

ADVANCES AND RETREATS IN SPECIFYING THE CONSTRAINTS ON INTAKE IN GRAZING RUMINANTS

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ABSTRACT

Considerable progress has been made in elucidating the physical interactions between grazing animals and vegetation. Differences among animal species considered over a wide range of measures of grazing behaviour can largely be accounted for by allometric scaling with body mass. This has increased our understanding of the constraints under which animals operate while grazing, and led to improvements in the prediction of intake. Ironically, just as these constraints are coming into clearer focus, their utility is questioned by the recognition that they do not take fixed values, but depend on the interplay of external and internal states. Without progress in understanding how animals reconcile the costs and benefits of grazing activity, the accuracy of our intake predictions will remain limited.

KEYWORDS

Ruminant, Grazing, Intake, Foraging behaviour, Constraint, Body size.

INTRODUCTION

The rate at which animals can extract nutrients from their environment determines their scope for growth and reproduction. Nutrient intake rate is a function of both the rate of intake of dry matter (DM) and of diet quality, or, broadly speaking, its digestibility. Diet digestibility can typically vary over a two-fold range (roughly 40-80% OMD), whereas dry matter intake can vary more widely: from nothing, under starvation conditions, up to some maximum intake set by physical or metabolic constraints. Therefore, daily dry matter intake rate is probably the single most important variable determining animal performance. This paper examines the physical mechanisms controlling intake, separating them into constraints on the gathering and processing of food: ingestive and digestive constraints, respectively. Considerable progress in understanding these has been made in recent years, and one theme of this review is the effect of body size, and the way that most of the differences among animal species in the operation of constraints can be reconciled by allometric scaling with body mass. The use of this knowledge to make predictions of intake is a second theme of this review. Hitherto, the concept of constraint has been useful both in thinking about the control of intake and in predicting intake in relation to vegetation properties. However, both of these are severely undermined by the sensitivity of intake parameters to variation in the animal's physiological state, and the consequent flexibility of constraints.

INGESTIVE CONSTRAINTS

An animal's short-term intake rate while grazing ('instantaneous' intake rate, IR) is the product of the mass of DM in each bite and the rate of biting. Its daily intake rate (daily intake, DMI) is the product of IR and grazing time (GT). These variables are components of the functional response, which is the relationship between food intake and food abundance, and will be reviewed in turn.

Bite mass. Both experimental and theoretical analyses of the functional response of mammalian herbivores show that bite mass is the variable exerting the greatest effect on intake rate (Hodgson, 1985; Spalinger and Hobbs, 1992; Parsons et al., 1994). Grass swards consist of a three-dimensional array of plant tissues, and bite mass varies with the volume of the sward which the animal can enclose in

each bite and with the bulk density of the grazed horizon (Black and Kenney, 1984; Illius and Gordon, 1987; Burlison et al., 1991; Laca et al., 1992). Bite volume is determined by the horizontal area of the sward covered by each bite and the depth to which the incisors penetrate into the sward.

Bite area is related to size of the animal's mouthparts, and incisor arcade breadth in a mature animal of mass A kg, is given by $8.6A^{0.36}$ mm (Illius and Gordon, 1987). Comparing animals covering a range of body size, Gordon et al. (1996) showed that bite area in sheep and goats scales with the square of incisor breadth. Bite area is also positively related to sward height, being progressively restricted on shorter swards. On short swards, only herbage in the immediate proximity of the incisor row can be prehended. From a mathematical model of these interactions, and assuming that bite depth did not vary with animal size, Illius and Gordon (1987) predicted that the allometric exponent relating bite mass to body mass should therefore tend from 0.72 to 0.36 as sward surface height was progressively reduced. Comparing bite mass with animals' metabolic requirements, which scale with $A^{0.73}$, large animals would be predicted to be at a disadvantage to smaller ones when grazing short swards, because each bite represents a smaller proportion of daily requirements. Comparison of the incisor arcade morphology of 89 species of ruminant supported this conclusion, since large-bodied grazers, such as cattle and African buffalo, have broader and flatter incisor arcades (which, arguably, are an adaptation to grazing short swards) than smaller and more selective animals (Gordon and Illius, 1988). This prediction was tested by Murray and Brown (1993), who compared bite mass in two species of similar body size but different incisor arcade breadth: the wide-mouthed wildebeest (a short-grass specialist grazer) and the topi, a narrower-mouthed grazer which prefers swards of intermediate height. Comparison of bite mass over a range of sward heights showed no significant difference between species in the slope of the mass-height relationship, but restricting the analysis to short swards (to which the hypothesis applies) shows that wildebeest bite mass was nearly twice that of the topi (Murray and Illius, unpublished). Illius et al. (in prep) tested the prediction using six species, ranging in size from 20 kg Soay sheep to 500 kg cattle. Incisor breadth in this group scaled with an allometric exponent of 0.42. On swards below 5 cm, bite mass scaled with an exponent of 0.63, not substantially less than the scaling of metabolic requirements. However, because of the slower rate of biting by larger animals (see below), IR scaled with an exponent of 0.50. This shows that large animals would have to graze short swards for longer to obtain the same fraction of their metabolic requirements as small animals, the effect of which would accord with that predicted by Illius and Gordon (1987).

The main reason why the original prediction was not borne out more strongly is that the experiment invalidated the assumption that bite depth is constant with animal size. Large animals bit more deeply into the sward than small ones, and grazing height was found to scale with an allometric exponent of -0.15. This is a robust result, applying both between and within species (Illius et al., 1995; Gordon et al., 1996). Large animals are capable of severing herbage closer to the ground surface than small animals, and it thus appears that they are less constrained by the resistance posed by physical

properties of the vegetation.

Bite mass increases greatly with increasing bite depth, since the vertical distribution of biomass in a sward is highly skewed, with most of the biomass at the base of the sward (eg Fig. 2 of Hodgson, 1985; Illius et al., 1995). Because the mouthparts encounter more plant tissue with increasing bite depth, and therefore greater forces have to be applied to sever the herbage, it has been suggested that the physical structure of plant tissues, particularly tensile strength, plays some part in the control of bite depth (Hodgson, 1985; Hughes et al., 1991). The importance of vertical variation in sward composition was recognized by Barthram (1981), who showed that sheep seldom bite into the lower sward stratum in which pseudostem predominates and which thus appears to form a physical barrier limiting the depth of the grazed horizon. The profile of sward tensile strength is a function of the vertical distribution of plant tissues, such as leaf lamina and sheath bundles (pseudostem), and of their tensile strength. Illius et al. (1995) compared the variation between five temperate grass species in the vertical distribution of the forces exerted in grazing, and argued that two aspects of canopy structure limit bite depth: the population density of tillers and the presence of pseudostem. The grass species studied varied more widely in canopy structure than their tissues varied in mechanical characteristics. The evidence for the effect of sward physical properties on the bite depth of goats was that the animals never grazed into the pseudostem horizon, which would have resulted in sharply increased bite force; that larger animals bit more deeply, presumably because they could exert greater force than small animals; and that animals grazed more deeply after a limited period of food deprivation, implying greater motivation to overcome the effort of grazing. It was calculated that the great majority of energy expenditure during grazing is in chewing the ingested vegetation, rather than in removing plant tissue from the sward. Since energy gain would exceed predicted energy use during grazing to any depth in the sward, it cannot explain why animals limit bite depth to the surface layer. Bite force varied widely between grass species, which argues against maximum force as a common factor limiting bite depth. Instead, Illius et al. (1995) suggested that consideration of the balance of costs and rewards would be more likely to lead to an explanation of what determines bite depth.

Bite rate. Our understanding of what determines rate of biting was transformed by the work of Spalinger and Hobbs (1992), who recognised that bite rate could be limited either by the animal's need to search for its next bite or by its need to chew ingested herbage. They derived equations for the functional response under conditions where intake rate is limited by one of three processes: rate of encounter with cryptic food items (Process 1); rate of encounter with apparent items (Process 2); and rate at which food can be chewed and swallowed (Process 3). Given an animal with maximum foraging velocity V_{max} , maximum eating rate R_{max} , minimum handling time per bite in the absence of chewing h and width of search path W , foraging on plants offering bites at density D (per m^2), and offering a bite of mass S , then the rate of biting B can, adapting Spalinger and Hobbs (1992) slightly, be written as:

$$\text{Process 1: } B_1 = \frac{V_{max} WD}{(1 + nV_{max} WD)} \quad (1)$$

$$\text{Process 2: } B_2 = \frac{V_{max} \sqrt{D}}{(1 + nV_{max} \sqrt{D})} \quad (2)$$

$$\text{Process 3: } B_3 = \frac{R_{max}}{(S + R_{max} h)} \quad (3)$$

Intake rate is simply the product of B and S . In (1) and (2), n is a coefficient describing the time lost to future encounters whilst pausing to take a bite, and can probably be approximated by h . The first two equations describe rate of biting as limited by encounter rate, and distinguish cases where (1) potential bites can only be detected at close range, perhaps because obscured by dead herbage, from (2) those where bites can be detected at a distance. Process 1 applies where the average distance between plants is greater than the detection distance, ie where $1/D > W$. Equation (3) describes the case where encounters with large S are sufficiently frequent to cause bite rate to be limited by chewing rate. Thus, as bite mass becomes restricted, bite rate can increase up to a maximum, h . The actual rate of biting will be governed by whether finding or chewing bites is slower. Fig. 1 describes how bite rate increases with increasing density and decreases with increasing bite mass, and the discontinuity in the surface shows the combinations of bite density and mass above which biting rate is governed by chewing rate. Not surprisingly, the parameters of these functional responses vary with animal size. V_{max} is $0.5M^{0.13}$ (Pennycuik, 1979), although an empirical test in 9 foraging herbivores by Shipley et al. (1996) found that V_{max} was the same regardless of size. Small animals tended to move relatively rapidly between patches, possibly because of greater risk of predation. Illius and FitzGibbon (1994) assumed that search path width W scales with animal stature, and so with limb length, or with $M^{0.25}$ (Alexander, 1977). Shipley et al. (1994) found that R_{max} scaled with $M^{0.69}$, but that h was constant across 12 species of herbivore ranging from 0.05 to 550 kg. However, Illius et al. (unpub) found that h scaled with $M^{0.125}$ in 6 species of ruminant, an exponent which is consistent with the scaling of the periodicity of limb movements and mastication (Druzinsky, 1993).

The conclusion which may be drawn from these studies is that understanding of the principal mechanical interactions determining IR in a ruminant of any size is now sufficiently advanced to have predictive value.

Grazing time. For a given intake rate, the animal's daily intake depends on the length of time it spends grazing, and therefore understanding the determinants of GT is important for predicting intake. Allden and Whittaker (1970) demonstrated that GT can increase to compensate for low IR, but that the ability or willingness of animals to compensate in this way is limited, and at sufficiently low IR animals may actually reduce GT. Likewise, Chacon and Stobbs (1976) observed that cattle increased GT in response to the initial depletion of the sward they were grazing, but, as depletion became severe, GT was reduced. The hypothetical explanations of these responses are that GT is constrained to some upper limit, perhaps by fatigue, and that animals may reduce GT when grazing becomes uneconomic. Not surprisingly, there is little direct evidence that fatigue limits GT, although the observation that animals bearing heavy vibracorders on their heads have shorter GT than controls (P.D. Penning, pers. comm.) is certainly suggestive. If there were an upper limit to GT, set by fatigue of the jaw muscles, then we would expect it to be affected by rumination, which is also a component of 'eating time' and of the daily total of jaw movements, and would therefore be expected to contribute to the overall fatigue of eating. Consistent with this is the observation that GT in horses is roughly comparable to the sum of GT and rumination time in ruminants (Martin-Rosset and Dulphy, in prep). Penning et al. (1991) imposed differences in bite mass on ewes by varying sward height, and showed that the allocation of jaw movements to prehension, mastication and rumination is largely a function of bite mass, with the total daily number of jaw movements showing only slight variation ($\pm 10\%$) across treatments and seasons (Fig. 2). GT (ie, the time spent in

prehension and mastication) varied inversely with sward height and bite mass, but because GT was largely interchangeable with rumination time, total oral processing time remained roughly constant. This supports the idea that the time or effort involved in oral processing (rather than GT *per se*) may have some upper limit, and that its allocation to grazing and rumination is a mechanical function of sward state. It seems unlikely, however, that a fixed upper limit to eating time or effort applies regardless of motivational state, since we might expect hungry animals (eg in lactation) to exceed limits observed in animals which have less drain on their nutrient status. This fundamental weakness of the idea of fixed constraints is discussed further below.

If a limit to grazing activity, such as total jaw movements, could be defined, it could form the basis of a prediction of DMI. A related approach has been to identify the time left over from grazing and rumination (termed 'idling'), and to assume that that is fixed (Woodward, 1997). Although both approaches offer improved predictions over those assuming that prehension bite numbers or GT are constrained to a maximum, there are a number of objections to them, not the least being that neither maximum daily jaw movements nor minimum idling time is readily quantifiable. 'Idling' is in fact made up of a number of vaguely-defined activities (such as social interaction, grooming, movement, resting), and such activities are likely to be more variable than feeding, because they probably matter less to the animal (Lawrence and Illius, 1997). The sense of deprivation of the less essential components of idling is likely to be less clearly perceived by the animal than the fatigue arising from jaw movements. The data of Penning et al. (1991) show that there is variation in idling time (by approximately $\pm 30\%$); that it was not inconsequential, being negatively correlated with live weight change (Fig. 3), and that variation in idling time was not consistent with sward height. Like fatigue, idling time remains an elusive variable on which to base predictions of grazing activity.

It could be argued that the decline in GT under conditions of severely limited IR could be the result of energy intake rate exceeding expenditure. This can be evaluated using the Spalinger-Hobbs functional response, together with data on the costs of travel and of eating (Taylor et al., 1982; Osuji, 1974). Fig. 4 shows how net energy intake minus expenditure per bite varies with bite mass and density, using the example of an animal of 50 kg and foraging for bites with a digestibility of 0.6 OMD. Negative energy balance is predicted to occur for low bite mass and with less than one bite/m². This reveals how sward conditions affect the economics of grazing, but it also reminds us that there is an abrupt threshold dividing energy gain from energy loss. Depending on sward conditions, animals should either graze because energy balance is positive, or they should not graze at all because it is negative. This does not therefore solve why animals' response of GT varies continuously with sward conditions, instead of reflecting the economic optimum of being either maximal or minimal. A possible explanation is that animals may not perceive accurately their short-term energy balance, and may reduce GT progressively as the profitability of grazing approaches zero.

DIGESTIVE CONSTRAINTS

Modelling digestive constraints. *Ad libitum* intake is reduced by low digestibility and it is assumed that low rates of ruminal digestion and passage impose physical constraints on intake (e.g. Laredo and Minson, 1973). Although this interpretation of the factors controlling intake of low-quality foods has been questioned (Tolkamp and Ketelaars, 1992), considerable progress in predicting intake and digestion in ruminants has been achieved by modelling (reviewed by Illius and Allen, 1994). Illius and Gordon (1991; 1992) developed

a model of rumen kinetics integrating animal size and plant characteristics. They showed that both the time taken to comminute large fibre particles and the small particulate retention time scale with $M^{0.27}$, in the manner of other temporal variables, and that the digesta load of gastrointestinal tract compartments is isometric with mass (M^1). These allometric relations account for much of the inter-specific variation in intake with mass, while much of the variation in intake of different foods can be accounted for by plant cell wall content and digestion rate. By assuming digesta load to be a fixed constraint, the model allows the maximum daily intake, digestion and ME intake to be predicted. Fig. 5 compares observations of intake in cattle and sheep with intake predicted from NDF and animal mass. When compared on a single food, large animals are predicted to be able to obtain a greater proportion of their daily energy requirements than small ones, with ME intake scaling as $M^{0.88}$ (Illius and Gordon, 1991). The consequently greater severity of digestive constraints in small animals explains their need to obtain higher-quality diets than large animals (Jarman, 1974).

Combining ingestive and digestive constraints. Although low-quality vegetation can only be eaten in limited daily quantities, its abundance is usually high, so it can be eaten rapidly if the animal is not being selective. Conversely, selection and intake of more digestible vegetation components is more likely to be limited by low IR rate than by digestive constraints. The trade-off between the two which maximizes daily energy intake can be used to predict foraging behaviour, and shows good agreement with experimental observation (e.g. Wilmshurst et al., 1995; Shipley et al., *subm*). Fig 6 shows an example of the trade-off between selectivity and IR, illustrating how the models of bite dimensions and of ingestive and digestive constraints, reviewed above, can be combined. Increasing selectivity by avoiding low-quality plant items relaxes the digestive constraint, but after a certain point, reduces IR. Optimal selectivity depends on how deeply the animal grazes, and occurs at the boundary between regions where digestive and ingestive constraints apply (dashed line). In this example, there is little advantage to grazing below 35 mm unless the animal is capable of being highly selective, which the size of its mouthparts may prevent. This might explain the deeper, more selective grazing of sheep than cattle grazing temperate hill swards with marked vertical heterogeneity (Hodgson et al., 1991).

THE STATE-DEPENDENCE OF CONSTRAINTS

The metabolic state of an animal, and particularly its degree of hunger, has often been shown to affect a number of ingestive behaviour variables, despite the more obvious importance of mechanical interactions with sward physical properties, reviewed above. For example, Greenwood and Demment (1989), Penning et al. (1991) and Newman et al. (1994) showed that IR is generally below the maximum possible, since it can be increased substantially by hunger. Illius et al. (1995) found that bite depth was increased in animals after a limited period of food deprivation. Penning et al. (1995) found that lactating sheep had higher bite mass, IR, GT and DMI than dry ewes. In spite of the physical determinants of grazing variables, the evident flexibility of ingestional strategies leads to the conclusion of Newman et al. (1994) that "a large, and often neglected, component of grazing intake is behavioural". Without better understanding of this, prediction of DMI will remain inaccurate. Furthermore, it calls into question the widely-used notion of fixed constraints on intake.

A constraint is usually defined as a limit or bound to a variable. For example, aerobic metabolism is entirely constrained by oxygen intake, and it is thus possible to predict the maximum feasible rate of metabolism, subject to that constraint. Belovsky (1978) used linear programming to show that diet composition in moose could be

predicted from constraints describing maximum GT and digestive capacity and minimum sodium requirements. For 'constraints' that are mediated by the animal's cognition and affected by its state, such as the perception of fatigue or rumen distension, it is harder to argue that a fixed value will apply in all circumstances. If animals will tolerate greater rumen distension when they are in a state of hunger, then the notion of a fixed constraint is invalid. Accordingly, Owen-Smith (1993, 1994) has questioned whether it is permissible to assume that constraints really operate as fixed bounds, by arguing that commonly-accepted 'constraints' such as GT and rumen load are not actually fixed, but may be modified by animal state and season. Chacon and Stobbs (1976) tested whether rumen fill constrained GT by removing the rumen contents of grazing cattle, and observed that this increased GT when the pasture was in the early stages of defoliation, and offered high IR, but had no effect on heavily-defoliated swards which restricted IR. Their interpretation was that motivational state determined whether the constraint was operative. Fixed constraints are therefore convenient, but strictly incorrect, approximations which are useful in predicting DMI. The flexibility of constraints throws open again the questions of what determines their settings and how constraints interact with one-another.

Recognition of the state-dependence of grazing behaviour leads to a simple economic formulation of decision-making by grazing animals: that they weigh the costs and benefits of their actions. Such an approach, while poorly researched at present, has the potential to explain why animals alter their ingestive strategies according to their state, and accords with McClymont's (1967) dictum that a balance is struck between all the negative and positive stimuli, rather than there being separate set-points or thresholds for each (see Hodgson, 1981, and Hodgson et al., 1997). This model of the control of intake would require a knowledge of the interaction of internal and external state, going beyond the elaboration of mechanical interactions between animal and vegetation which has been the main preoccupation of the last 25 years.

Although considerable achievements have been made in understanding grazing mechanisms, particularly the physical interactions of grazing animals with vegetation, the integration of signals from grazing with those from the animal's physiological and motivational state is fundamental to the control of intake. Thus, future work will have to investigate the interaction between the physical and the psychological aspects of grazing behaviour. Without progress in understanding how animals reconcile the costs and benefits of grazing activity, the accuracy of our intake predictions will remain limited.

ACKNOWLEDGEMENTS

Thanks to I.J. Gordon, M.B. Hardy, J. Hodgson, P.J. O'Reagain and P.D. Penning for discussions and for comments on an earlier draft.

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Figure 1

Spalinger-Hobbs functional response, showing how bite rate in a 50 kg ruminant varies with bite mass and the environmental density of bites (bites/m²). As density increases, less time is spent searching (ascending part of surface; Process 1 or 2), while as bite mass increases, more time is spent chewing (descending part of surface; Process 3).

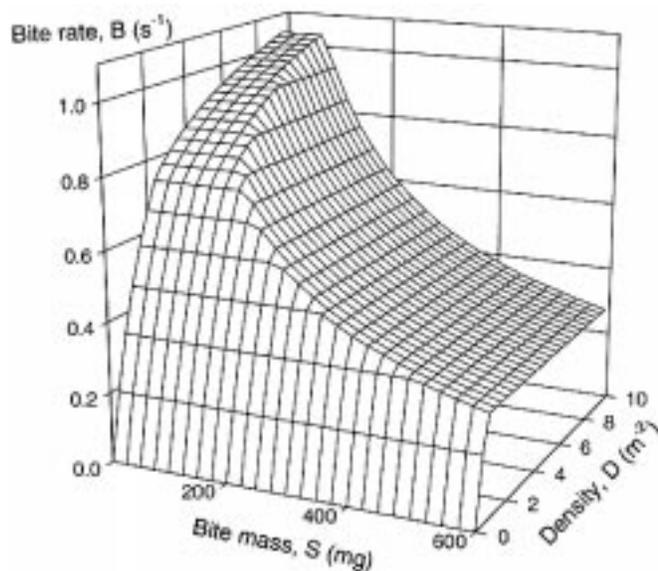


Figure 2

The allocation of jaw movements in ewes continuously stocked on a range of sward heights, either when lactating in spring or when dry in autumn (data of Penning et al 1991).

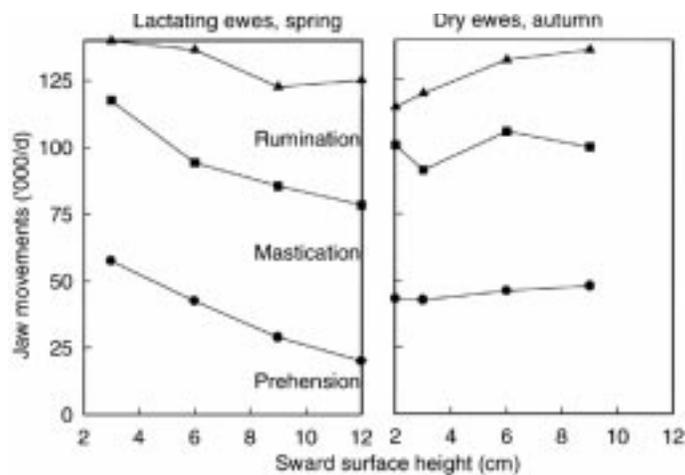


Figure 3

Weight change in grazing ewes is a function of idling time (data of Penning et al 1991).

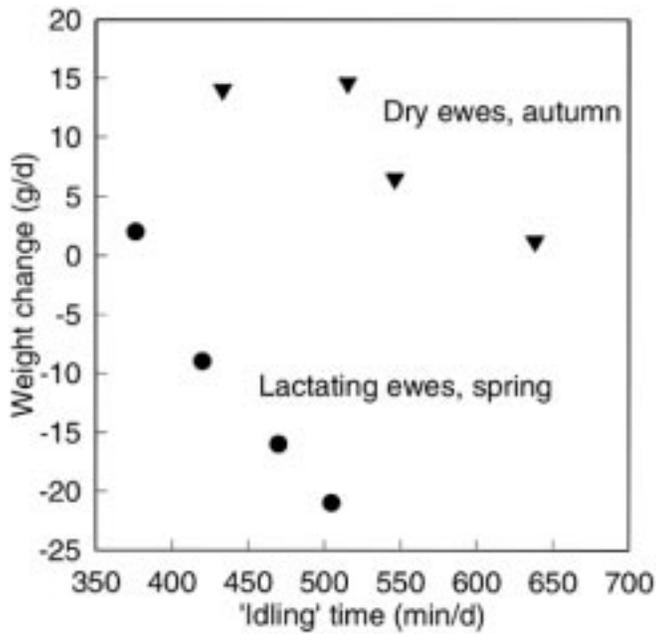


Figure 5

Forage intake constrained by NDF in animals of mass (M) 30, 250 and 500 kg. Solid lines show observations of Laredo and Minson 1973; Poppi et al 1980; Hovell et al 1986 and Orskov et al 1988, as summarised by: $DMI=0.014NDF^{-1.8}M^{0.89}$, $r^2=0.94$, $n=55$; Dashed lines show predictions from the model of Illius and Gordon (1991,1992) using M and NDF as inputs ($DMI=0.02NDF^{-2.2}M^{0.81}$).

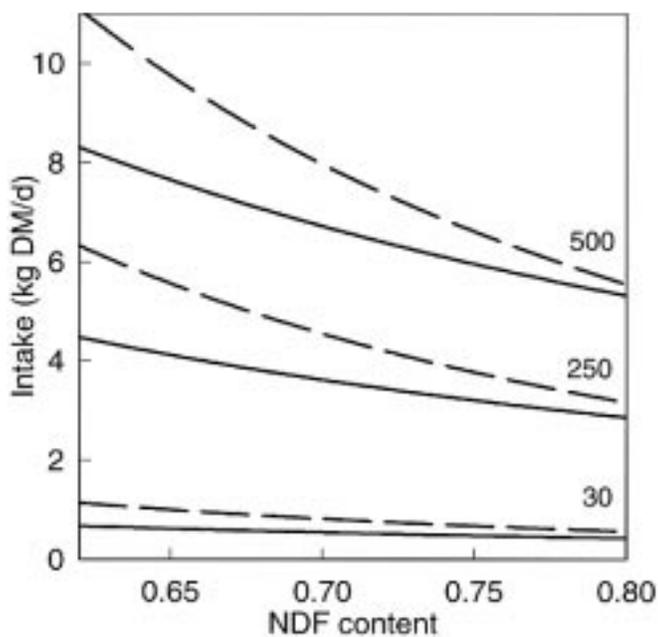


Figure 4

Predicted energy balance (J ME/bite) is determined by bite mass and density (bites/m²). The contours connect combinations of bite mass and density giving equal energy balance for a 50 kg ruminant taking bites with 0.60 OMD.

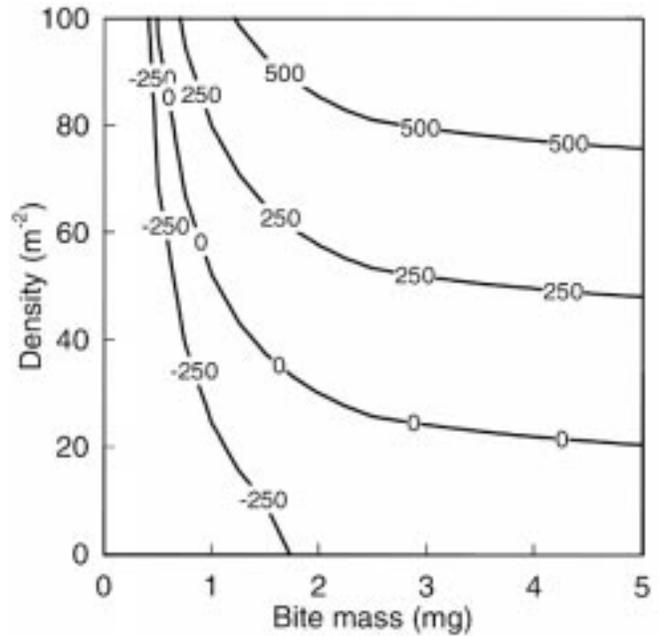


Figure 6

Predicted daily energy balance in relation to vertical selection (obtained by varying grazed height from 50 to 15 mm from ground level) and horizontal selection (by progressively reducing the inclusion of stem and dead leaf). The dashed line separates the regions where digestive (○) and ingestive (◐) constraints apply. Modelled conditions: 50kg animal grazing for up to 10 h/d on a sward of 100mm in height, and containing dead stem, dead leaf and green leaf at 20, 60 and 60 g/m² and OMD = 0.35, 0.5 and 0.7 respectively.

