learning, sensitive recognition of the feeds allows anticipation of nutritional and physiological consequences of intake. This is essential to determine motivation to eat and meal size when one feed is offered, and also feed preferences and foraging behaviour in more complex situations, such as heterogeneous swards and rangelands.

Learning the post-ingestive effects of feeds

The senses that are stimulated in the presence of feed enable the animal to anticipate the postingestive effects of feed. Provenza *et al.* (1992) proposed a schematic representation of the processes involved in the learning of feed preferences. The affective system integrates the taste of a feed with postingestive feedback and the cognitive system integrates the odour and appearance of the feed with its taste. Learned food aversions towards toxic plants or feeds experimentally laced with several compounds that cause malaise have been clearly established in ruminants (du Toit *et al.,* 1991). Learned preferences based on positive nutritional postingestive feedback are undoubtedly also important for ruminants. After 10 days adaptation, lambs developed a strong preference for non-nutritive flavours paired with glucose over the same flavours paired with saccharin (Burrit and Provenza, 1992). Thus ruminants, like other mammals, develop preferences for feeds that are richer in energy (Provenza, 1995). However, in a free-choice situation, diet selection does not always maximise energy density in the diet. Sheep eat some straw to prevent rumen disorders, even when a more concentrated feed is also on offer (Cooper *et al.*, 1995). Sheep fed with a "long-fibre-free" diet will eat 10 mm polyethylene fibre to restore normal rumination activity (Campion and Leek, 1997). It was even observed that dairy goats can buffer seasonal variations in available vegetation composition. For example, at turn out, goats seek herbage species relatively low in protein and rich in fibre; it is likely that animals select vegetation to reduce the variation in ingesta composition as far as possible in the face of large seasonal variations of vegetation composition (Fedele *et al.*, 1993; Morand-Fehr, unpublished). Moreover, post-ingestive stimuli need to be periodically reinforced, and so the animal has regularly to re-evaluate the cost/benefit ratio of the different choices.

Dietary experience, particularly early in life, modulate feeding behaviour and diet selection. Processes of learning from the mother, from other animals of the same species and through trial and error have been reviewed by Provenza (1995). For example, naive sheep, cattle and goats may eat up to 40% less than experienced animals in the same environment (Provenza and Balph, 1987). When feeding, animals adapt to their environment by developing their ability to recognize plant species and their grazing skills (Flores *et al.*, 1989), and by learning and memorising the distribution of resources (Dumont and Petit, 1998). Learning from the dam and social partners (Thorhallsdottir *et al.*, 1990), and recognition of postingestive consequences of diet choices are important in this adaptation and in the acquisition of appropriate dietary habits. Lambs accustomed to graze either clover or grass with their dam have a stronger post-weaning preference for the species they had previously experienced (Ramos and Tennessen, 1992). After weaning, lambs reared by goats spent less time eating clover than those reared by ewes, consistent with the stronger preference for clover of ewes compared with goats (Orr *et al.*, 1995). For adults, short-term neophilia may temporarily modulate preferences. Sheep that had grazed either clover or grass swards for 3 weeks subsequently showed a stronger preference for the species previously lacking in their diet; nevertheless, after 3 days, they reverted to a stronger preference for the species they had been previously accustomed to eating (Parsons *et al.*, 1994). However, when an unknown feed is offered to goats, sensory evaluation can take a long time and intake begins at a low rate, which can limit the size of the first meal.

Hedonic behaviour

Mechanisms of brain reward can to some extent induce hedonic feeding behaviour, which competes with physiological factors controlling intake. Sensory properties of the feed will stimulate hedonic behaviour to some extent. Total intake of sheep was only 0.4 kg/d when they ate straw and received grass in the rumen but rose to 0.9 kg/d in the reverse situation, although the digestibility of the total diet was similar (Greenhalgh and Reid, 1971). Unpleasant sensations when eating straw may explain its very low hedonic value. Hedonic behaviour can explain voluntary intakes greatly in excess of requirements in wethers fed good quality forages (Baumont *et al.*, 1997). The sensory motivation induced by a second distribution of fresh hay will override the satiety signals associated with the first distribution (Baumont *et al.*, 1990b). However, the size of the second meal depends on the relative palatability of the two hays distributed. Sheep satiated with low-quality meadow hay will eat 400 g of lucerne hay. However, they are reluctant to eat meadow hay when satiated with lucerne. In goats, hedonic behaviour may explain why they make refusals even when this selectivity prevents them meeting their energy requirements (Morand-Fehr *et al.*, 1991b). At pasture, the pleasant experiences associated with the consumption of a new food have been suggested to explain preference for novelty or for rarity (Newman *et al.*, 1992). Hedonic behaviour, however, competes with the effort that has to be expended to earn the reward. In a test situation, when animals have to walk to obtain a good forage, the preference for the good forage depends on the amount offered the animals in reward (Dumont *et al.*, 1998).

In conclusion, Fig. 1 summarises the main relationships between forage characteristics, short-term control of intake, feeding behaviour and finally forage intake. Modelling intake behaviour is a good tool to test our knowledge of what controls intake. Forbes (1980) developed the first mechanistic model of intake in ruminants. More recently, Sauvant *et al.* (1996) proposed a mechanistic model of intake and chewing activities that integrates relationships between feeding behaviour and digestive processes. Decisions between eating, ruminating and resting are taken according to the relative values of the functions of motivation to eat and of satiety, which integrate the signals described above. The forage is characterised by the cell wall content and its potential digestibility, and by the proportion of large particles. A palatability index and a coefficient of heterogeneity take into account non-nutritional characteristics and selection possibility in the forage and are combined to estimate instantaneous palatability of the forage. This model accurately predicted intake kinetics of sheep fed different types of hay indoors.

Role of plant characteristics on forage ingestibility

Forage ingestibility is defined as the maximum quantity of the feed that can be eaten by the animal when this is supplied *ad libitum* as the sole feed. When given indoors, ingestibility of green forage depends mainly on its nutritive value and fill effect and on its sensory properties, assuming it does not contain toxic compounds (Fig. 1). Conservation of forage generally modifies ingestibility. Compared with the original green forage, making hay depresses the nutritive value and consequently ingestibility. Making silage does not alter the digestibility, but ingestibility is depressed if the quality of conservation is poor and the silage contains large amounts of fermentation end-products.

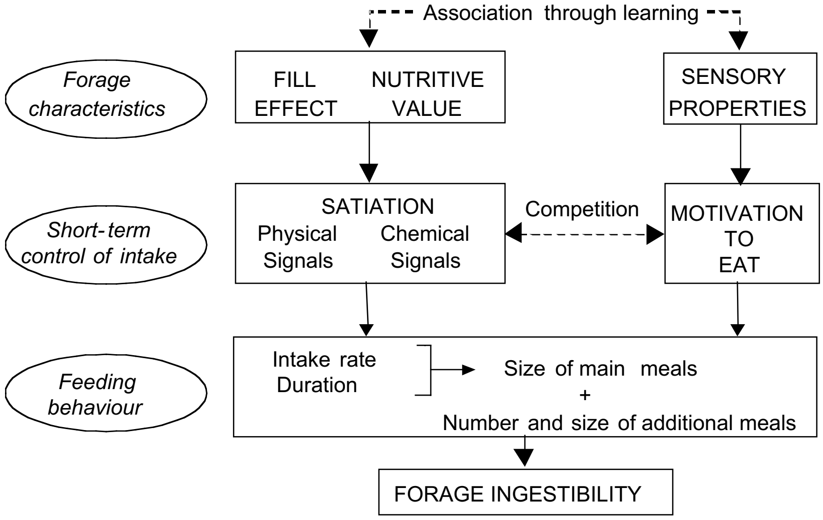

Fig. 1. Relationships between forage characteristics, short-term control of intake, feeding behaviour and forage ingestibility.

Nutritive value and fill effect

For a given plant, ingestibility, like digestibility, is dependent on the vegetation stage and the number of the vegetation cycle. During the first vegetation cycle, ingestibility decreases with the age of the plant. Relationships between age, digestibility, chemical composition of forage and their ingestibility are linear or slightly curvilinear according to the species (Demarquilly *et al.*, 1981). With the same digestibility voluntary intake of legumes is about 20% higher than that of grasses due to a lower cell wall content. Also, for the same age and digestibility, voluntary intake differs among grasses. Taking into account the main variations in forage ingestibility allowed the development of the fill unit system to predict feed intake for ruminants fed indoors (Jarrige *et al.*, 1986).

The decrease in ingestibility with age of forage is the consequence of the increase in its fill effect. As the plant ages, its morphological and histological development decreases the amount of cell content, which is soluble, rapidly degraded and has almost no fill effect, and increases the amount of cell walls. Consequently, forage retention time in the rumen and thus fill effect increases. In addition, tissue lignification increases the undegradable fraction of the cell walls and decreases the degradation rate of the degradable fraction (Grenet et Demarquilly, 1987). The time needed to reduce particle size before ruminal escape is also increased. Retention time in the rumen depends mainly on the degradation rate of the degradable fraction and on the proportion of the undegradable fraction, since its outflow rate does not vary widely among plant species (Baumont *et al.*, 1997). Residence time of dry matter in the rumen is closely related to forage ingestibility (Baumont *et al.*, 1996).

Sensory properties

Sensory properties of the feed are associated by a learning process with the nutritive value and the toxicity of the feed. How much sensory properties affect feeding behaviour and intake independently of these two major components remains an open question.

Physical characteristics

Since the work of Arnold (1966), it has been recognised that the sense of touch plays a role in the response of the animal to the feed. Physical characteristics of the forage such as dry matter content and particle size, and resistance to fracture are known to affect ease of prehension and thus intake rate (Inoué *et al.*, 1994). With dried forages, relative preferences for mixtures with varying proportions of long and short particles were closely related to the differences in intake rates (Kenney and Black, 1984). Discrimination between the different mixtures decreases as intake rates of the feeds being compared increase. Accordingly, preference for short particles is more pronounced in slowly ingested forage like straw than in rapidly ingested hay. Small ruminants are also sensitive to particle size of concentrates. Ground feeds with a large percentage of fine particles (<0.5 mm) are clearly less well accepted than coarse ground feeds, (Morand-Fehr *et al.*, 1994). The preference for coarse particles may be due to greater ease of prehension. The water content in feed modifies dry matter intake very little except with ground cereals that can be changed into compact pastes with a high water content. Nevertheless, high humidity can result in a better acceptability of dusty, finely ground feeds. Thus choice of diets by animals can be affected by interactions between particle size and humidity.

Chemical characteristics

The effects of various odoriferous compounds naturally present in plants were analysed by Arnold *et al.* (1980) by sprinkling the chemicals onto cotton wool pads placed in the manger. Effects of odoriferous compounds are difficult to interpret because they can vary in amplitude and sometimes in sign according to whether the animals are in choice situations or not. Arnold *et al.* (1980) added to pelleted hay small quantities of several compounds recognised to decrease intake by their odour or decrease preference for a water solution by their taste. Over a three-day period, significant depressions in intake were obtained with coumarin, gramine, tannic acid, malonic acid and glycine. However, sheep that were both anosmic and agustatory were affected in the same way as normal sheep. *In vitro* digestibility of the pelleted hay was drastically depressed by tannic acid and gramine, and slightly by coumarin and glycine, but was unaffected by the other compounds. Small ruminants can also be sensitive to flavours added to the diet (Morand-Fehr *et al.*, 1991a) and to sugar, salt, urea and hydrochloric acid at various levels, which correspond to the four primary tastes: sweet, salty, bitter and sour (Morand-Fehr *et al.*, 1993). However, animals in the same flock display a very wide range of response to the 4 taste components. Grovum and Chapman (1988) showed that animal response to added chemicals varies with feed management.

Low intake of silage is often attributed to low palatability, since digestibility is only slightly different from that of green forage. Effects of smell and taste on silage intake were studied with anosmic and agustatory sheep (Michalet-Doreau, 1975). The increase in silage intake by anosmic compared with normal sheep was more pronounced with poorly preserved (+33%) than with well preserved silages (+6.4%). Silage intake by agustatory sheep was not modified. Acetic acid added to the silage had a clear negative effect on intake (Buchanan-Smith, 1990). Amines are suspected to decrease palatability, because in sheep initial eating rate at the beginning of the meal was depressed by addition of amines in silage (Van Os *et al.,* 1995). Low palatability of silages probably results from learning the negative post-ingestive signals due to high amounts of fermentation end-products. Like other ruminants, sheep and goats are very sensitive to concentrate palatability. Preference tests under standard conditions in goats showed that fats, rapeseed meal and urea can lower the palatability of compound concentrate feeds (Morand-Fehr *et al.*, 1991b). Giger-Reverdin and Sauvant (1991) established a scale of palatability for concentrate feeds.

Role of vegetation characteristics on grazing behaviour

Behavioural constraints are different and more diversified at pasture than indoors. Animals have to search for feed (search constraint) and they have to harvest the plants (prehension constraint). Even so, animals are free at pasture to develop their own foraging strategy. They exploit environmental heterogeneity by grazing selectively. Prediction of intake and of the impact of animals on vegetation needs an understanding of their foraging decisions. When shepherds drive their flocks on grazing circuit, their strategy of resource utilisation influences the animal's behaviour and interacts with the foraging strategy of the flock.

Foraging strategy and diet selection

On homogeneous swards, the importance of prehension constraints first caused herbage intake to be represented as the product of intake rate and grazing time (Allden and Whittaker, 1970), assuming spatio-temporal stability of intake rate. As this approach is inappropriate on heterogeneous swards, a hierarchical approach is now preferred, that organises the grazing process into different levels corresponding to animal decisions, which are then integrated over wider spatio-temporal levels (Bailey *et al.*, 1996).

Representation of the grazing process and theoretical bases of foraging behaviour

When an animal begins to eat, it selects a feeding site and a patch within that site. Selection of bites within the patch continues so long as Instantaneous Intake Rate (IIR) remains above a certain threshold. When IIR falls below this threshold, the animal selects a new patch, and when acceptable patches in the feeding site become scarce, a new feeding site is selected. This representation of the grazing process proposed by Laca and Ortega (1995) enables foraging behaviour to be formalised in terms of a hierarchy of scales where animals make decisions and integrate these over different spatio-temporal levels. A patch is defined as a spatial aggregation of bites over which IIR remains relatively constant (Illius and Hodgson, 1996). Thus patch size can range from an area from which one bite is taken to a homogeneous paddock.

Two approaches to foraging decisions have been proposed. Synthetic approaches assume animals organise their behaviour towards an objective, whereas analytical approaches assume that behaviours arise from cause-effect relationships. The basic axiom of the main synthetic approach, Optimal Foraging Theory (OFT), is that present-day animals forage optimally as a result of natural selection, because optimal foraging enables the animal to maximise its reproductive output ("fitness") (Krebs and McCleery, 1984). Fitness maximisation has often been translated into efficiency of foraging, which, for practical reasons, has often been equated with short-term dry matter intake rate (Laca and Demment, 1996). The recent model of Newman *et al.* (1995) base foraging decisions on maximisation of fitness and include a simplified mechanistic sub-model of digestion. Another synthetic approach, the principle of "satisfying", hypotheses that a behavioural option may be taken, not only when it is optimal, but when it is of sufficient benefit to the animal (Ward, 1992). This raises the problem of defining a satisfaction threshold if predictions are to be made under this principle.

Analytical approaches explain foraging behaviour in a complementary manner. For example, patch choice may be motivated by sensory stimuli, by post-ingestive feedback resulting from previous choices, and by dietary experience. Synthetic and analytical approaches should be perceived as complementary rather than exclusive. Although OFT stresses the importance of natural selection in determining behaviour, it cannot exclude the importance of short-term dietary experiences. Optimisation-based predictions should, therefore, include animals' dietary experiences. The difficulty in dissociating the different approaches is well illustrated by the question posed by Illius *et al.* (1998): do animals eat a plant species faster because they prefer it (sensory stimulus) or do they prefer it because they can eat it faster (optimisation of behaviour)?

Optimisation is an elegant approach because it is a functional synthesis of foraging behaviour and it allows quantitative predictions. However, it may be a simplified representation of reality and the basic theoretical axiom has generally been simplified. The few experimental tests of intake rate maximisation hypothesis have not completely validated it, and this has led to suggest different explanations, such as the search for a balance of nutrients and dilution of toxins (Newman *et al.*, 1994; Parsons *et al.*, 1994), necessity for the animal to sample its environment (Demment *et al.*, 1993), and constraints on the animal's ability to evaluate the cost/benefit ratio of different behavioural options (Illius *et al.*, 1998).

How do vegetation characteristics influence foraging decisions?

In the light of the proposed representation of foraging behaviour, we discuss how vegetation characteristics influence animals' foraging decisions, including the bites prehended on the patch, the length of time spent grazing a patch before moving to another, the further choice of a new patch, and how these decisions contribute to total daily intake.

Patch level: IIR on the patch is determined by the mass of the bite and the functional relationship relating bite mass to the time required to handle it. Time per bite may be split into prehension and mastication times. This representation, based on the time budget, considers the animal as subject to two constraints: (i) the time required to prehend a bite, which is independent of bite mass; and (ii) the time required to masticate the harvested material, which is proportional to bite mass (Newman *et al.*, 1994; Prache, 1997) and varies with plant species (Newman *et al.*, 1994). Bite mass is determined by the ease with which the sward can be gathered into the mouth and sheared; these determinants have been reviewed by Prache and Peyraud (1997). On vegetative swards, sward height and bulk density are the main determinants of bite mass and IIR (Black and Kenney, 1984; Burlison *et al.*, 1991). On complex swards, bite mass is also affected by the presence of "barrier" components in the sward such as stems and dead material. Green leaf mass per unit area has been shown to be the best predictor of bite mass and IIR across different phenological stages of the sward (Prache *et al.*, 1998). However, sward height or green leaf mass do not take into account all the factors involved, because they are one-dimensional (sward height) or two-dimensional (green leaf mass) descriptors, while bites are taken in three dimensions (Ungar, 1996).

Patch departure: Forage depletion in the patch and perception or expectation of intake opportunities in other patches will motivate the animal to move on. The animal has to make a trade-off between continuing to graze a patch where it is experiencing diminishing marginal rewards, and moving to another patch, thereby incurring a time cost. If the animal seeks to maximise intake rate, the Marginal Value Theorem (MVT), Charnov (1976) predicts that the animal will leave the patch when intake rate within the patch equals the average intake rate for the whole environment. Demment *et al.* (1993) and Laca *et al.* (1993) have globally validated MVT, but Bazely (1988) observed a longer residence time than predicted by MVT.

Multi patch level: Factors such as vegetation characteristics, distance to water, climate or shelter, and social and predation factors may influence patch choice. Considering vegetation characteristics, two situations may be distinguished: (i) those where the animal can express its preferences, i.e., can graze the preferred patch without having to search; and (ii) those where preferences are modified by a cost of searching.

When searching costs are negligible, for example on a feeding site that offers easily found discrete patches, animals generally prefer patches where they can eat rapidly (Black and Kenney, 1984; Illius *et al.*, 1998), i.e., they will concentrate grazing on patches that offer greatest intake rate potential. However, preference is not absolute and intake rate is often less than predicted from optimisation theory. For example, on a field consisting of adjacent monocultures of grass and clover 6 cm tall, the proportion of clover in the diet of sheep is about 70%, even though sheep generally eat clover faster than grass (Newman *et al.*, 1994). Why do animals express partial preference and choose mixed diets? In the short-term, the necessity for the animal to consume the different patches to evaluate their profitability, difficulty or lack of interest of the animal in discriminating, and discrimination errors, have been proposed as explanations (Illius *et al.*, 1998). On a daily scale basis, diurnal pattern in preferences, search for a balance of nutrients and digestive constraints have been proposed as explanations of partial preferences and mixed diets (Newman *et al.*, 1995).

Preference is sensitive to relative vertical availability of the different plant species. Animals may trade off quality for quantity and switch to the less preferred item, when greater benefit is obtained on it (Harvey and Orr, 1996; Prache *et al.*, 1996). If one assumes that animals seek to maximise intake rate, the switch to the less preferred patch may be predicted from potential intake rate on each patch. For example, sheep rotationnally grazing swards containing reproductive patches in a vegetative background, should consume the vegetative patches as long as their green leaf mass will allow a higher intake rate than the reproductive ones (Fig. 2). Thus, if animals seek to maximise intake rate, they should switch to reproductive patches when the green leaf mass on vegetative patches becomes lower than 300 kg DM/ha (i.e., 9 cm height in this study). This result is in agreement with the preference measurements of Dumont *et al.* (1995). However, animals may also make a trade-off between biomass and digestibility, i.e., short-term intake rate and long-term intake rate, because of digestive constraints (Wilmshurst *et al.*, 1995).

In natural conditions, additional constraints of searching for preferred patches may limit intake rate. These constraints are determined by the total herbage availability, the relative horizontal abundance of the preferred species and their spatial distribution. They make the environment more difficult for the animal to search and induce it to consume less preferred but easier-to-reach food patches. Faced with these constraints, the animal may develop search strategies: it may walk faster (Roguet *et al.*, 1998), increase daily grazing time (Prache *et al.*, 1998), or learn about the location of food and use its spatial memory together with visual cues (Laca and Ortega, 1995; Edwards *et al.*, 1997; Dumont and Petit, 1998). The cost of searching is difficult to assess. Indirect indicators may be used, such as the animal's degree of selectivity expressed as the difference between diet and sward composition, intake per distance walked and proportion of potential bites encountered removed (Laca and Ortega 1995; Prache *et al.*, 1998; Roguet *et al.*, 1998). A decrease in the horizontal availability may affect encounter rate. For example, when grass/clover swards contained 20% clover per ground area, sheep spent 44% of their grazing time on clover vs. 73 and 67% when the clover represented 50 and 80% of the area (Parsons *et al.*, 1994).

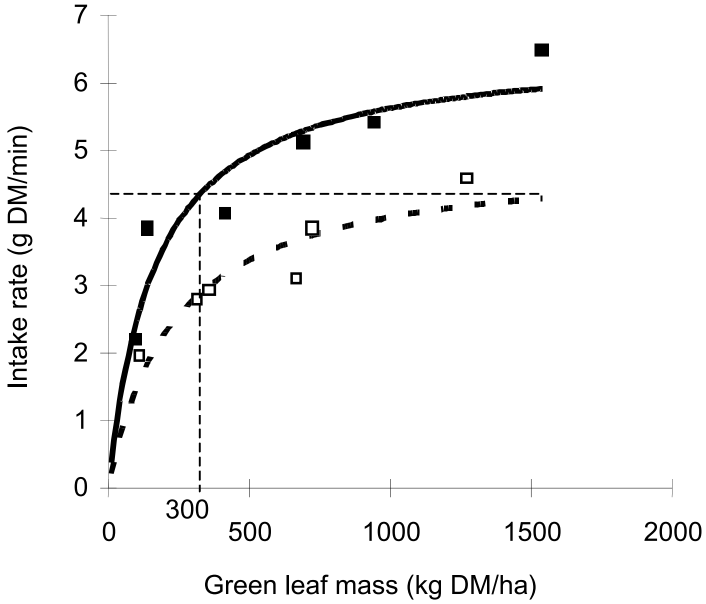

Fig. 2. Prediction of diet choices based on dry matter intake rate maximisation: an example on swards containing reproductive patches (dotted curve) in a background of vegetative patches (solid curve) (from Prache *et al.,* 1998).

The effect of scale of patchiness may have marked effects on animal's foraging decisions, although it has not, as yet, received much attention. Two types of patchiness may involve searching costs: small-scale, with constraints due to selection of preferred from less preferred food items, and larger scale with constraints due to moving and locating alternative patches. Fine mixtures reduce the opportunity for selection, whereas large patches offer maximum opportunity for selection. Sheep grazing grass/clover swards select more clover when the species are offered in separate strips than in an intimate mixture (Clark and Harris, 1985). Larger scale heterogeneity may impose a constraint on moving to reach the chosen patch, which may affect intake rate (Laca *et al.*, 1993), unless moving time is completely devoted to mastication. Larger scale heterogeneity may also impose constraints on the visual perception of alternative patches and spatial knowledge. In an operant conditioning test, sheep walked with the same frequency to resources that had the same edible biomass relative to the distance to the patch (Dumont *et al.*, 1998). Use of visual cues may enable the animals to increase efficiency of search and intake rate (Laca and Ortega, 1995). Patchiness also offers animals trade-off opportunities, because when they move within a heterogeneous sward, they can choose to eat a less preferred but neighbouring plant species, rather than move to a preferred but distant one (Clarke *et al.*, 1995).

When a shepherd organises patch selection

Shepherding consists in interacting with spontaneous animal's decisions. At first sight, the herder's interventions could be considered simply as new constraints to the expression of the behavioural trends of the flock. In fact, rather than trying to inhibit selective feeding behaviour, an experienced shepherd has to identify spontaneous behavioural trends to avoid countering them too often (Deffontaines *et al.*, 1989). While building a strategy for both animal feeding and resource management, the shepherd has to some extent to follow the movements of the flock to maintain the confidence of the animals. Effective management by a shepherd can upgrade dietary motivation on heterogeneous pastures (Meuret, 1993a,b).

Shepherding interact with the animal's foraging response patterns (Senft *et al.*, 1987). Transhumance, is a repeatable, scheduled response to predictable seasonal shortages in forage availability. Nomadism, is an adaptation to unpredictable forage production. Both have developed a wide range of informal and formal rules (Westoby *et al.*, 1989; Niamir-Fuller, 1995). For anthropologists, working on pastoral systems based on livestock mobility, there is a need to reconsider the leader paradigm that promotes settling process, coming from land carrying-capacity evaluation (Scoones, 1994). Animal nutrition scientists have devoted little attention to how a shepherd can manoeuvre an animal's appetite, taking advantage of spatial heterogeneity at scales of feeding sites and vegetation patches (Bailey *et al.*, 1996).

Rangelands are patchy environments. Within a single day, a flock may well come across extremely diverse vegetation, and each of its members may decide to distribute thousands of bites over hundreds of sometimes highly contrasted plant parts, from a tiny grass regrowth to a large mature leafy branch. Such broad diversity can motivate feeding. First, it offers the animal many ways to solve the usual conflicting problems: obtaining maximal quality and adequate quantity (Owen-Smith and Novellie, 1981). Secondly, most of the shrubs and leafy branches are easily prehended, allowing small ruminants high rates of intake up to 0.4 g dry matter/min/kg $LW^{0.75}$ (Meuret, 1997). Black and Kenney (1984) showed that high intake rate is an important factor in motivation to graze. Finally, motivation is increased if the diversity of plant material on offer during a grazing bout is high, especially when the material is of medium or low potential palatability (Meuret and Bruchou, 1994).

Shepherds who have developed their own expertise in stimulating animals' appetite on patchy environments organise in a grazing circuit the succession of encounters of the different patches. A model of shepherded circuit design, based on farm surveys together with intake kinetics analysis has been developed (Meuret, 1993a,b). The grazing circuit may be viewed as an ordered sequence of patches offered during one main meal, the objective being to optimise the animal's feeding motivation (Fig. 3).

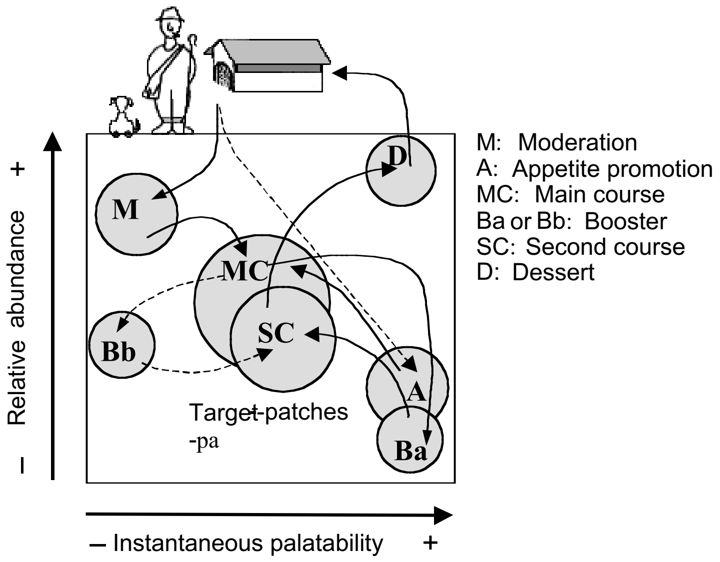

Fig. 3. The Menu model: A shepherded grazing circuit is an ordered sequence of offered patches during one main meal, the objective being to constantly revive the animal's eating motivation on coarsest resources ("target-patches") (from Meuret, 1993a,b).

This model, which draws on the "menu" concept in a restaurant, is based on two rules: (i) creation of synergetic sequences within the foraging bout; and (ii) follow spontaneous behavioural trends while developing flock's confidence in shepherd's interventions. When intake must be stimulated in a particular patch ("target-patch") with rough and less palatable material (e.g., a patch to be cleared of scrub), the shepherd has to detect and use complementary resources, sometimes contiguous patches in the feeding site. The different patches could play six distinct roles during a circuit, and their use value for a specific phase during the meal is assessed individually according to two simple criteria: the relative abundance and the instantaneous palatability of the resources for a given flock (Sauvant *et al.*, 1996). A moderation-patch, with abundant but not highly palatable plants, could be used at the beginning of the circuit to reduce the appetite of the flock. In contrast, an appetite promotion patch, with highly palatable but not abundant resources, has to be used at the beginning to stimulate a flock that has a low appetite. The target-patch, with medium plant abundance and palatability, is then used as a main-course, for the bulk of the meal. When animals are losing interest in this patch, a booster-patch (or booster-action) has to be used to add diversity and revive appetite. There are few ways of boosting appetite: offering a patch with low plant abundance but high instantaneous palatability, markedly different from the main course; conversely, grazing the animals on a patch with medium abundance of biomass and very low instantaneous palatability; watering the flock or offering it salt licks. When the booster-action is successful, another target-patch with slightly better instantaneous palatability than the main course-patch is used for a second course. At the end, if the shepherd considers there is not enough time for a new booster-course sequence, a dessert-patch, with high plant abundance and palatability, can be used.

The organisation of a "menu" by a shepherd, that takes full advantage of a patchy environment and emphasises the concept of instantaneous palatability, seems consistent with the role of aversions in diet selection at pasture hypothesised by Provenza (1996). This shows that the feed value of such an environment results largely from proper feeding management at the level of the feeding site and feeding bout, that could manoeuvre the appetite. Experienced shepherds observe their flock's attitudes to evaluate initial hunger, intermediate disaffection for food and signs of satiety. A shepherd who succeeds in designing a menu becomes a "mobile attractant" for the flock, being able to generate a "build-up" pastoral value from a heterogeneous and variable vegetation (Meuret, 1996).

Conclusions

Over the past twenty years great progress has been made in the knowledge of the forage characteristics that influence behaviour and intake in small ruminants. Meal size and diet composition are mainly controlled by anticipation of postingestive effects to avoid nutritional excesses or deficiencies. The role played by sensory properties of the diet is still not completely understood as it is partly confounded with the role of nutritive value after learning, but it is essential in explaining the control of feeding behaviour. Ruminants generally develop preferences for feeds that provide a high satiety level rapidly. Feeds that can be ingested fast and that are rapidly and highly digested are very palatable provided they do not contain toxic compounds. Nevertheless, for a given nutritive value, sensory properties of the feed *per se* can stimulate or depress hedonic behaviour and thus intake.

A more efficient foodstuffs utilisation necessitates to improve prediction of forage ingestibility. Residual variation in predictive models of voluntary intake based on nutritional characteristics (i.e., energy and nitrogen values, fill effect) remains generally high. Fill effect of a forage can be expressed as its ruminal retention time and can be predicted using *in situ* degradability or laboratory methods. A so-called "hedonic value" of feed is probably much more difficult to predict, and to a first approximation can be assessed by the difference between observed and predicted intake.

At pasture, intake, diet composition and the impact of grazing on the vegetation is the result of a complex interaction between the animal and the vegetation. The livestock farmer has to organise this interaction within a pastoral strategy adapted to local conditions. Through selective grazing, the animal consumes a diet of a higher nutrient quality than that on offer, and distributes its impact on the vegetation. Nevertheless, the determinants of foraging decisions remain a matter of debate. In simple experimental situations (very short-term, simple dietary choices), diet selection is generally well predicted by intake rate maximisation. However, short-term prediction of diet selection is not completely validated on a daily scale basis, which may be affected by discrimination and digestive constraints, balance of nutrients, diurnal pattern of diet selection, sampling, social effects within the flock, flock-farmer interactions. Prediction of total intake is further impaired by the difficulty of predicting grazing time. General trends in the prediction of diet selection might be sufficient to enable prediction of a switch from grazing preferred to less-preferred patches, and reduce further decline in forage quality. Predicting diet selection is further complicated in more complex situations such as rangelands, with a large diversity on offer, making the environment more difficult for the animal to perceive, and offering it opportunities for trade-offs between behavioural options.

Selective behaviour of small ruminants is very important in coping with variability and heterogeneity of forage resources. A question that arises is whether feed preferences can be modified by conditioning. So it could result in a better management of grazing areas or enhanced forage intake in intensive feeding situations. Offering choice to animals might stimulate forage intake and so forestall some pathological problems. The nutrient requirements of each individual could be more precisely met. However, research is needed to determine appropriate conditions for choice feeding.

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