

Minimal Total Discomfort; an integrating framework for food intake and selection (Minimierung des Unbehagens: ein Steuerungssystem der Futteraufnahme und Futterselektion beim Wiederkäuer). J. Michael Forbes*, Institute of Integrative and Comparative Biology, University of Leeds, Leeds LS2 9JT, UK.

The control of voluntary food intake has been the subject of wide interest from the point of view of human obesity and anorexia, for which laboratory animals have been the usual models. This interest has also encompassed farm animals and most particularly ruminants because of the unique aspects of their anatomy and physiology and because of their enormous economic importance. If ruminants by-and-large ate the amounts of foods required to meet their nutrient requirements, as do pigs and poultry, then there might not be a need to focus so much on these differences. However, for ruminants the amounts of forage eaten are often insufficient to meet their nutrient requirements, and expensive supplementation is necessary.

It was proposed more than 70 years ago that the inadequate intake of forages was due to physical limitation by rumen capacity – the slow rates of digestion of fibre meant that the rumen was ‘full’ before requirements had been met. The pathways for such an effect were traced, including characterisation of mechanoreceptors in the rumen wall with afferent pathways to the CNS. Although it was suggested that ruminants therefore had a completely different method of intake control than simple-stomached animals, it was not long before it was shown that metabolites such as volatile fatty acids (VFAs) both depressed food intake and stimulated receptors in the rumen wall. Also, it was observed that with finely ground and concentrated foods ruminants could control their intake to approximately meet the requirements for energy.

It was on this basis that what became known as the two-phase hypothesis (TPH) was founded: ‘ruminants eat to meet their nutrient requirements unless prevented from doing so by physical limitation’. Although there was serious questioning of this hypothesis (PITTROFF and KOTHMANN, 1999; TOLKAMP and KETELAARS, 1992) it has continued to have its backers (e.g. OLDHAM, EMMANS and FRIGGENS, 1998), usually because no widely-accepted alternative has been available. Poppi et al, (1994) broadened the theory by including several factors in their model, but still retaining the ‘first limiting factor’ principle. It is hard to reconcile this independence of factors affecting intake – how can an animal that one moment is limiting its intake only by rumen fill, ignoring VFA concentrations for example, suddenly depend solely on the latter when a small reduction in rumen fill occurs due to onward passage of some digesta?

Several years ago I was visiting Brazil for a month to give a course of lectures at the Veterinary Faculty of the University of Sao Paulo. I had set myself the task of giving serious thought to the question of the control of intake, given that I had more free time than I was accustomed to. One evening I was taken to a famous fish restaurant by a good friend and his wife and advised which was the best fish to sample. A large fish and its accompaniments duly arrived and was greatly enjoyed, assuming that this was the main course. However, I was then put in the position of having to take several different fish courses which, to avoid disappointing my hosts, I duly ate. During the night I awoke with a considerable feeling of abdominal discomfort! This was not nausea and I could not pin it down to any particular organ, although I suspected it was my liver suffering from an overload of protein. There was a ‘Eureka’ moment when it suddenly occurred to me that this might be an extreme example of ‘discomfort’ generated by the mild excesses (or deficiencies) of resources that occur normally. Perhaps animals eat to reduce these discomforts rather than directly to meet their nutrient requirements! Perhaps these discomforts are combined to provide an overall message that the CNS uses as a major drive of whether or not to eat. Over the next days and weeks this was developed into the Minimal Total Discomfort framework now to be presented, the scheme for which is derived from a recent review (FORBES, 2007).

The Minimal Total Discomfort (MTD) framework

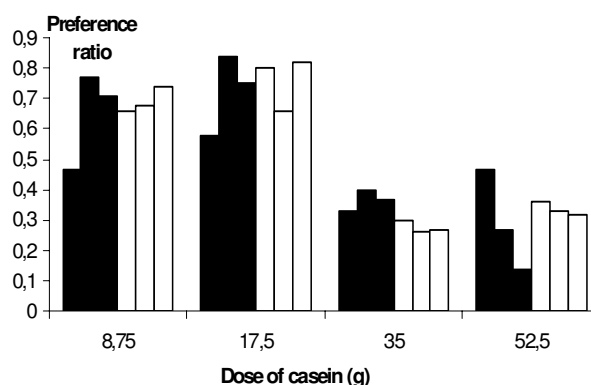
Optimal supply of nutrients

The 'requirement' for a resource is the rate of supply of the resource from its food or environment that most closely matches the rate at which it is programmed to utilise that resource, i.e. the 'optimal' rate of supply of that resource. 'Programming' is determined by the genetic potential of the animal and any deviation from this caused by previous malnutrition.

Deficiency or excess

Any imbalance between current supply of one or more resources and the optimal supply will create 'discomfort' related to some function of the magnitude of the deviation. The term 'resources' is used to indicate not only nutrients but such things as time spent eating and distension or other physical stimulation, above certain thresholds. It could also be expanded to include non-food items such as space allowance and social competition. There is evidence that either excess or deficiency of an essential nutrient causes avoidance of the food associated with that imbalance and Fig. 1 shows preference developing for small doses of casein while high doses cause aversion.

Fig. 1. Preference for flavour associated with administration of four doses of casein into the rumen of sheep in the first, second and third tests during conditioning (solid bars) and 7, 21 and 35 days post-conditioning (open bars) (ARSENOS and KYRIAZAKIS, 1999).



Transformation of discomforts

How can such diverse stimuli as rumen fill (kg), oxidation of substrates in the liver (mmol/min) and space allowance (m²) be expressed in the same currency so as to allow them to be combined? Discomforts can be brought into the same units by expressing them as proportions of the optimal supply for each resource (similar to FISHER, 1996).

What is the function relating these discomforts to their contribution to the total discomfort signal? It is to be expected that the effects of stimuli become proportionately more severe the greater the deviation of the current level of the resource from the ideal, i.e. a curvilinear relationship. The function should also encompass the idea that both excesses and deficiencies of supply of resources contribute to discomfort. The simplest way by which these objectives can be achieved is by squaring the deviation between supply and 'demand' for each resource.

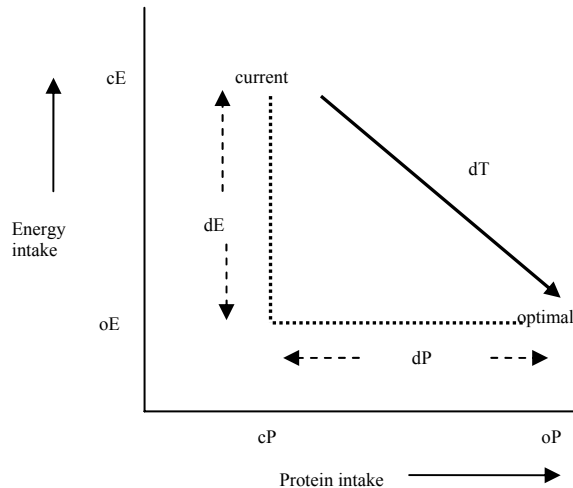
It seems highly unlikely that the same proportional deviation in supply of several resources will have the same discomforting effect, so that a different function for each resource may well be found to be necessary. Thus far the quadratic function has been used without weighting.

Summation of discomforts

How should the separate 'discomforts' then be combined? We will use as an example two food resources, energy and protein, plotted one against the other (Fig. 2). The current food intake provides energy and protein in amounts represented as 'current' while its optimal intakes of energy and protein are shown as 'optimal'; to get most directly from 'current' to 'optimal' it follows the thick arrow from

the former to the latter. The proportional deviations in energy supply ($dE = (cE - oE)/oE$) and protein supply ($dP = (cP - oP)/oP$) give a combined deviation (Pythagoras) of the square root of the sum of $(dE)^2$ and $(dP)^2$. More resources are represented by additional dimensions, again by adding in the squares of their proportional deviations from optimal.

Fig. 2. Diagram of connection between current and optimal intakes of energy (E) and protein (P). cE and cP are the current intakes of E and P, respectively and oE and oP are the optimal intakes. dE is the proportional deviation of energy $((oE - cE)/oE)$ while dP is the proportional deviation for protein $((oP - cP)/oP)$. Application of Pythagoras's theory allows dT , the overall deviation between the current and optimal positions represented by the diagonal solid arrow, to be calculated as $\sqrt{(dE)^2 + (dP)^2}$.



There are, in addition, physiological grounds (FORBES, 1996) that these deviations can then be added together, rather than being multiplied.

Minimisation of total discomfort

Having calculated total discomfort at one level of food intake, the model is iterated through a range of intakes (and combinations of intake where more than one food is included) until the MTD is reached; this gives the predicted intake (and choice) of food(s).

Implementation

For an arbitrary starting rate of intake, for each of the resources being considered, the quantity of the resource provided by this rate of intake is calculated, the requirement for that resource subtracted, the difference expressed as a proportion of the requirement, squared and multiplied by the weighting factor for that resource (if weightings are to be used); the results are summed and the square root of the sum taken to calculate the Total Discomfort; this is repeated with different rates of intake until Minimal Total Discomfort is attained.

Food resources to be considered

In the first numerical example three resources are included: energy, protein and dietary bulk; the 'standard' food used is a typical forage containing 10 MJ ME/kg DM, 0.12kg CP/kg and 0.60 kg NDF/kg. Energy and protein (crude protein, CP) generate discomforts whether in deficiency or excess. Neutral detergent fibre (NDF), on the other hand, only generates discomfort when in excess of a threshold for bulk in the rumen. It is assumed that the foods are balanced for minerals and vitamins.

Animal 'requirements'

The animal is a rapidly growing lamb at a weight of about 35 kg, with an optimal ME intake ('requirement') of 20 MJ/d on the basis that lambs of this type grew best on a food which gave an intake of 19.6 MJ ME/day (KYRIAZAKIS and OLDHAM, 1993). Similarly, the 'requirement' for

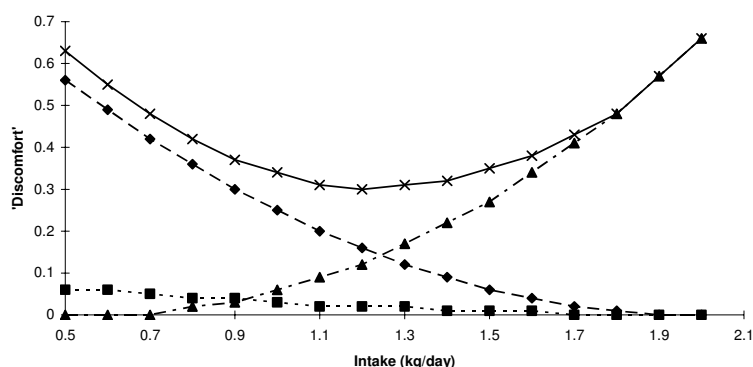
CP is 0.25 kg /day and NDF induces discomfort when its intake is greater than 0.35 kg /day (an educated guess).

Solution

Discomfort is plotted against intake with as many lines on this graph as there are resources being considered (Fig. 3). The optimal intake for providing ME is 1.75 kg/day while for CP it is 2.25 kg/day (the food is imbalanced). Neutral detergent fibre (NDF) is used as an index of dietary bulk and discomfort is only generated if current supply exceeds optimal supply. The three discomforts are added and the minimum discomfort is achieved at a daily intake of 1.2 kg DM, i.e. both ME and CP intake are limited by NDF.

Changing the animal's requirements, and/or changing the concentration of one or more of the resources in the food, results in curves with different positions on the graph, a different total discomfort curve and thus a different prediction for daily food intake. The minimum of the total discomfort curve can be found rapidly using the Solver function in Microsoft Excel®.

Fig. 3 Proposed discomfort due to ME (◆), CP (■), NDF (▲) and the sum of these (x) against intake of a forage food by growing sheep (see text for details).



In reality there are many more factors involved in the control of intake and selection, including amino acids, minerals and vitamins. In addition many external factors affect intake, including social factors, weather and animal/plant interactions including rate of eating and ease of selection between different plants or parts of the same plant.

Of the many shortcomings of this model perhaps the most serious is that it does not deal with interactions between nutrients. For example, protein provides not only amino acids but also energy and the latter can be quantitatively important when protein is supplied in excessive amounts, or is imbalanced in its amino acid composition. One way to deal with this is to add another factor to the model: the CP:ME ratio, generating additional discomfort when the food was less than 0.0125 g/MJ (0.25 kg CP/20 MJ ME), on the grounds that protein deficiency reduces the animal's ability to deal with energy-yielding substrates, leading to an excess of energy. It is this 4-factor model that has been used for the examples describe below.

Model exploration

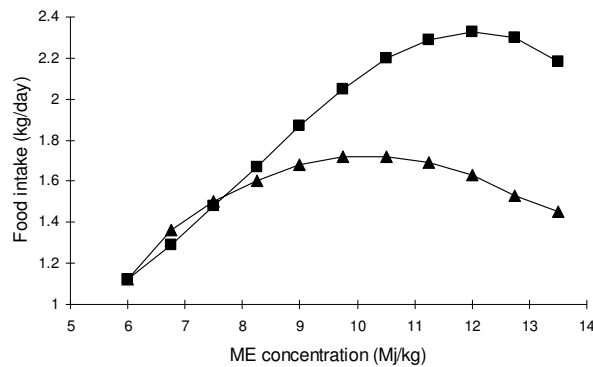
This model is intended to be a research tool, designed to explore new concepts, and, unlike multiple regression 'models' based on real data, it cannot can be tested under conditions similar to those in which it is intended they are to be used. It should, however, perform reasonably over a much wider range of conditions than regression models. The following is a selection of situations typical of those of interest in studies of food intake and selection.

Food quality

Much emphasis has been placed on the physical limitation of intake imposed by rumen capacity coupled with slow rates of digestion and passage of forages. Metabolic control has also been invoked for more concentrated foods and those with small particles and the assumption has usually been that one or other are operative at any one time, leading to the TPH. To test the how the MTD framework copes with the interaction between physical and metabolic controls of intake, the Model was run for foods with different qualities in which ME content ranged from 6 to 13.5MJ ME/kg in parallel with which CP was gradually increased from 90 to 200g CP/kg and NDF decreased progressively from 600 to 100g/kg. The predictions of intake plotted against food quality (expressed here as ME concentration) of the food for sheep with standard requirements (20 MJ ME/d, 0.25 kg CP/d and 0.35 kg NDF/day) are shown in the lower line of Fig. 4. It can be seen that intake increases with improvements in energy yield up to about 10.5 MJ ME/kg (0.15kg CP and 0.33 g NDF/kg) but then decreases with the highest quality foods. The TPH involves a sudden change from intake positively related to food quality in the 'physical' phase to intake negatively related to quality in the 'metabolic' range. MTD, however, gives a gradual change-over, as envisaged by Owen et al (1969) and observed in practice (BINES, 1979; N.R.C., 1987, p 57).

An increase of 50% in the ME and CP requirements of the animal was imposed to simulate lactation (NDF threshold stayed the same) and the upper line in Fig. 4 shows that the maximum DM intake was predicted to be achieved at an ME content of about 12MJ ME/kg (0.18 kg CP and 0.20 kg NDF/kg). An increased productive energy output was thus predicted to increase food intake with diets of high ME content, as commonly observed.

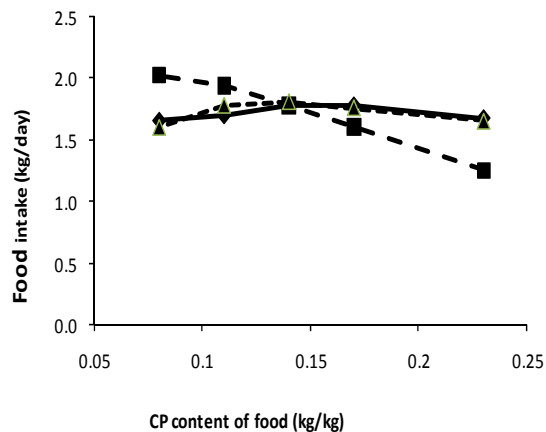
Fig. 4. Predicted intake of foods of a range of nutrient values (see text) for a growing sheep (◆) and another with nutrient requirements increased by 1.5 times (■).



Food protein

The MTD model was run with parameters for growing sheep and foods ranging from 0.08 to 0.23 kg CP/kg, ME of 11.0MJ/kg and NDF varying between 0.19 to 0.21 kg/kg (KYRIAZAKIS and OLDHAM, 1993).

Fig. 5. Intakes of food (◆) by growing sheep offered single foods of various CP contents (KYRIAZAKIS and OLDHAM, 1993) and predictions of the MTD model without (■, 3-factor model) or with (▲, 4-factor Model) optimal CP:ME ratio.

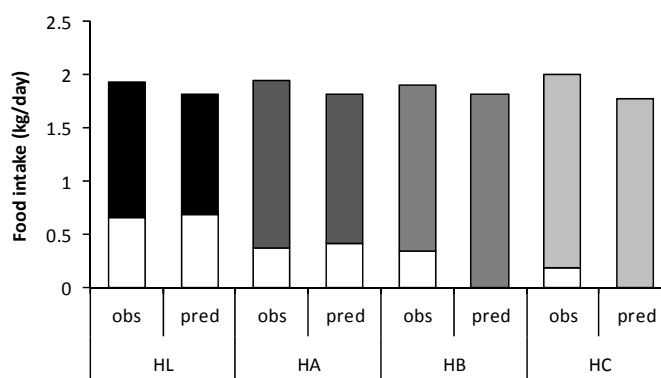


It can be seen that the 4-factor model performs much better than the 3-factor model, compared to observed intakes by these sheep and this seems to vindicate the addition of the CP:ME factor. Note that the foods offered in the experiment had low NDF content so that discomfort due to NDF was negligible.

Choice feeding

Offering animals a choice of foods is a particularly good way to investigate animals' abilities to adapt as they learn about the nutritional qualities of foods. The MTD model was programmed to 'experiment' with two foods by changing the rates of intake of each food until minimum discomfort is reached, thereby predicting both daily food intake and the proportion of each of the two foods eaten. The experiment of Kyriazakis and Oldham (1993) has again been used to provide the animal and food specifications for simulations of diet selection. The animal is a sheep with high growth potential and ME, CP and NDF 'requirements' of 20MJ ME, 250g CP and 350g NDF/d, as described above. The highest protein food (0.23 kg/kg) was always on offer along with one of the other foods with protein contents of 0.17, 0.14, 0.11 or 0.08 kg/kg. Fig. 6 shows good agreement between observed and predicted except that foods B and C were eaten in small amounts by the sheep even though they did not need to do so to fulfil their 'requirements' for CP; the model predicted zero intake of these two foods. It is characteristic of animals that they sample each available food from time to time and this appears to be what was happening in this experiment and the resulting excess intake of CP was not sufficient to cause undue discomfort.

Fig. 6. Observed and predicted intakes by growing lambs when offered ad libitum access to two foods, one (H) with a CP content of 0.23 kg/kg, the other with a CP of 0.08 (L), 0.11 (A), 0.14 (B) or 0.17 (C) kg CP/kg DM (KYRIAZAKIS and OLDHAM, 1993).



Choice-fed lambs were observed to eat more in total than similar sheep offered single foods (KYRIAZAKIS and OLDHAM, 1993) while the model predicted daily intakes of single- and choice-fed animals to be similar. The model does not include any explicit means whereby choice feeding might affect total intake in comparison with a balanced single food, and there is no part of the current theory that would provide such a means. However, it is likely in some situations in which no food is balanced when offered by itself, that an appropriate choice will allow a better match between supply of and demand for resources, and total intake could be higher.

Improvements and developments

The MTD approach seems to work reasonably well under a variety of conditions, both animal and food. It is far from complete, however, and the author hopes that others will take sufficient interest to correspond with him concerning further developments.

There is almost no end to the number of factors that could be included in the MTD approach. Rate of eating and grazing time have already been briefly explored (FORBES, 2001). Ease of prehension, walking distance and heat load would further adapt the application of MTD to the outdoor situation.

Social factors such as group size can also be included and space allowance has tentatively been used in once instance of the model (FORBES, 2006). Additional dietary factors affecting intake and choice include individual amino acids, minerals, vitamins, toxins, fibre type, flavours previously associated with foods with different properties. A major problem with many of these potential additional factors is how they should be weighted – it seems unlikely that an intake of half the optimal level of protein, for example, would generate the same discomfort as a space allowance of half the optimal. Arbitrary weightings of 0.33 for CP and NDF relative to ME have been used when the MTD approach was first described in detail (FORBES and PROVENZA, 2000) but this was not justified as it was not based on factual evidence.

Ruminants have a ‘requirement’ for fibre in that their digestion is impeded when given finely-ground foods and, if given the opportunity, they will invariably choose to eat some long fibre. This can easily be included in the MTD model by specifying that discomfort is caused by very low intakes of long fibre.

Mention has been made of the interactions between resources, using protein and energy as an example. One way to explore this area further would be to use existing models of ruminant digestion and metabolism as sub-models to provide a more dynamic representation of the animal/food relationship.

At present the MTD approach has not incorporated feedbacks from body reserves. This could be achieved by assuming that deviations from the ‘ideal’ body fat content (and fat: lean ratio) generate discomforts (via insulin or leptin?) which could then be added into the total discomfort.

Although Pythagoras’s Theorem has been invoked to support the quadratic relationship between stimulus and response used in the model presented above, better evidence is required. It seems likely that a deficiency in the supply of a resource might cause greater discomfort than the same proportional excess of that resource. Is there information in the literature that might allow a better assessment of the appropriate function(s) relating stimulus to response?

Conclusions

It is generally accepted that the control of intake and choice of food, including by ruminants, is multifactorial. For many decades, however, most attempts to incorporate more than one factor have been with ‘first limiting factor’ models, typically physical limitation vs. metabolic control. One development was the use of six limiting factors (POPPI et al., 1994) and another involved multiplication of factors (FISHER, 1996), which is physiologically unlikely, and an artificial device was invoked for increasing the importance of chemostatic control at lower levels of rumen fill, which is unnecessary if the additive approach is adopted. The approach adopted for the MTD framework scales any number of factors according their deviation from optimal which allows them to be manipulated together because they are all in the same currency. Addition is chosen because it is the simplest way in which to combine the various factors and has some experiment support. Critically, intake is predicted not as the dependent variable, but as independent and causing variations in discomfort, which is seen as being the controlled variable. Food intake and selection are observed to vary widely from day to day (FORBES, 2007) and this can provide the inputs whereby animals learn to eat that amount (and mix) of food(s) that cause MTD over periods of several days.

The MTD framework is put forward to encourage further development and as a challenge to devise experiments to show areas in which it fails. Failure would not be an inability to predict intake to the nearest few percent, but rather the failure of the broad concept of how different factors are integrated to predict more generally ways in which intake and selection cope with changes in diet, physiology or environment.

It remains to be seen whether the approach will be useful in assisting the practical management and ration formulation for ruminants. It may be found that either the approach is wrong in principle, or that its parameters (functions and weightings) can never be estimated. In the meantime, if it serves to

stimulate thought and experimentation leading to advances in our understanding then I will be well satisfied.

For a spreadsheet on which the MTD model is programmed, or to discuss any aspect of the approach, please contact the author at j.m.forbes@leeds.ac.uk.

References

- ARSENOS, G. and I. KYRIAZAKIS (1999): The continuum between preferences and aversions for flavoured foods in sheep conditioned by administration of casein doses. *Animal Science* 68: 605-616.
- BINES, J. A. (1979): Voluntary food intake. *Feeding Strategy for the High Yielding Dairy Cow*. ed. W. H. Broster and H. Swan, Granada: 23-48.
- FISHER, D. S. (1996): Mathematical integration of distension and chemostatic feedbacks for regulation of ruminant intake in diets with varied dietary protein. *Journal of Animal Science* 74: 3076-3081.
- FORBES, J. M. (1996): Integration of regulatory signals controlling forage intake in ruminants. *Journal of Animal Science* 74: 3029-3035.
- FORBES, J. M. (2001): Consequences of feeding for future feeding. *Comparative Biochemistry and Physiology* 128: 461-468.
- FORBES, J. M. (2006): Conclusion and perspectives. *Food and Feeding in Domestic Vertebrates. A Comprehensive Approach from Structure to Behaviour*. ed. V. L. Bels, CABI Publishers: 349-358.
- FORBES, J. M. (2007): A personal view of how ruminant animals control their intake and choice of food: Minimal Total Discomfort. *Nutrition Research Reviews* 20: 132-146.
- FORBES, J. M. (2007): Voluntary Food Intake and Diet Selection in Farm Animals. CAB International, Wallingford:453.
- FORBES, J. M. and F. D. PROVENZA (2000): Integration of learning and metabolic signals into a theory of dietary choice and food intake. *Ruminant Physiology: Digestion, Metabolism, Growth and Reproduction*. ed. P. B. Cronje, CAB International: 3-19.
- KYRIAZAKIS, I. and J. D. OLDHAM (1993): Diet selection in sheep: the ability of growing lambs to select a diet that meets their crude protein (nitrogen x 6.25) requirements. *British Journal of Nutrition* 69: 617-629.
- N.R.C. (1987): Predicting feed intake of food-producing animals. National Academic Press, Washington D.C.:85.
- OLDHAM, J. D., G. EMMANS and N. FRIGGENS (1998): Development of predictive systems to relate animal and feed characteristics to amounts and patterns of forage, and total food intake, by cows. *Optimisation of Forage Quality and Intake by Ruminants*. ed. M. Gill, Natural Resources International Ltd: Report to MAFF on DS04.
- OWEN, J. B., D. A. R. DAVIES and W. J. RIDGMAN (1969): The control of voluntary food intake in ruminants. *Animal Production* 11: 511-520.
- PITTROFF, W. and M. M. KOTHMANN (1999): Regulation of intake and diet selection by herbivores. *Nutritional Ecology of Herbivores*. ed. H. G. Jung and G. C. Fahey, American Society of Animal Science: 366-422.
- POPPI, D. P., M. GILL and J. FRANCE (1994): Integration of theories of intake regulation in growing ruminants. *Journal of Theoretical Biology* 167: 129-145.
- TOLKAMP, B. J. and J. J. M. H. KETELAARS (1992): Toward a new theory of feed intake regulation in ruminants. 2. Costs and benefits of feed consumption: an optimization approach. *Livestock Production Science* 30: 297-317.

j.m.forbes@leeds.ac.uk