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FORAGING BEHAVIOUR AND INTAKE IN TEMPERATE CULTIVATED GRASSLANDS

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Introduction

In temperate areas, grazing provides a large part of the nutrient requirements of ruminants and may be an important form of land use. In Europe, grassland occupies some 150 million hectares, and grazing provides about 60 to 75% of the nutrient requirements of cattle (Wilkins and Vidrih 2000). From the end of the 80's, agricultural surpluses in Europe have led to production quotas and increased interest in more extensive systems. At the beginning of the 90's, the emergence of the notion of sustainable agriculture combining economic, social (concerns in dereliction of less-favoured rural areas), and environmental issues (pollution, loss of biodiversity arising from intensification, environmental degradation...) strengthened the emphasis on livestock farming systems based on grazing. The challenge is to develop grazing systems that contribute to the economic sustainability of agriculture, that able to ensure the preservation of the rural landscape, with minimum recourse to non-renewable resources, while preserving and/or improving the environment. Grazing systems are further favoured by the 'green' image of their products, grassland-based food production being considered as safe, 'natural' and respectful towards animal welfare. Recent findings demonstrated the nutritional advantages of grassland-based food products (Demeyer and Doreau 1999), and the possibility of tracing grass-feeding in animal products by the use of biomarkers (Prache and Theriez 1999).

In the milk production systems of Europe, milk quotas have increased the pressure on production costs so emphasizing the interest in increasing the animals' voluntary intake from grazed swards. Environmental concerns have questioned N fertilisation and cattle waste management. Both renewed interest in increasing the use of legumes in swards. In grasslands areas that are devoted to beef cattle and sheep, systems are generally more extensive; farmers have to manage larger flocks on larger and more diversified areas, and to conciliate production with environmental objectives (maintaining open landscapes, contributing to landscape biodiversity).

One of the main problems coming up to the grazing science is the increasing diversity in management objectives and the diversity of situations (grassland areas, management and production systems, herbivores species,...). The challenge is, then, for the grazing scientist to provide fundamental principles and biological laws that may both be generalized under a broad range of conditions and allow concrete applications to the majority of situations.

The process of herbivores' foraging is of major importance because it determines the nutrient intake of the animals as well as the location and intensity of the animals' impact on the vegetation. Therefore, a better understanding of its determinants is of fundamental interest to the management of both animals and vegetation and in the dynamics of the grazed

ecosystem. A grazing animal has a much greater control of its decisions than a stall-fed one, particularly when resources are heterogeneous and human intervention is low. Animals exploit the heterogeneity of the resources through selective grazing, choosing a diet which is of better quality than the average vegetation on offer (Jamieson and Hodgson 1979, Prache et al 1997) that will benefit performance. Hence, predictions of both nutrient intake and the effects of animals on the vegetation needs an understanding of animals' foraging decisions. However, the determinants of foraging decisions remain obscure since many studies have been largely descriptive and failed to provide generality. Recently, increased effort has been made to develop models of the grazing process supported by theoretical basis. This approach should allow a better understanding of the determinants of animals' foraging decisions and their impact on the vegetation, and should facilitate a generalization of the research results to a broader range of situations.

1. Representation of the grazing process and theoretical bases of foraging behaviour

The importance of prehension constraints during the grazing process first caused herbage intake to be represented, on homogeneous swards, as the product of bite mass, biting rate and feeding time (Allden and Whittaker 1970), assuming spatio-temporal stability of bite mass and biting rate. This approach is no more appropriate on swards that are heterogeneous, such as pastures associating different plant species, or swards that became heterogeneous because grazing was unevenly distributed. A hierarchical approach is now preferred that organises the grazing process into a hierarchy of scales where animals make decisions, that are then integrated over spatio-temporal levels (Senft et al 1987, Laca and Ortega 1995). We focus in this paper on the following levels of decisions : i) short-term decisions, such as selection of the bites on the patch, the length of time grazing a patch before moving on, the selection of a new patch, and ii) longer-term decision, i. e. the length of time to spend feeding.

A patch may be defined as a spatial aggregation of bites over which the instantaneous intake rate (IIR) is relatively constant (Illius and Hodgson, 1996). Thus, two adjacent patches are considered to be distinct when the variability of the animal's instantaneous intake rate between the two patches is sufficient compared with the intra-patch variability. There still remains the problem of how to fix a threshold. Hence, a fine scale of heterogeneity, although it might be perceived by the animal, is not necessarily functional if the animal can not select at that scale. For example, cattle are able to visually discriminate leaf from stem or green from dead material, but contrary to sheep, they might not be able to actively select them because of the shape of their incisor arcade breadth. This example illustrate the need to characterize spatial heterogeneity from a functional point of view.

There are two main theoretical ways of looking at foraging decisions. Synthetic (or ultimate) approaches assume that animals organize their behaviour towards an objective, while analytical (or proximate) approaches explain behaviours from cause-effect relationships.

The basic axiom of the main synthetic approach Optimal Foraging Theory (OFT) is that, because animals that forage more efficiently have a greater reproductive output (fitness), present-day animals forage optimally as a result of natural selection (Krebs and McCleery 1984, Laca and Demment 1996). Fitness maximisation has often been translated into efficiency of foraging, which has often assumed to equate with rate of nutrient intake. However, the recent model by Newman et al (1995) include instead the maximization of fitness. An alternative to the OFT hypothesis, the principle of 'satisficing' hypothesizes that a behavioural option may be taken, not only when it is optimal, but when it is sufficient to overcome some threshold requirement for the animal (Ward 1992). However, this view presents a problem as to how to define a satisfaction threshold if one wants to predict foraging

behaviour. Analytical approaches stress rather than cause-effect proximate relationships determine foraging behaviour, such as sensory stimuli (for example, perception of the height or the brightness of the vegetation) (Bazely 1988, Provenza and Balph 1990), post-ingestive feedbacks resulting from previous choices (Provenza 1995) and dietary experiences (Flores et al 1989, Distel et al 1994).

Synthetic-ultimate and analytical-proximate approaches may be perceived as complementary rather than exclusive. For example, if OFT stresses the importance of natural selection in the determinism of behaviour, it cannot exclude the importance of short-term dietary experiences. Optimization-based predictions should therefore include the animals' dietary experiences. The difficulty in dissociating the two approaches is well illustrated by the question posed by Illius et al (1999): do animals eat a plant species faster because they prefer it (sensory stimulus) or do they prefer it because they eat it faster (optimization of behaviour)?

Optimization is an elegant approach because it is a functional synthesis of foraging behaviour and it enables quantitative predictions (Parsons et al 1994a, Newman et al 1995, Wallis de Vries, 1996). However, it may be a simplified representation of the reality and the basic theoretical axiom has generally been simplified. Actually, maximization of reproductive fitness has been simplified into maximization of various surrogate currencies (instantaneous intake rate of DM, the instantaneous intake rate of a nutrient, daily DM intake, daily nutrient intake, or daily intake of net nutrients., which may prescribe different foraging strategies and behaviours. Moreover, there are still very few experimental tests of this theory, which have generally not completely validated it (Black and Kenney 1984, Demment et al 1993, Illius et al, 1999). This has led to inconclusive explanations, such as the necessity for the animal to sample its environment (Demment et al 1993), constraints on the animal's ability to evaluate the profitability of different behavioural options (Illius et al 1999), search for a balance of nutrients and dilution of toxins (Illius and Gordon 1993, Newman et al 1994a, Parsons et al 1994b, Wallis de Vries and Schipper 1994). These factors do not deny the optimization principle, but underline the importance of constraints that may be difficult to assess.

The weakness of early optimization models lay in the extrapolation from small to larger spatio-temporal scales. These models were developed to describe short-term foraging behaviour. As spatio-temporal scales become larger, foraging behaviour becomes more complex to describe and understand, as it integrates trade-offs with other processes and behaviours. The stochastic dynamic programming approach proposed by Newman et al (1995) is a first attempt at integration. Further steps needed are i) integration of digestive processes, ii) refinement of constraints and the animal's abilities to face them, and iii) integration of interactions of foraging with other motivations such as shelter, social interactions and predator avoidance.

2. How do animals respond to their foraging environment?

Foraging involves the interactions between the characteristics of the animals and the characteristics of the food in the environment. We consider some of the animals' foraging decisions within the vegetation, morpho-physiological, digestive, and behavioural constraints they face, but we mainly focus in this paper on the effects of vegetation characteristics, as animal factors are mainly addressed in the Foraging Strategy session.

2.1. How do vegetation characteristics influence short-term foraging decisions?

In the light of the representation of the grazing process proposed above, we discuss how vegetation characteristics influence the animals' foraging behaviour, including the characteristics of the bites prehended on the patch, the time required toprehend and masticate

bites, the length of time grazing a patch before moving to another, and the further choice of a new patch.

2.1.1 - Patch level

Here, it is assumed that the sward structure is homogeneous in the horizontal plane. The instantaneous intake rate on the patch (IIR) is determined by the mechanical interactions between the grazing animal and the physical properties of the vegetation. It is represented as the quotient of the mass of the bite (BM) and the time required to perform it (T). Bite mass is considered as the primary determinant of IIR, as under many circumstances it constrains the time required per bite.

Bite mass is determined by the ease with which the herbage can be gathered into the mouth and sheared, by the possible presence of 'barrier' components and by the herbage's dry matter content. As grass swards consist of a three dimensional array of plant tissue, bite mass varies with the volume of the bite and the bulk density of the vegetation in that volume. The bite volume is further represented as the product of bite depth and bite area.

Bite mass determines mastication requirement per bite. A linear relationship has been demonstrated between the number of mastication jaw movements and bite mass in sheep and cattle (Newman et al 1994b, Laca et al 1994). In sheep, where prehension and mastication jaw movements are mutually exclusive, time per bite may be split into two components $T=a+bBM$, with a = prehension time, and bBM =mastication time. This functional representation, based on the time budget concept (Spalinger and Hobbs 1992), considers the animal as subject to two constraints: i) the time required toprehend and sever a bite, which is considered as independent of the bite mass, and ii) the time required to masticate the harvested material, which is constrained by bite mass (Newman et al 1994b, Prache 1997, Prache et al 1998) and fiber content of the herbage. In cattle, prehension and mastication jaw movements are not exclusive and compounds jaw movements may represent up to 90% of total jaw movements for high bite masses (Ungar 1996). Hence, in contrast to sheep, the total number of jaw movements required per bite is rather determined by the greatest of the prehension and the mastication requirements than by their sum. As a result, the relationship between time per bite and bite mass in cattle is curvilinear: for low bite masses, it is constrained by prehension time whereas for higher bite masses, it is constrained by chewing time that is proportional to bite mass (Laca et al 1994).

The relationship between IIR and sward structure is most frequently a saturation curve which is easily derived from the relationships described above (Spalinger and Hobbs 1992, Prache et al 1998).

2.1.1.1. Sward determinants of bite characteristics and instantaneous intake rate

Sward height and density

On vegetative patches, the ease of gathering herbage into the mouth is mainly determined by height and density of the sward and by the stiffness of the herbage, which interact with animal's grasping movements (Black and Kenney 1984, Burlison et al 1991, Laca et al 1992). The respective effects of height and density of the herbage have been clearly established owing to the original technique of 'hand constructed swards' (HCS) pioneered by Black and Kenney (1984) and further adapted by Laca et al (1992). This method allowed both to avoid the difficulties encountered in 'real swards', i.e. the strong correlation between height and bulk density of the sward and the barrier effects, and to precisely control the structure of

the sward offered to the animals.

Height is the main sward determinant of bite depth, which tends to be a constant proportion of it. This response is well established experimentally, but questions remain regarding the underlying reasons for such a biting 'rule of thumb'. Illius et al (1995) recently argued against a maximum force being a common factor limiting the bite depth, a hypothesis that has been frequently suggested before.

Within studies, bite depth tends to be a constant proportion of sward height, but this proportion varies from 30 to 50% between studies. Variations may be due to different experimental conditions, the highest values being observed on HCS composed of green leaves, whereas 'real' swards may present some barrier to defoliation and a high bulk density at the base. However, variations are also due to methodological differences in defining and measuring bite depth. On HCS swards composed of green leaves, bite depth is simply calculated as the mean difference in extended length of grazed leaves before and after grazing, in which case the proportion defoliated is about 50% (Ungar et al 1991, Laca et al 1992, Flores et al 1993, Ginnett et al 1999). On 'real' swards, bite depth measurements relate to the variation in either sward surface height (SSH) (Illius et al 1995, Orr et al 1997a) or in extended tiller height (Wade 91, Carvalho et al 1998, 1999) or a combination of both (Edwards et al 1995). Tillers are composed of organs that may be defoliated to different extent; hence, measurements may relate to the depth where all the tiller has been grazed (minimum bite depth, BDmin), or to the maximal depth where the tiller has been, even partially, defoliated (maximum bite depth, BDmax). In both cases, bite depth tends to be a constant proportion of sward height, but the constant of proportionality differs: Wade (1991) for dairy cows obtained values of 35% and 45% for BDmin and BDmax respectively. Carvalho et al (1998 and 1999) using the BDmax method obtained values of 48% for sheep. In the case of bite depth estimates based on SSH measurements, the proportion defoliated is about 35% (Burlison et al 1991, Orr et al 1997a). None of these three methods on 'real' swards are completely satisfying for absolute estimations of bite depth; those based on tiller measurements may, respectively, underestimate (BDmin) or overestimate (BDmax) bite depth and bulk density of the grazed horizon, and that based on SSH may be liable to bias in the mapping of the grazed area (Orr et al 1997a) and in the variability in SSH. As bite mass increases with increasing bite depth, this point remains a methodological problem in the estimation of bite depth and bulk density of the grazed horizon and in the mechanistic modelling of intake.

Bite area results from the interactions between mouth size, herbage grasping movements, sward height and density. It is related to mouth size, but animals are able to collect herbage from an area larger than that of the open mouth by using their tongue (cattle) or jaw and lip movements (sheep and goats). Hence, bite area is positively related to sward height (Burlison et al 1991, Edwards et al 1995 for sheep; Ungar et al 1991, Laca et al 1992, Flores et al 1993 for cattle). On tall swards, it scales with the product of incisor arcade breadth and mouth gape (assumed to be equal to the incisor arcade breadth), but on short swards, it scales with incisor arcade breadth as only a narrow band of tillers can be prehended (Illius and Gordon 1987). In cattle, the relation of bite area to sward height depends strongly on sward density (Laca et al 1992), because animals reduce the amplitude and the number of tongue movements with increasing sward density. This interaction has not been experimentally quantified for sheep, although it is probably different than for cattle because of the different herbage gathering motions in the two animal species.

Bite mass may be represented as the product of bite depth, bite area and bulk density of the grazed horizon. It increases with sward height and density, each variable acting independently and additively (Black and Kenney 1984, Burlison et al 1991 for sheep; Ungar et al 1991, Laca et al 1992, Demment et Laca 1993, for cattle). Effects are generally linear for

cattle and curvilinear for sheep (Laca et al 1992, Black and Kenney 1984, Penning et al 1991a and 1994). Studies with HCS demonstrated that bite mass cannot be predicted solely on the basis of herbage mass, but that both height and density have to be taken into consideration. Actually, herbage mass is a two-dimensional description of a sward whereas bites are taken in three dimensions: a given herbage mass is indeed more accessible to the grazing animal (higher bite mass) when it is tall and sparse than when it is short and dense (Burlison et al 1991, Laca et al 1992). It derives that IIR is influenced independently by sward height and density.

Mechanical properties of the herbage

The mechanical properties of the herbage may influence IIR. Mac Kinnon et al (1988) and Inoue et al (1993) observed that IIR tended to increase by 15 to 25% when sheep grazed ryegrass in which the resistance to fracture was reduced by 40%. First, stiffness of the herbage may affect the effectiveness of herbage gathering (Flores et al 1993). It has been suggested that the higher ease of prehension of white clover as compared to grass may be due to a greater pliability of the herbage, so allowing a higher bite area and mass (Edwards et al 1995, Orr et al 1997b). Secondly, a higher resistance to fracture may affect time per bite. The mastication cost per unit herbage mass ingested has been shown to vary with plant species, being higher for ryegrass than for clover (26 mastications g^{-1} DM vs 15 for clover, Newman et al 1994b) and for *Festuca arundinacea* as compared to *Lolium perenne* (Prache and Damasceno, unpublished). Mechanical properties of the herbage could be further predicted by an index of fibrosity, such as NDF.

Barriers to defoliation: potential IIR inhibitors

The pseudostem has been suggested to form a physical barrier to bite depth. Such an effect can be explained by the greater resistance to defoliation due to its layered structure and its higher fibrosity (Wright and Illius 1995, Illius et al 1995). This barrier effect depends upon pseudostem characteristics. When it is young or when it is below the horizon that is normally grazed by the animal, its presence does not affect bite depth (Flores et al 1993). Experimental quantification of this barrier effect, according to the fibrosity of pseudostem and in interaction with its height relative to the sward height is further required.

Stemmy material affects IIR. The imbrication of vegetative and reproductive tillers in swards that are in an advanced stage of maturity greatly affects the bite mass in selective animals such as sheep (Prache et al 1998). This effect appears to be mediated via a decrease in bite area and bulk density of the grazed horizon rather than a decrease in bite depth (Carvalho et al 1999). The presence of stubble stems in the grazeable horizon also greatly alters bite mass in sheep and cattle because i) animals restrict bite depth to the leafy horizon and ii) bite area is impaired by the increased stiffness of the plants. Instantaneous intake rate on reproductive swards is further impaired by an increased time required to form andprehend the bite and to masticate it (Prache et al 1998, Ginnett et al 1999). Green leaf mass per unit area has been shown to be the best predictor of bite mass and IIR in sheep and cattle across different phenological stages of the sward (Flores et al 1993, Prache 1997, 1998) or sward management (Penning et al 1994).

The presence of dead material at the bottom of the sward may also reduce bite depth and IIR, but its effect has never been quantified, probably because it is difficult to study experimentally.

Dry matter content of the herbage

Surface water reduces the ease of prehension and palatability of the herbage, particularly in sheep where this is very sensitive, whereas internal water may cause a bulk effect on rumen fill. Orr et al (1997b) observed an increase in dry matter intake per bite and intake rate by sheep over the day and suggested that this may be related to an increased DM content of the herbage, a loss of water surface making the herbage less slippery and easier to harvest. As they observed constant fresh dry matter intake per bite throughout the day, they suggested that the amount of fresh herbage per bite may determine bite mass. Increased surface water may also reduce biting rate (Butris et Phillips 1987, Laca et al 1992, for cattle; Prache and Carvalho, unpublished, for sheep).

2.1.2. Patch depletion and 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 maximize 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) and Roguet (1997), although agreeing with the qualitative predictions of MVT, observed a longer residence time and a lower intake rate than predicted by MVT. Imperfect knowledge of the environment and social constraints have been given as possible explanations of a sub-optimal behaviour (Bazely 1988).

Optimal patch residence time depends on the characteristics of the environment. It increases with interpatch travel time (Laca et al 1993, Distel et al 1995) and depends strongly on the shape of the gain function (Astrom 1990). Gain functions have rarely been measured. Stephens and Krebs (1986) suggested the most likely shape would be an asymptotic curve. That was confirmed experimentally by Wallis de Vries (1998) on swards of variable height, but Ginnett et al (1999) obtained different forms by manipulating the architecture of the vegetation. These authors derived habitat grazing predictions in the field on the basis of optimal behaviour, from the gain functions they measured on hand-constructed swards. Their predictions on stemmy *vs* non-stemmy swards agreed with the results of Roguet et al (1998b) and Prache et al (1998) obtained in a field situation: for a given green leaf mass per ha, the animals grazing vegetative swards had a shorter residence time, removed more herbage from each patch and visited fewer patches per day, while obtaining higher intake rates than animals foraging on stemmy swards. On the contrary, their predictions on tall *vs* short swards differed from the results of Roguet et al (1998a and b). These discrepancies may be due to imprecisions in estimating the gain function's shape, which is, nevertheless, a key factor when linking spatiotemporal hierarchical scales.

An initially uniform patch may be viewed as superposed grazing horizons, each with a characteristic bite depth, area and IIR, that are successively defoliated. This representation is probably over-simplistic. Firstly, bite depth impact is rather hemispheric especially in cattle, secondly, the animals do not strictly graze horizon by horizon. Recent studies have shown that when the fraction of the horizon area remaining ungrazed decreased below a threshold of about 25-30%, the bite area and hence the bite weight taken within an horizon tended to decline, and there was a significant entry into the next horizon (Ungar 1998). This has been explained by a non-systematic bite placement, border effects and overlap between bites (Ungar and Ravid 1999). In the field, homogeneous patches are often greater than a single feeding station (FS), and the question remains as to whether or not a depletion occurs at the

feeding station level within homogeneous patches. This is an important question, as local FS depletion may cause a reduction in bite dimensions and intake rate as compared to the assumption that depletion does not occur at the FS level. However, it is difficult to study experimentally because it necessitates working under very short-term tests, and in conditions (grazing sods indoors) where behaviour may be different compared to field situations (Roguet et al 1998a, b, Wallis de Vries 1998). Roguet et al (1998b) observed that ewes removed 6 to 9 bites per FS in continuous pastures of variable herbage availabilities and stages of maturity. If we assume a maximum bite area of 20 cm^2 (Edwards et al 1995) and an FS area of 3500 cm^2 (Roguet et al 1998a), this represents 3 to 5% of the area of the FS, so that it is unlikely that depletion has occurred at the level of the FS in this study with sheep. Little comparable information is available for cattle. Wallis de Vries et al (1998) observed in a field situation with large patches that cattle took an average of 7 bites per FS, so a value comparable to that observed with sheep. Maximum bite area is about eight-fold higher in cattle than in sheep, but the size of the FS is probably not of comparable increment between the two animal species. Hence, it might be that cattle, in contrast to sheep, present a risk of depletion at a lower level to that of an homogeneous patch, i. e. feeding station level. Nevertheless, Wallis de Vries et al (1998) observed no significant reduction in average bite weight over a series of 5 bites when compared to a series of 10 bites on grazing sods 1500 cm^2 in area, and Ginnett et al (1999) observed no significant reduction in bite mass and IIR over a series of 10 bites as compared to a series of 20 bites on 20cm-high hand constructed swards 2100 cm^2 in area. The question still remains for cattle as to whether or not the FS level is relevant in the hierarchical representation of the grazing process.

2.1.3. Multi-patch level

Patch choice may be influenced by factors such as vegetation characteristics, distance to water, climate or shelter, social and predation factors. When considering the vegetation characteristics, two situations may be distinguished: i) those where the animals can express their preferences, i. e. can graze the preferred patch without having to search and, ii) those where choices are affected by a cost of searching.

When searching costs are negligible, for example on a feeding site which offers easily found, discrete patches, animals generally prefer patches where they can eat at the faster rate. This has been shown by using a combination of paired feeding short-term tests of the same species, by varying the height and density of the sward (Black and Kenney 1984, Demment et al 1993, Distel et al 1995). Studies on plurispecific patches are very few, but a recent study by Illius et al (1999) with pairs of turves of different plant species also confirmed the short-term preference of goats for the higher intake-rate alternative. Hence, animals concentrate grazing on patches that offer the greatest energy intake rate potential, that allow them to increase their rate of food intake. Therefore, it is of importance to consider the spatial heterogeneity of the sward, when predicting intake rate. However, preference is not absolute and intake rate is often less than predicted from the optimization theory (Dumont et al 1995, Prache et al 1997, Baumont et al 1998, Illius et al 1999, Prache and Damasceno, unpublished). On fields consisting of adjacent monocultures of grass and clover of the same height, the proportion of clover in the diet of sheep, heifers and lactating cows is consistently about 70% (Parsons et al 1994a, Harvey and Orr 1996, Penning et al 1995, Rutter et al 1999) even though animals generally eat clover faster than grass (Newman et al 1994b). In the same way, dry ewes offered a choice between adjacent ryegrass (preferred species) and festuca (disliked species) monocultures 20 cm-high include approximately 20% festuca in their diet (Prache and Damasceno, unpublished).

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, the difficulty or a low interest by the animal in discriminating, and discrimination errors, have been proposed as explanations (Illius et al 1999). Actually, the choice between patches depends upon the ability of the animal to discriminate between them (Laca et al 1993, Illius et al 1999). On a daily scale basis, the diurnal pattern in preferences, the search for a balance of nutrients and digestive constraints have been proposed as explanations of partial preferences and mixed diets (Newman et al 1995, Wallis de Vries and Schippers 1994). Moreover, if OFT stresses the importance of the efficiency of foraging in the reproductive success of an animal species, the capacity to diversify its diet under food scarcity may also contribute to the species's strategy to increase its reproductive output.

The preference for a plant species or patch is sensitive to its relative availability (Carrere et al 1995, Harvey and Orr 1996, Prache et al 1997). Animals may trade-off quality for quantity and switch to the less-preferred item when greater benefit is obtained from it. If one assumes that animals seek to maximize intake rate, the switch to the less-preferred patch may be predicted from the potential intake rate on each patch. The figure 1 gives an example for sheep rotationally grazing swards containing reproductive patches in a vegetative background. Functional responses on vegetative and reproductive patches (fig1a) lead to predict that, if using a short-term DM intake rate optimization rule, animals should switch to reproductive patches when the green leaf mass on vegetative patches becomes lower than 300 kgDM. ha⁻¹ (i. e. 9 cm height in this study). This prediction is in agreement with the results of choice tests using similar patches (fig 1b). 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. For example, wapitis offered choices between 2, 4, 6, 8 and 10 weeks regrowth patches preferred patches of medium biomass and quality (4-weeks regrowth), rather than better quality but lower biomass patches or higher biomass but lower quality patches (Wilmhurst et al, 1995). Solving an optimal policy for the herbivore from the potential intake rate on each patch leads to the prediction that the switch to the less-preferred patch will be abrupt and rapid, and there will be no preference for either patch after the switch. These predictions agree with the results of Prache and Damasceno (unpublished) on swards consisting of adjacent monocultures of ryegrass and festuca monocultures, and Prache et al (1997) on swards containing vegetative and reproductive tillers (Figure 2). During the grazing down of a reproductive sward, ewes first selected vegetative tillers as long as these were taller than 8-9 cm, the relative mass of vegetative tillers in the diet being 28% higher than in the sward; thereafter, the animals changed their choices radically and rapidly, showing no preference for either type of tillers, but without reversing, on average, their choices in favour of the reproductive tillers. However, further research is required i) to describe the functional response (potential intake rate) of herbivores on different types of patches (plant species, particularly) according to their height and density, and ii) to test the validity of the optimal hypothesis to explain the process of diet choices against real data.

In natural conditions, there are often additional constraints in searching for preferred patches, which may limit intake rate and alter diet choices. These constraints are determined by total herbage availability, relative horizontal abundance of the preferred species and their spatial distribution. They make the environment more difficult for the animal to perceive and increase the probability to consume less-preferred but easier to reach food patches (Clarke et al 1995, Dumont et al 2000). 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 bites encountered removed (Laca and Ortega 1995, Roguet et al 1998b). Prache et al (1998) demonstrated and quantified a negative relationship between dietary selectivity and intake rate, because of a decreased bite mass and an increased time cost of searching. Roguet et al (1998b) observed

that the distance walked for a given bite mass was always higher on reproductive as compared to vegetative swards, ranging from 5.4 to 6.9 cm and from 3.6 to 5.6 cm respectively.

The proportion of a preferred food item in the diet is generally related to its proportion in the sward, i.e. there is a tendency towards frequency-dependent selection (Clark and Harris, 1985, Prache et al, 1997). A decrease in 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 1994b).

The scale of patchiness may have marked effects on animal's foraging decisions. A small-scale of patchiness may involve constraints due to selection of preferred from less-preferred food items, whereas a larger scale may involve constraints due to moving and locating preferred patches. Fine mixtures reduce the opportunity for selection whereas large patches offer maximum opportunity for selection. Sheep grazing on grass/clover swards select less clover when the species are offered as an intimate mixture rather than in separate strips (Clark and Harris 1985). Gordon and Illius (1997) observed no differences in the diet selected by sheep on four dispersions of clover and grass, but a higher intake rate on larger patches. Large-scale heterogeneity may impose various constraints, which may affect foraging behaviour, dietary choices and the impact on the vegetation (Montossi et al 1994). It may impose constraints on moving to reach preferred patches, which may affect intake rate (Laca et al 1993), unless the moving time is completely devoted to mastication. There may also be constraints on the visual perception of alternative patches and spatial knowledge making the value of the environment more difficult to perceive. Consequently, spatial distribution of preferred patches influences efficiency of search and intake rate. Both increase with patchiness, from random and uniform distribution to aggregated distribution (Laca and Ortega 1995, Dumont et al 2000). When the preferred patches are distant and out of the sight of the animals, the use of visual cues may enable animals to increase their efficiency of search and intake rate (Laca and Ortega 1995).

2.2. From short-term to daily intake rate

Integration from short-term IIR to daily intake necessitates the linking of instantaneous feeding behaviour with satiation processes together with the animal's motivation to eat. Great progress in integrating ingestion and digestion has been achieved by mechanistic modelling (Illius and Gordon 1991, Sauvant et al 1996). However, determinants of daily feeding time are much less well elucidated, which impairs our ability to predict feeding bouts and daily intake from short-term intake rate.

2.2.1. Integration of ingestion and digestion

Post-ingestive signals coming from feed (rumen fill, fermentation products and nutrients) contribute to the satiation process. Ingestion and digestion are linked by the nutritive value and the fill effect of the forage. Nutritive value is determined by the characteristics of the forage available and the degree of selectivity of the animal. Animals are able to learn the post-ingestive consequences of their dietary choices, and hence to appreciate indirectly the nutritional value of the plant they have selected, feedbacks acting as positive or negative stimuli in subsequent choices (Provenza 1995). This author demonstrated that ruminants develop preferences for feeds that are richer in energy and that post-ingestive feedbacks enable animals to avoid toxins and nutritional unbalances.

Beyond its ease of prehension, ingestibility of the selected plant, like its digestibility, decreases with its age, as a consequence of the increase of its fill effect (Figure 3). Retention time in the rumen depends mainly on the degradation rate of the degradable fraction and on

the proportion of the undegradable fraction (Baumont et al 1997). As the plant ages, its morphological and histological development decreases the amount of cell content, which is soluble, rapidly degraded and with almost no fill effect, and increases the amount of cell walls. Consequently, forage retention time in the rumen and fill effect increases. Tissue lignification further increases the undegradable fraction of the cell walls and decreases the degradation rate of the degradable fraction, which further increases retention time in the rumen (Baumont et al 1997). For animals fed indoors, the plant cell wall content has been shown to be a good criterion for predicting forage's fill effect and ingestibility (Baumont et al 1997).

Animals grazing heterogeneous pastures frequently have to trade-off between forage quantity and forage quality. Forage of low quality is generally more abundant, so it can be found more easily and eaten more rapidly if the animal is not selective, but daily intake may be limited by digestive constraints. Conversely, greater selectivity yields a higher quality of diet, but may limit intake rate and daily intake. Thus, ingestive and digestive constraints define an area of possible daily quantity and quality of diet, the specific intake and diet quality depending finally on the strategy of the animal; solving an optimal policy depends, for example, on the surrogate currency that the animal seeks to maximize (Demment et al 1995).

2.2.2. Motivation of the animal to eat: feeding time

Factors controlling feeding time (FT) remain poorly understood. There are, actually, inherent difficulties in assessing the complexity of its determinants and their possible interactions, from rumen load, to level of nutrient intake and thermal load, in interaction with the motivational state of the animal.

Bulk in the rumen has been demonstrated to constrain both FT and intake for high availability of low-quality pasture, but to have no effect on highly defoliated pastures, in which case, the constraint to FT was rather the animals' unwillingness to further graze (Chacon and Stobbs 1976). There is clear evidence that animals can increase FT to compensate for a low intake rate, whether this decrease is due either to a low herbage availability or an increased selectivity (Alden and Whittaker 1970, Chacon and Stobbs 1976, Prache et al 1998, Champion et al 1998). This compensation may be total or partial, depending upon the actual intake rate, the animal's requirements and the ability/willingness to further graze, as well as daylight length, though beyond a certain threshold, FT may actually drop sharply. This pattern is widely recognized for rotational grazing (Chacon and Stobbs 1976, Hendricksen and Minson 1980, Prache et al 1998) and strip grazing (Le Du et al 1981).

This pattern has been explained by i) FT being a compensatory mechanism that is constrained by upper limits such as gut fill, thermal load and fatigue, and ii) animals evaluating the profitability of grazing and reducing FT when it becomes uneconomical (Illius and Gordon 1999). It has been proposed that prehension bite numbers or feeding time may have an upper limit set by jaw muscle fatigue. However, Illius (1997) rather suggested the total jaw movements (or time involved in oral processing, i.e. grazing+ruminating) as a limit to FT. Actually, Penning et al (1991) observed an almost constant oral processing time and daily jaw movements across seasons and sward treatments. The hypothesis that has been put forward to explain the decline in FT under conditions of severely limited intake rate is that grazing becomes uneconomical, i.e. the energy cost of travel and eating exceeds energy intake. Actually, the animals do not abruptly cease grazing, but rather reduce their feeding time; so, it might be that they do not accurately weigh the costs and benefits of grazing in the short-term, and might progressively reduce FT as the grazing profit approaches zero (Illius 1997). We evaluated these hypotheses using the data of Roguet et al (1998) and Prache et al (1998), who quantified the moving profit, quality of the diet and FT of ewes progressively

defoliating a reproductive sward, together with the data on the costs of travel and eating of Osuji (1974) (Figure 4). Feeding time first increased from 312 min to a maximum of 616 min, as a compensatory mechanism to a decreased IIR, the decrease in mean digestible intake rate being totally compensated by an increase in FT. Feeding time then dropped to 523 min and 504 min. The moving profit decreased from 3.65 kcal. m⁻¹ to 1.34 kcal.m⁻¹ respectively at the beginning and the end of the grazing down, being 1.39 kcal.m⁻¹ at the time of the maximum FT. The energy balance was always positive, but the results indicated that a moving profit of about 1.39 kcal.m⁻¹ may be a threshold value below which the sheep reduce their feeding time. However, further evaluation of these hypotheses is still required.

2.2. Interactions with the animal's characteristics

Here, we focus on the interactions with morpho-physiological characteristics and animal state, whereas other animal's characteristics, such as dietary experiences and social environment which also influence both the foraging abilities and the decisions of animals are addressed in the Foraging Strategy session.

3.3.1. Morphological characteristics

The body mass of herbivores induces differences in energy requirements together with differences in ingestive and digestive capacities. These characteristics explain most of the between-species differences in foraging behaviour. They have been extensively reviewed by Illius and Gordon (1999).

The efficiency of prehension depends upon the incisor arcade breadth, on the force the animal can exert when biting, and in cattle, on the degree of protrusion of the tongue. The efficiency of mastication per unit herbage mass ingested depends on the molar surface area, being greater for cattle than for sheep (Parsons et al 1994a).

General relationships between morphological characteristics and efficiency of grazing have been derived from data on various ruminant species showing that body mass influences most of the variables related to intake rate. Variations in body mass induce differences in mouth size and in maximum bite area. Illius and Gordon (1987) proposed the following equation: incisor arcade breadth (IAB, mm) = 8.6 W^{0.36}, W being the animal's liveweight, but Taylor et al (1987) proposed a greater allometric constant for cattle than sheep (IAB, mm = 9.84 W^{0.33} for cattle, 8.44 W^{0.33} for sheep). Sward structure and animal body mass interact, bite mass increasing faster with sward height for larger animals (Ferrer Cazcarra et al 1995). This is explained by the allometric relationships of bite area with sward structure (Illius and Gordon 1987). On short swards, where only a narrow band of tillers in the immediate proximity of the incisor row can be prehended, bite area is determined by incisor arcade breadth (proportional to W^{0.33} to W^{0.36}); on tall swards, bite area scales with the product of incisor arcade breadth and mouth gape (assumed to be equal to the incisor arcade breadth), hence it increases proportionally with W^{0.67} to W^{0.76} (Gordon et al 1996). Assuming that bite depth does not vary with the animal's size, these mechanical interactions led Illius and Gordon (1987) to predict that the allometric exponent relating intake per bite to body mass should tend from 0.72 on tall swards to 0.36 on short swards. However, these authors further examined the allometry of bite mass and intake rate from data on ruminant species ranging from 20 kg sheep to 500 kg cattle, and found that bite mass scaled with an exponent of 0.74 on tall swards and 0.63 on short swards (IB=8.16 W^{0.74} and 4.04 W^{0.63}, respectively). They explained the discrepancies between their predictions by a greater bite depth in large animals that was not allowed for in the first predictions (Illius and Gordon 1999). However, variations in bite depth with animal body mass still needs further investigation. Illius and Gordon (1999)

recently argued that bite depth scaled with the animal's liveweight, indicating that large animals may be less constrained by the resistance posed by the physical properties of the vegetation. However, Orr et al (1997a) did not find any differences between heifers and ewes, and Carvalho et al (1999) found almost similar proportionality coefficient between bite depth and tiller length with ewes than Wade (1991) with dairy cows (48% vs 45%).

Considering the slower rate of biting by larger animals, short-term dry matter intake rate has been estimated to range from $7.66 W^{0.71}$ on tall swards, i.e. close to the scaling of the daily energy requirements, to $8.63 W^{0.50}$ on short swards (Illius and Gordon 1999). The increase in intake with age and weight is mediated via an increase in intake rate, as feeding time generally decreases with age and weight. In dairy cows, herbage intake increases by 1.0 to 1.5 kg OM per 100 kg W (Peyraud et al 1996), which is similar to the incremental increase reported for cattle differing in size (Zoby and Holmes 1983). This is mediated by an increase in the rate of intake of $3 \text{ g OM} \cdot \text{min}^{-1}$ per 100 W, whereas FT decreases as the liveweight of the animal increases ($-40 \text{ min per } 100 \text{ kg W}$, Delagarde 1997). Similar results have been observed in cattle differing in age and liveweight (-23 to $-35 \text{ min per } 100 \text{ kg W}$, Zoby and Holmes 1983)

According to the scaling of intake rate with sward height, large animals are more handicapped on short swards where intake rate increases more slowly with body mass than do the energetic requirements ($W^{0.75}$) (Illius and Gordon 1987). These prehension constraints may partly explain why cattle switch earlier than sheep from short digestible patches to patches with greater biomass, but lower digestibility (Dumont et al 1995). The shape of the incisor arcade also determines the ability of the animal to select between food items or plant parts, which is greater for sheep than for cattle (Gordon and Illius 1988). Hence, large animal species may be handicapped when the accessibility of the preferred food items is poor; in this case, the quality of the diet selected by cattle may be much lower than that selected by sheep. Consequently, the heterogeneity of the vegetation in a sward may change in a different way depending upon the body size of the animal species that grazes it, because of the different impact on the colonizing plant species at the boundaries of patches (Illius and Hodgson, 1996). However, the lower selective ability of large animals is outweighed by their greater digestive capacity and efficiency. Actually, the energetic requirements of herbivores increase proportionally to $W^{0.75}$, whereas the gut volume increases linearly with W (Demment and Van Soest, 1985). Hence, large animal species can tolerate lower quality forages than small species, as the ratio of energetic requirements to gut volume is lower (Demment and Van Soest 1985, Demment and Greenwood 1988). Moreover, small animal species are less efficient at digesting rough forages because of the shorter residence time of material in the rumen (Dulphy et al 1994), which scales with $W^{0.27}$ (Illius and Gordon 1999).

2.3.2. Internal state

There is evidence for a diurnal pattern in diet selection in cattle and sheep. It has been explained by a desire to eat rapidly during the morning meal after the relative fast of the night and avoidance of having to graze during the night, preference for the species having the lower rate of passage being higher in the evening (Penning et al 1991b). When animals were given a choice between adjacent patches of clover and grass, they showed the greatest preference for clover in the morning and ate more grass and less clover during the evening meal (Parsons et al 1994b, Newman et al 1994b on sheep, Rutter et al 1998 on cattle). Likewise, sheep having the choice between adjacent vegetative and reproductive patches spent more time grazing the reproductive patch during the evening meal (Dumont et al 1995).

The animal is able to use its behaviour as a flexible means to face both vegetation and physiological constraints. Actually, some volitional control of intake rate exists, as shown by

experimental data relating foraging decisions to the animal state. After a period of food deprivation or when the time of access to the food is decreased, the animal is able to increase its rate of food intake (Greenwood and Demment 1988, Penning et al 1991b, Newman et al, 1994a, Prache et al 1998), by increasing its bite mass (Newman et al 1994a, Prache et al 1998), and/or decreasing the time taken to masticate each unit of DM (Laca and Demment 1996). Fasting has also been suggested to alter bite depth because of an increased motivation of the animal to overcome the effort of grazing (Illius et al 1995). In the same way, during feeding bouts, the motivation to eat and intake rate are maximum at the beginning and decrease continuously during the process of satiation until the end of the feeding bout which corresponds to satiety.

Lactating animals achieve a greater intake than dry animals essentially through an increase in feeding time, but as time available to forage may be an important constraint, high-producing animals are able to adapt their behaviour by grazing more efficiently. Higher feeding time, intake rate and bite mass have been reported in lactating compared to dry ewes (Penning et al 1995), and Prache (1997) observed that ewe's bite mass and intake rate increased with lambs' growth rate, i. e. level of ewe's milk production. The mechanisms by which high-producing animals achieve a greater mean bite mass requires further investigation. It does not seem to be mediated through an increased biting depth, as Carvalho et al (1999) did not find any differences in bite depth between dry ewes and ewes rearing twins. A higher intake rate may be further mediated via a decreased time devoted to mastication (Prache 1997). In lactating cows, a higher intake by medium-producing as compared to dry animals is mostly mediated by an increase in feeding time (from 5 to 8 min/kg milk, Journet and Demarquilly 1979), but for high-producing animals, because the time available to forage is constrained to a plateau at 9-10h per day, an increased intake is mostly mediated through a higher intake rate (Rook and Huckle 1996, Delagarde 1997).

2.3. Limits of the idea of fixed constraints

Beyond the physical and searching constraints imposed by the vegetation that have been reviewed above, the animal is hence able to adapt its behaviour to overcome these constraints to some extent. Consequently, though the idea of vegetation constraints has helped to build a general framework from which to represent the interactions between the grazing animals and the vegetation, and the control of intake, there is convincing evidence that these constraints do not always have fixed values (Illius and Gordon 1999). Prehension and mastication constraints on the patch may be overcome to some extent by hungry animals. Likewise, facing searching constraints in a heterogeneous environment, the animals are able to develop search strategies, such as walking faster (Roguet et al 1998b), learning about the location of food and using its spatial memory together with visual cues (Laca and Ortega 1995, Edwards et al 1996, Edwards et al 1997, Dumont and Petit 1998). In the same way, there is no absolute threshold for the different post-ingestive signals involved in the satiation process, i.e. rumen fill and nutrients (Faverdin et al 1995).

This evident adaptability in foraging behaviour question us on the validity of the notion of absolute thresholds and fixed constraints adding separately and additively, and further complicates the prediction of diet selection and intake. It highlights the need to further integrate the interaction between the animal's internal state and the constraints of the vegetation. Beyond the conventional view of grazing behaviour being governed by the constraints of the vegetation, an alternative view is emerging that represents feeding behaviour as being the result of the balance between all the positive and negative stimuli. Feeding continues as long as positive stimuli have a higher intensity compared to negative stimuli; when the intensity of the negative stimuli exceeds that of the positive stimuli, feeding

is inhibited (Faverdin et al 1997). The model by Sauvant et al (1996) that has been further adapted to grazing situations by Baumont, Cohen-Salmon, Prache and Sauvant (unpublished) is a first attempt to manage two antagonistic forces, the motivation to eat and the satiation process. It consists of two interconnected submodels, a ruminal digestion submodel together with a feeding decision submodel, the choice of grazing, ruminating or resting depending on the relative values of the functions of intake motivation and of satiety. If the motivation to eat is high enough, physical regulation can be delayed, because it is not based on a fixed value of rumen fill as assumed in previous models (Forbes 1980, Illius and Gordon 1991). Conversely, on heavily defoliated swards, the decrease of the index of palatability of the sward greatly lower the motivation to eat. When the animal eats, its potential intake rate is determined by the characteristics of the sward, the dynamic simulation then predicts an actual intake rate integrating the animal's satiety status. Interplay between characteristics of the vegetation and internal state of the animal is hence dynamically taken into account from the level of a few bites to several following days.

3. Daily intake

Modelling the interaction of the grazing animal and its pasture to predict intake has been attempted either by the classical way using empirical equations of predictions based on animal and sward characteristics (Peyraud et al 1996), or by a mechanistic approach based on a comprehensive synthesis of the lower-level processes involved (Baumont et al unpublished), but a recent simple mechanistic model has also been developed by Stuth et al (1999) in order to provide tools for management purposes. These models have mainly focused on swards which can be considered as homogeneous patches. However, conceptual and mechanistic approaches should allow further development on more complex swards.

As considerable work has been made in recent years with dairy cows, we mainly use this literature to review the different factors affecting herbage intake. We focus in this paper on the sward factors that affect herbage intake, animal factors having been recently reviewed by Peyraud and Gonzalez-Rodriguez (2000).

3.1. Sward factors affecting daily herbage intake

Main sward factors influencing herbage intake are the availability of herbage, its architecture (spatial array) and its nutritive value in relation to rumen transactions.

3.1.1. Sward availability and architecture

Daily intake is influenced by sward availability and architecture of the herbage. Height and density of the sward have positive effects, whereas stemmy and dead material have negative effects because they reduce IIR.

For continuous stocking maintained at a given sward height, a characteristic sward structure develops and herbage availability may be simply described in terms of sward height or herbage mass. In this case, herbage intake (HI) increases asymptotically with sward mass and/or height, a maximum intake being reached for a sward height of 8 to 9 cm in dairy cows (Le Du 1980) and from 6 cm onwards for lactating ewes (Penning et al 1994).

Under rotational and strip grazing conditions, sward structure is different as compared to continuous grazing, it is much more variable and may change rapidly. Moreover, when herbage mass/height declines significantly during the day (intensive rotational or strip grazing) or when it is measured only prior to grazing, this description of herbage availability is insufficient. In that case, it is generally described by a combination of herbage mass and

herbage allowance prior to grazing.

A number of studies have demonstrated a strong curvilinear relationship between herbage allowance (HA), herbage intake and animal performance (Greenhalgh et al 1966, Combellas and Hodgson 1979, Peyraud et al 1996 in dairy cattle, Gibb and Treacher 1978, in sheep). With vegetative perennial ryegrass swards grazed by adult dairy cows, Peyraud et al (1996) and Delaby et al (1999) observed an average increase in HI of 0.25 kg OM day⁻¹ per kg increase in HA when it ranged between 11 to 16 kg OM day⁻¹, and a much smaller increase (+0.05 kg OM day⁻¹) above 20 kg OM day⁻¹. High herbage allowance is therefore required to achieve maximum intake and performance. However, an increased herbage allowance early in the season leads to an increase in residual sward height and this may result in a deterioration of sward quality in mid and late season. Hoogendoorn et al (1992) have observed an increased proportion of stem and dead material and reduced digestibility following lax grazing in the early season. From a practical point of view, the room for manoeuvre is small. Hoden et al (1991) found that HI can be increased by 1 kg OM cow⁻¹ day⁻¹ by a 1 cm-high increase in residual sward height in spring without noticeable effects on sward quality later in the season. Beyond this value, alternative strategies could be used to manage residual herbage, such as topping, grazing by low-producing animals or reducing HA together with providing supplements. An alternative strategy would be to develop sward structures allowing the maintenance of high intake levels together with a low residual sward height, which is a challenge for research.

Beyond herbage allowance, pregrazing herbage mass (HM) does have an independent additive effect on herbage intake, the relation being curvilinear, with a slight decrease in HI for high biomass even when it is not associated with a decrease in digestibility. Hence, intake by dairy cows is maximal between 4.0 and 5.5 tOM.ha⁻¹; it may be reduced by 2 kg.day⁻¹ when HM falls from 4 to 3 tOM.ha⁻¹ or increases from 5.0 to 6.5 t OM.ha⁻¹ (Peyraud et al 1996). Furthermore, by pooling data obtained under different grazing conditions (rotational and continuous grazing, different ages of regrowth, different sward phenological stages under rotational grazing), Penning et al (1994), Prache (1997), Prache et al (1998) on sheep and Parga et al (unpublished) on dairy cows showed that grazing behaviour and daily intake of ewes and dairy cows were better correlated with the availability of preferred plant organs (green leaves) than with the total herbage availability. The availability of green leaves therefore, could be a better criterion than the total herbage availability to predict HI for swards changing rapidly in leaf to stem ratio, such as rotationally or strip-grazed swards. However, as seen above, the three-dimensional structure of the herbage is important to consider. Herbage mass or green leaf mass per ha are actually two-dimensional descriptions of the sward, whereas intake is a three-dimensional process. As height and density are always closely correlated within a sward, they cannot be separately introduced in the multiple regressions aimed at assessing the relative effect of each factor. A greater range of sward structures permitting an increased degree of independence of sward characteristics and splitting herbage mass into its two components, together with a more detailed description of sward structure and morphology, may lead to further improvements in the prediction of intake.

The pseudostem has been suggested to form a barrier to defoliation. Actually, on rotational systems, because the sward height declines during the grazing down process as a function of herbage allowance, HI may be greatly determined by the characteristics of the last horizons grazed by the animal. Wade (1991) first suggested that in addition to sward height, pseudostem height may alter herbage availability. He studied the grazing down process in rotationally grazed swards that were initially tall or short (Table 1). Intake and milk yield started falling when tiller height reached a higher value in initially tall than in initially short swards, but milk yield and intake started to reduce when the free lamina was approximately

55 mm in both swards. An optimal pregrazing height remains to be found: cows grazing very short swards are unable to eat sufficient quantities of DM even if the area offered is large, whereas on tall rotationally grazed swards other limiting factors, such as the pseudostem barrier (and decrease in digestibility, see above) may have negative effects on daily intake. The positive effect on HI of a high proportion of green leaf lamina in the deep horizons was shown by Parga et al (2000). These authors prepared two contrasting swards by different cutting policies. The swards differed in green leaf mass in the 5-15 cm horizons, but had similar height, herbage mass and green leaf mass above 15 cm. At high herbage allowance, HI was similar in both swards, but when the herbage allowance was decreased from 17 to 12 kg OM, HI was less affected on the leafy compared to the control sward. Increasing green leaf mass in the deep horizons of the sward by appropriate grazing management or selection of varieties may have a major role in increasing herbage intake, while allowing the maintenance of a low residual sward height.

3.1.2. Quality and nature of the sward

In housed animals, OM digestibility of the forage determines its filling effect (e.g. rate of comminution, digestion and passage) and ad libitum intake. The relation between OM digestibility and intake per metabolic liveweight is linear or slightly curvilinear according to plant species (Figure 3), with a decrease of 0.99 to 1.56 and 0.86 to 0.95gOM. kgW^{0.75} per percentage unit of OMD decline for grass and legume species respectively (Demarquilly et al, 1981, in sheep). At pasture, changes in digestibility are most often associated with changes in sward structure, such as sward height and vertical distribution of plant organs within the horizons, which may lead to difficulties in quantifying the relative importance of prehension and rumen fill constraints. Moreover, the nutritive value of the forage ingested is further mediated by the animal's selectivity, which depends upon its ability/willingness to be selective, i.e. its foraging strategy. At generous herbage allowances (ease of prehension of the herbage being not a limiting constraint on intake), Hodgson et al (1977) demonstrated a close, linear relationship between herbage intake of young cattle and OM digestibility of the selected herbage, over the range 0.50 to 0.80. In dairy cows, a 2.2 kg.day⁻¹ decrease in HI has been reported by Greenhalgh (1966) on vegetative as compared to reproductive ryegrass swards. This decline may be due to a decrease in the intake rate because of selective grazing (Flores et al 1993, Prache et al 1998), together with an increase in NDF content that affects rumen transactions. Under a range of data reasonably representative of pastures for dairy cows (d>0.75), Peyraud et al (1996) quantified a 0.2 kg OM increase in HI per unit increase in pepsine-cellulase digestibility.

At a given digestibility, ingestibility is higher for legumes than for grass (about +20% for confined sheep, Figure 3), because of their lower cell wall content. Likewise at pasture, markedly higher intakes have been observed on red or white clover than on ryegrass (Ulyatt 1971, Hodgson 1975, on lambs) and on lucerne compared to cocksfoot of a similar digestibility (Allder and Minson 1963, on beef cattle). This is explained by a higher intake rate, digestion and passage rates. Comparisons of grass species in grazing situations have been rare. Herbage intake and milk yield have been shown to be reduced by 1 to 2 kg. day⁻¹ when cows graze cocksfoot compared to perennial ryegrass (Greenhalgh and Reid 1969). Hageman et al (1990) observed a higher intake and milk production on tetraploid compared to diploid ryegrass varieties. A tendency to an increased IIR has been reported by Inoue et al (1993) on ryegrass the tensile and shear strength of which was reduced. However, although of likely importance in sward prehension and comminution, the effect of sward tensile strength on daily intake has not yet been demonstrated. Comparisons of ryegrass varieties under grazing have recently been undertaken to identify the plant attributes of importance for intake, and to

further evaluate and breed ryegrass cultivars. These studies showed that the potential value of ryegrass cultivars cannot be evaluated from indoors and/or cutting experiments. No correlations were found between intake of housed animals and intake at pasture (Hazard et al (1998) and between herbage production under cutting and grazing (Orr et al 2000). Large significant differences in daily intake by grazing sheep have been observed in both studies, but further investigation is needed to determine the plant attributes responsible for this variation that can be used to evaluate and breed grasses.

A number of studies have shown higher intake and animal production on mixed ryegrass/white clover when compared to pure ryegrass swards, the difference increasing with increased clover content. Mixed swards present also the advantage of allowing more flexibility in grazing management. Actually, between 28-days and 50-days regrowth, digestibility and content of protein flowing into the duodenum decreased for ryegrass (0.80 to 0.75 and 154 to 110 g. kgDM⁻¹), whereas they remained almost the same for white clover (0.80 and 180 g. kgDM⁻¹) (Peyraud 1993, Mambrini and Peyraud 1994). Considering the increased concern for pollution risks, mixed ryegrass/white clover swards provide opportunities to reduce mineral nitrogen fertiliser inputs and should be considered as an alternative option to pure grass swards, the challenge being to maintain a sufficient clover content within the sward. Moreover, offering simple choices to animals may further enhance intake. Champion et al (1998) observed that sheep offered adjacent grass and clover monocultures tended to have higher daily herbage intake than sheep fed pure clover, pure grass or intimately mixed grass-clover swards. More generally, intake has been demonstrated to be stimulated by some diversity in the diet offered unless searching constraints may come to limit intake rate (Baumont et al 2000, in sheep fed silage and hay indoors; Meuret and Bruchou 1994 in goats grazing rangelands).

The increased concern about the effects of intensive grazing systems on the environment may lead to reduced mineral N fertilisation. Beyond a reduction in herbage mass and height, herbage intake may, in this case, be affected by a decrease in grass crude protein content affecting microbial digestion of the cell walls through a decreased rumen-degradable protein supply. On soils having a low N supply capacity (2% OM), reducing N fertilisation from 320 U/ha to almost nil N led to a fall in HI (2 kg OM day⁻¹ in dairy cows), while the protein content in the grass fell below 12% DM. Reduced HI was mostly mediated through the reduction in grass crude protein, since feeding protein-rich supplements increased grass intake (Delagarde et al 1997). Conversely, the same reduction in N fertilisation did not affect HI on deep and rich soils (10% OM), where the crude protein content of the unfertilised sward remained higher than 15% DM.

The water content of fresh herbage can have a marked effect on herbage intake. Internal water may induce a physical limitation. Studies with housed cows have shown that a low dry matter content reduces HI at a rate of 1 kg per 40 g. kg⁻¹ fall in the DM content below a critical value of 180 g. kg⁻¹ (Verite and Journet 1970). The mechanism is poorly understood, but it is postulated that the water, which is predominantly intracellular, causes a bulk effect on rumen fill. The surface water may induce behavioural limitations. The greater dilution of DM in fresh material decreases the DM intake rate and may come to limit the daily intake for animals that have important constraints in the time available to forage because of their high nutritional requirements, the critical value being 140-150 g. kg⁻¹ for dairy cows (Demment et al 1995). Moreover, surface water reduces the ease of prehension and palatability of the herbage, as seen above. High rainfall and the corresponding high weight of herbage surface water have actually been shown to adversely affect herbage intake by cattle (Butris and Phillips 1987).

Although the regression models have advantages of simplicity, they are conditions-dependant and their descriptive framework does not allow the provision of a generalization

for other types of animals and other sward conditions. Moreover, empirical equations of HI predictions based on animal and sward characteristics are based on the assumption that the sward is homogeneous in the horizontal plane. When the sward is/becomes heterogeneous, the animal grazes selectively between patches and the sward can no longer be described 'on average'.

3.2. Mechanistic modelling approach

A simple mechanistic model has been developed in Australia to predict herbage intake and digestibility of the diet selected on temperate swards, with practical management objectives (Stuth et al 1999). The model predicts HI as the product of the animal's potential intake and the proportion of this potential that the pasture can supply. This proportion is estimated from the relative intake rate and feeding time and the relative ingestibility of the herbage. A selection submodel predicts the diet selected by the animal from the distribution of the herbage between pools of characteristic digestibility and the assumption that the animal attempts to satisfy its potential intake from the most digestible pool available. Inputs by the user are animal characteristics, herbage mass, digestibility of green and dead material and proportion of legumes in the sward. To our knowledge, it is the first model providing support to advisors of the grazing industry, but its limits stem mainly in the generalization to spatially heterogeneous swards.

More complex mechanistic models based on the integration of lower level processes and supported by theoretical basis should allow increased generality (broader range of conditions) although an increased complexity. Such a model has been further developed from that of Sauvant et al (1996), which was initially designed to dynamically model behaviour and intake of confined animals (Figure 5). The initial model comprised two interconnected submodels, a ruminal digestion together with a feeding decision submodel, the originality being to regulate the feeding decision from the balance between motivation to eat and satiety. The intake motivation function (FMI) is based on the energy balance of the animal on the previous day, diurnal cycle and an index of palatability of the sward that decreases as the sward is grazed down. The satiety function (FSAT) is determined by rumen load signals and the instantaneous energy balance. This model has been adapted to grazing situations on the basis of the general framework representing the grazing process discussed above, that views grazing as a hierarchy of scales where animals takes decisions. Two submodels were added: i) a sward-horizons submodel describing the sward as superposed grazing horizons, each with characteristic bite dimensions and potential instantaneous intake rate, and ii) a foraging decision submodel describing preferences between horizons. The sward-horizons submodel describes the structure and the nutritive value of each grazing horizon, assuming that there is an ungrazeable horizon at the base of the sward. Preferences between the horizons depends upon their relative availability and potential IIR. Actual intake rate then integrates the animal's choice between horizons of potential IIR and its satiety status. In this way, interactions between vegetation constraints and the animal's internal state are dynamically integrated from short-term decisions (scale of a few bites) to daily intake during the course of several days. Simulations of this model fitted satisfactorily with the behavioural and intake data of Prache et al (1998) and Penning et al (1994) obtained in different sward management conditions and different physiological stages of ewes (dry vs twin lactating). However, there is a need to clarify the mechanisms by which animal requirements and vegetation characteristics interact to determine bite geometry and potential intake rate, and to what extent preferences between horizons are affected by the physiological stage of the animal. A further development would be to simulate behaviour and intake on swards associating two plant species, by using a general framework from which to represent preferences rules (grazing

horizons or plant species).

Conclusions

Intake, diet composition and the impact of grazing on the vegetation is the result of complex interactions between the animals and the vegetation. Through selective grazing, the animals select a diet of higher nutrient quality than that on offer, and distributes their impact on the environment.

Facing this complexity, a recently increased effort has been made to develop a conceptual representation of the grazing process supported by theoretical bases, that both organizes the processes into a hierarchy of scales where animals make decisions, and provides their integration to intake. This representation may reconcile the way of looking at different grassland types, from paddocks considered as homogeneous to grasslands that are heterogeneous (height, phenological stages, botanical composition, etc...). Great progress has been made in understanding the physical interactions between the grazing animal and the sward structure, that determines the bite characteristics and the instantaneous intake rate on a homogeneous patch. The availability of green leaves and their spatial arrangement is a key determinant of intake rate and intake on homogeneous patches across different grazing management and type of animals. The determinants of foraging decisions at higher levels of organization remain less well understood. The complexity of the animal/vegetation interactions has led to the development of simple experimental situations (short-term, simple dietary choices) to test hypotheses. In this case, animals tend to maximise their rate of food intake, demonstrating that sward heterogeneity is an important consideration when predicting nutrient intake rate. However, short-term predictions are not completely validated on a daily scale basis, and predicting foraging behaviour is further complicated in more complex situations where searching constraints make the environment more difficult for the animal to perceive. Moreover, the widely used idea of fixed constraints undergone by the grazing animal is questioned as there is evidence that the animals are able to adapt, to some extent, to these constraints. Major challenges remain to integrate i) the interplay between the vegetation characteristics and the animal's internal physiological and motivational state, and ii) the short-term foraging behaviour to larger spatio-temporal scales. The first developments of a dynamic model for simple sward conditions is presented, the originality of which is in a feeding decision sub-model based on the relative values of intake motivation and satiety.

From a practical point of view, there are opportunities for the development of sustainable lower-input systems, by optimizing the use of grazed herbage. In dairy systems, the challenge is to improve the grass intake per animal while maintaining high quality swards throughout the grazing season. Increasing green leaf mass in the last horizons grazed under rotational or strip grazing conditions may have a major role in increasing herbage intake while maintaining a low residual sward height. The use of mixed grass/legume swards is well known to both allow increased intake and environmental benefits through reduced N fertilisation. Moreover, offering a choice to the animals, such as adjacent monocultures of grass and clover, may stimulate intake. Further confirmation of these results is needed together with an investigation of their practical utilization. Large differences in intake have also been observed between cultivars of perennial ryegrass and underlying factors responsible for high intake potential remain to be understood if criteria for evaluating and breeding grasses are to be developed.

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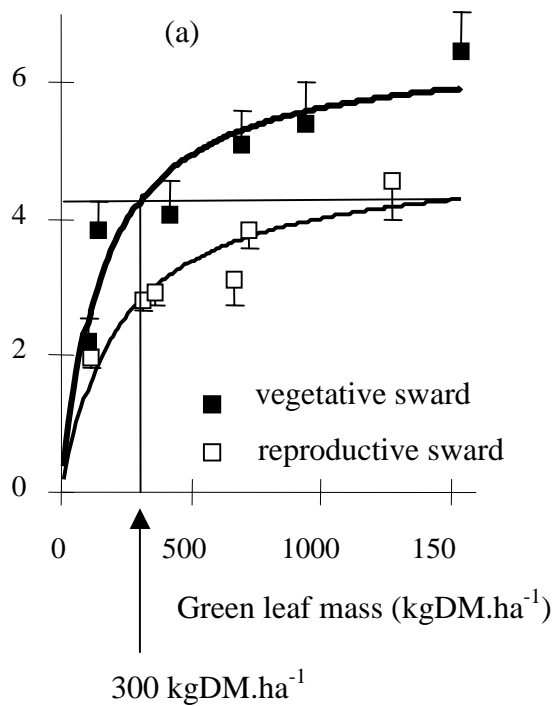
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Table 1 - Relation between dairy cows' performances and structure of the grazed tillers during a five days paddock grazing down of (herbage allowance : 25 kg OM. cow⁻¹. day⁻¹, perennial ryegrass)

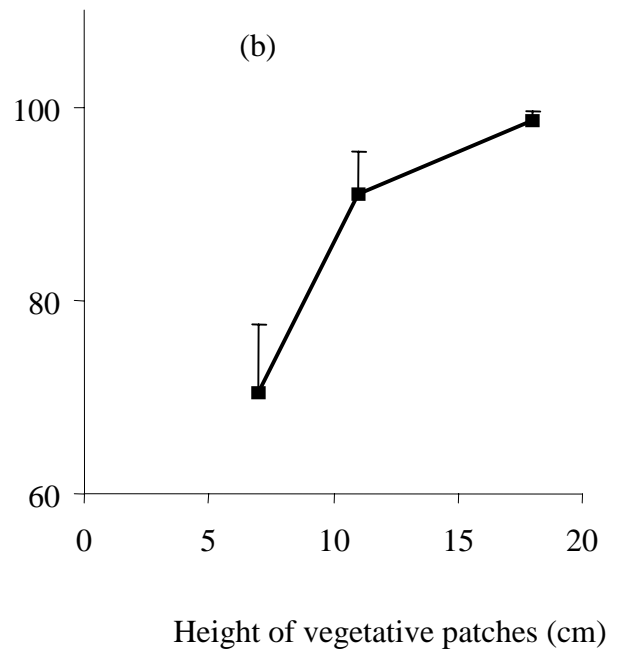
Day in paddock	Day 1	Day 2	Day 3	Day 4	Day 5
Herbage intake (% day 1)	100	100	97	92	89
Milk production (% day 1)	100	99	92	80	79
Mean extended tiller height (mm)					
Short sward (1)	154	130	116	98	90
Tall sward (1)	228	179	147	120	107
Free leaf lamina height (mm)					
Short sward (1)	99	72	55	43	36
Tall sward (1)	136	91	60	43	29

(1) pregrazing extended tiller height = 240 mm and 350 mm respectively for short and tall swards. Adapted from Wade (1991).

Short-term intake rate (gDM.min⁻¹)



Time spent grazing vegetative patches (%)



(i. e. 9 cm high for the vegetative patches)

Figure 1 - Prediction of diet choices from dry matter intake rate maximisation : an example on swards containing reproductive patches in a background of vegetative patches

- (a) : functional response of dry ewes on vegetative and reproductive patches (from Prache et al 1998)
- (b) : choice of sheep between vegetative and reproductive patches according to the height of the vegetative patches (from Dumont et al 1995)

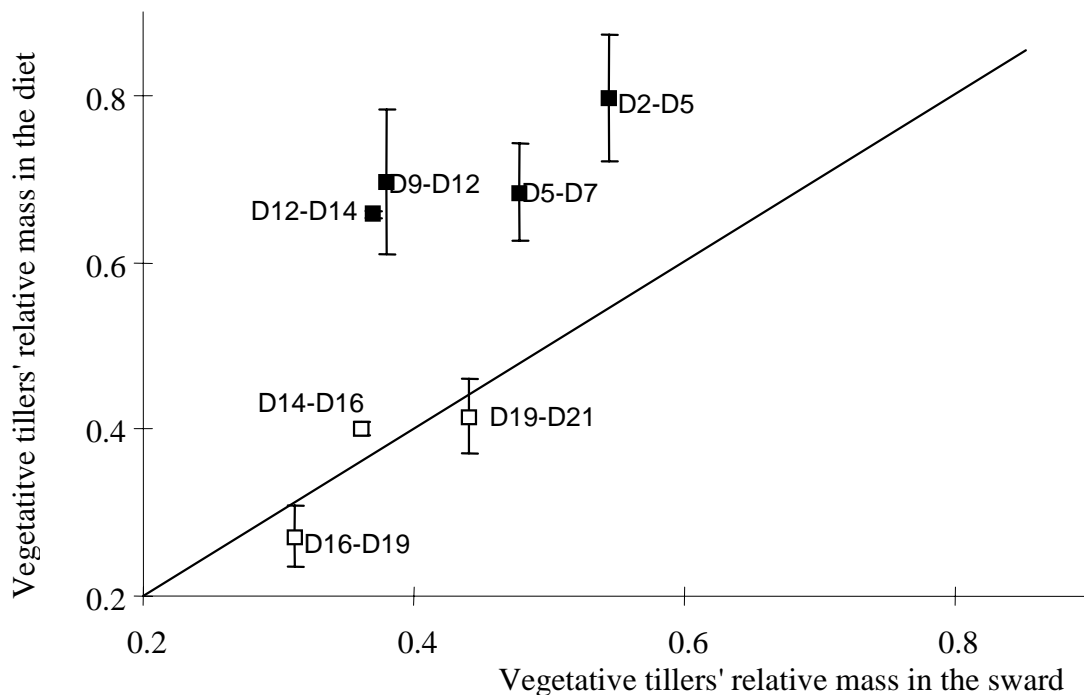
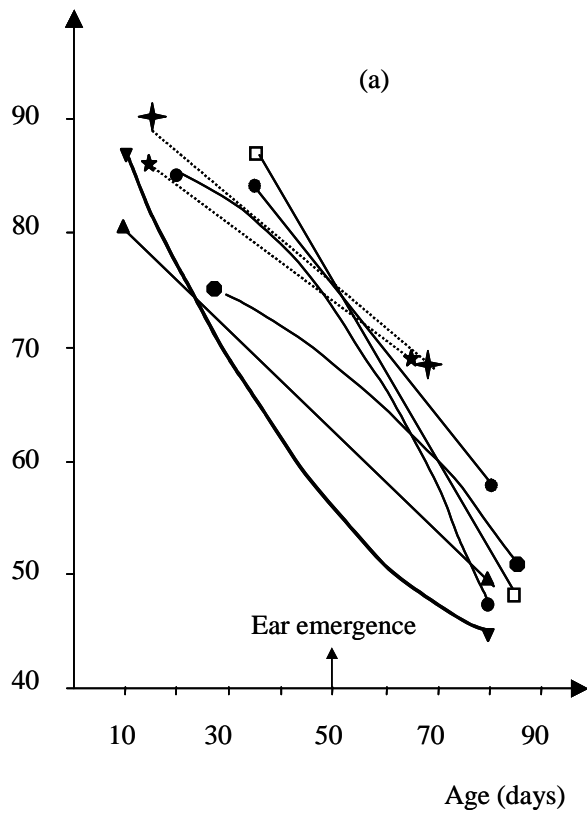


Figure 2 - Choice of sheep between vegetative and reproductive tillers when grazing a reproductive sward

Di signifies the number of days elapsed (i) since beginning of grazing of the sward. Di-Dj signifies the period of time (Day i - Day j) over which the composition of the diet have been

Ingestibility (gDM/kgW^{0.75})



Ingestibility (gDM/kgW^{0.75})

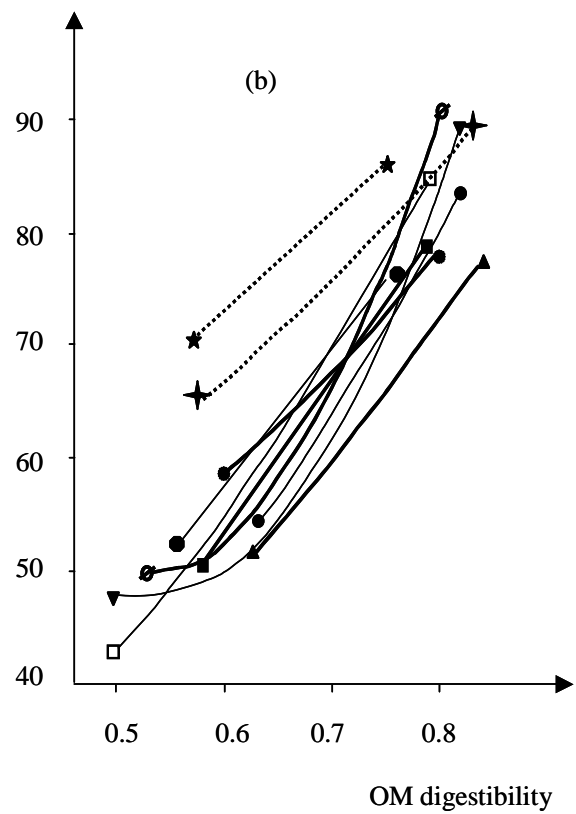


Figure 3 - Effects of age (a) and digestibility (b) of the forage on ingestibility in sheep (from Demarquilly et al 1981)

- *Dactylis glomerata* ● *Festuca pratensis* ▲ Late perennial ryegrass ★ Alfalfa ■ Highland natural sward
- ▲ *Phleum pratense* ● *Festuca arundinacea* ● Early perennial ryegrass ✦ Red clover ⦿ Lowland natural sward

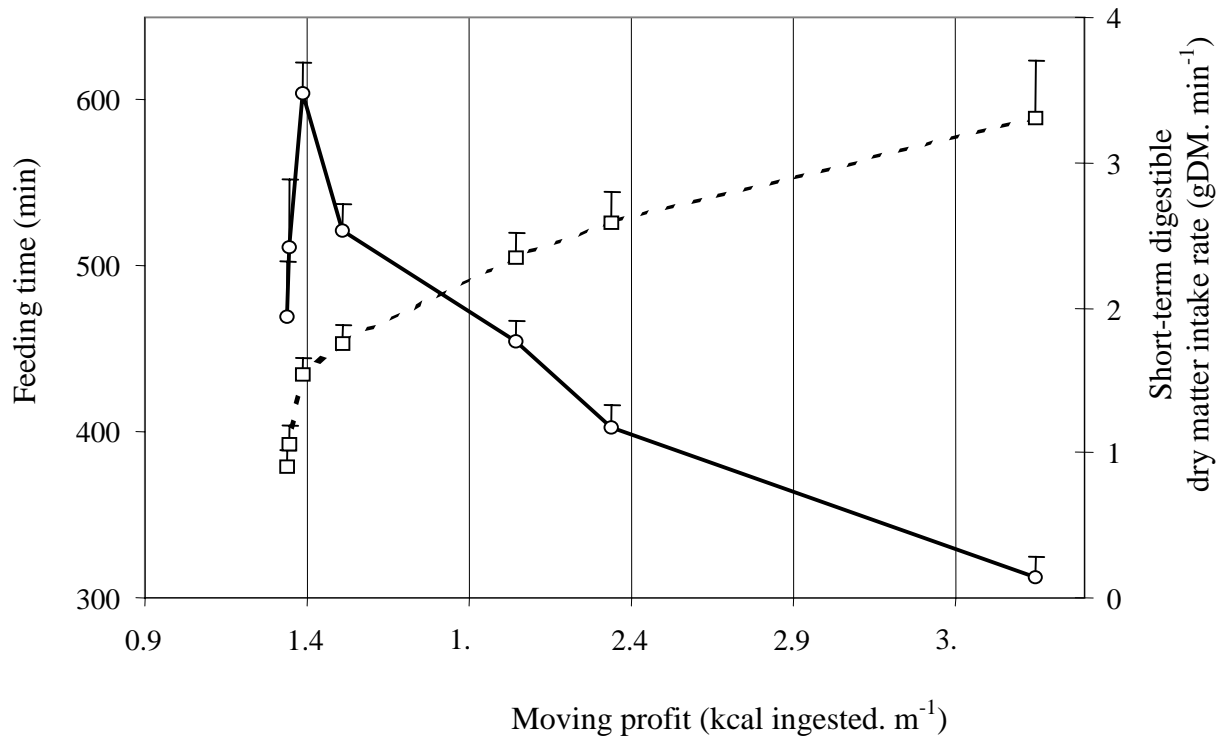


Figure 4 - Relationships between short-term digestible dry matter intake rate, moving profit and feeding time (from Roguet et al 1998b and Prache et al 1998)

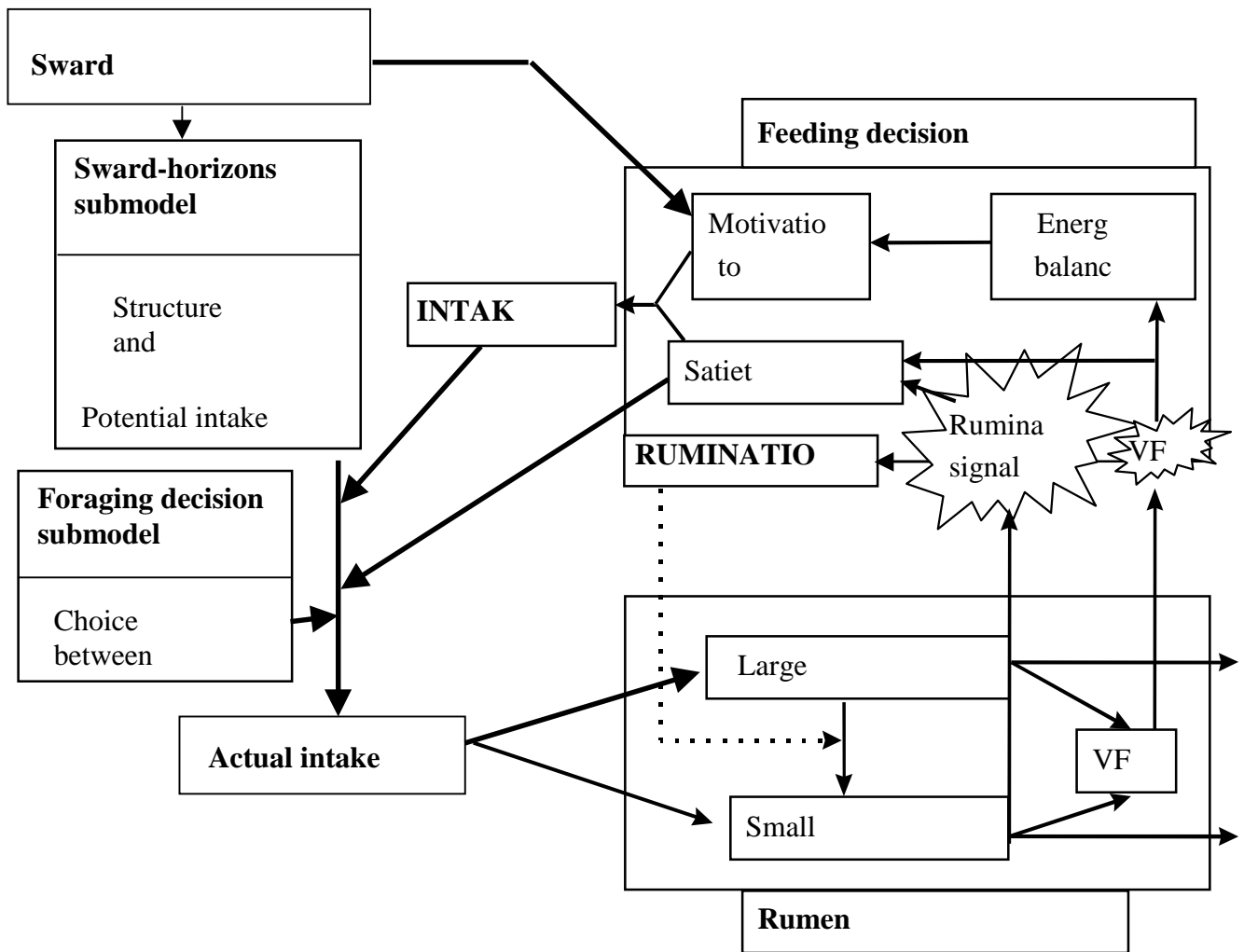


Figure 5 - Framework of the mechanistic model of behaviour and intake at pasture developed by Baumont, Cohen-Salmon, Prache and Sauvant from the model of Sauvant et al (1996)