# Genotype, Nutrition and Behaviour Interactions in Ruminants

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## Introduction

One of the main aims of research in animal nutrition is to provide information which can be used, in practice, to control animal performance. This does not deny the value of 'curiosity-driven' research as a worthy intellectual pursuit in its own right. But, in the main, the value of 'advances' in animal nutrition (especially farm animal nutrition) is the extent to which that information, at some time, will be useful to aid practice.

In this context, the application of 'advances' in animal nutrition needs to take into account the natures of the animals to which information is applied. By this I mean the genetic nature of the animal and the way it behaves in a particular environment (i.e., phenotype).

Much effort has been applied over many years to understand feeding behaviour in the grazing animal with, perhaps, somewhat less effort aimed at understanding other aspects of feeding behaviour. For ruminants, the influence of genotype on nutritional issues has been given relatively little attention - especially by nutritionists. In comparison with the situation with non-ruminants (especially pigs and poultry) it is quite startling that description of genotype plays rather little part in the structure of most ruminant nutritional schemes (e.g., CSIRO 1990; AFRC 1993).

As increasing emphasis is now being placed ion predicting the responses of animals to available feeds it is probably more important now, than ever before, that proper account is taken of the role of genotype and phenotype in determining future performance responses. This argument is given extra weight now that genetic tools to improve ruminant livestock are increasingly powerful and widely used.

The purpose of this paper is to provide a context within which ideas about relationships between genetics, feeding behaviour and nutrition might be expressed. Results of studies of genotype and feeding interactions in dairy cows and of the use of diet selection techniques as a means to gain understanding about some aspects of feeding motivation in ruminants are presented.

Figure 1 shows a general framework for considering the relationships between an animal, its feed and its environment. It could be used for any animal species,

**Figure 1** A general scheme to relate animal and feed characteristics for prediction of feed intake and animal performance.
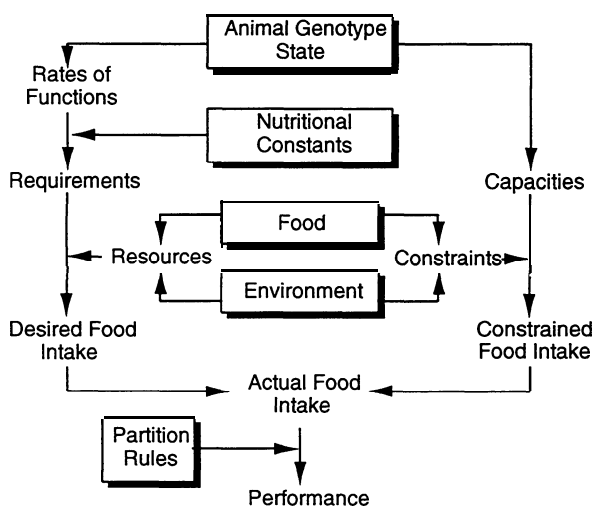


but will be considered here in the context of ruminants.

At the head of the framework is a description of the animal. Animals vary according to their genotype and their state. The important elements of 'state' are body composition, reproductive state and state of health. The left-hand side of the figure presumes that the animal is trying to eat sufficient of an appropriately balanced food to allow it to meet its 'targets' for performance as determined by genotype and current state. The demand for feed resources is a true statement of requirements, i.e. the amounts of nutrient and energy which are needed for the animal to achieve its target; this is a little different from the usual statement of requirements as the amounts of nutrient (and energy) which are needed for an animal to perform at a certain rate. The difference is one of perspective. The animal's perspective of its requirements identifies the amounts of resources (nutrients and energy) which it needs to achieve a 'preferred target performance'. The nutritionists, or animal managers' perspective is the amounts of resources which should be supplied to ensure a certain rate of performance. If the amounts of resource supplied to the animal are inappropriate to

meet *its* needs, the response, as animal performance, may be quite different form the performance which the manager or nutritionists expected.

Both feeds and environment provide resources which the animal needs in order, successfully, to attain its targets. But also both feeds and environment might constrain the ability of an animal to eat the right amount of the right balance of feeds in order to meet its targets. This is because animals have certain 'capacities' to accommodate feed or environmental constraints. Examples of such capacity might be for physical attributes of the feed, toxic factors, the thermal environment etc. Actual food intake is therefore predictable, either as a 'desired food intake' which is an amount of an ideally balanced food which allows the animal to meet its target (according to its genotype and state) or is constrained by features of the feed and the environment to be less than that which is desired.

A great deal of ruminant nutrition research has been expended on finding ways to predict the supply of nutrients (and energy) from the amount of food which is eaten. There continue to be considerable problems in that area, especially as regards prediction of metabolisable nutrient yields from feed ingested. But the subject remains as a practically important area of research.

Notwithstanding those problems of predicting metabolisable nutrient (or energy) yields from consumed feeds, the lower part of the diagram (Figure 1) shows that performance of the animal becomes predictable if partition rules are available to describe the fate of absorbed nutrients.

Thus, the main problems of ruminant nutrition are (as stated many times over the last few decades) a means to predict food intake and a set of rules to describe the partition of nutrients (and energy) made available from consumed food between alternative pathways of use. The most common practical situation is that the animal consumes a diet which is either inadequate in amount (undernutrition) and/or balance of metabolisable nutrients (malnutrition) so the question arises "what rules apply (or what processes regulate) the partition of limited and/or imbalanced nutrients between various pathways of use in an animal which cannot achieve its 'desired performance targets'"?

This general approach can be used to develop models of animal performance (Emmans and Oldham 1988). It has formed the basis of a substantial part of our research programme over the last few years. One of its key premises is that animals strive to eat in order to achieve a performance target. What evidence is there for this?

## Diet Selection in Pigs and Sheep

The clearest evidence comes from non-ruminants. Pigs will make dietary selections between pairs of highly digestible feeds of different protein:energy ratio to achieve their 'growth targets'. Kyriazakis and

Emmans (991) allowed small, recently weaned, pigs to become relatively fat or thin by offering, *ad libitum,* feeds of low protein:energy ratio or high protein:energy ratio respectively. From 16-3 3 kg liveweight the pigs had free access to both a low and high protein:energy ratio diet and the choices made by the pigs of different body composition differed in such a way that the fatter pigs became leaner and the leaner pigs fatter. By the time that the pigs reached 33 kg liveweight, pigs of a given sex had, effectively, achieved the same lipid:protein ratio in the carcase and that ratio differed between sexes. The pigs had chosen diets which allowed them to regain a performance path which was fixed by genotype, although they had been diverted from that path through being offered imbalanced single foods at an earlier stage.

In other work with boars, growing from 44 to 103 kg liveweight, Kyriazakis *et al.* (1993) found that the chosen crude protein concentration of a diet, selected from two feeds of different protein concentration, fell throughout the growth period, somewhat in line with expectations from the changing ratios of lipid and protein which would be growing in those animals over that period of time. In a comparison between different genotypes of pig (Large White x Landrace vs. Meishan) Kyriazakis *et al.* (1993) found that the slower growing, more adipose, genotype (Meishans) made radically different selections at a weight and over time from 'genetically improved' pigs. These three pieces of evidence (namely diet selection to regain a body composition at a stage of maturity; variation in selection over a growth path and difference between genotypes in diet selection at a weight) provide a good basis on which to accept the proposition (Figure 1) that animals are trying to eat sufficient of a well-balanced food to allow them to achieve a growth target. It would also appear that growing pigs will make a diet selection (between choices of feeds of different protein:energy ratio) which allows them to grow protein at a high (possibly maximum) rate, but to avoid an excessive intake of protein.

If the hypothesis appears to stand with pigs offered highly digestible feed, is it also applicable to ruminants?

Growing sheep, offered choices between pairs of digestible feeds which differ in their protein:energy ratio do make structured choices between feeds (Hou *et al.* 1991). It also appears that sheep will select a diet (where the food choices on offer are of high digestibility) which allows them to grow protein at a maximum rate and to avoid an excessive intake of nitrogen (Kyriazakis and Oldham 1993). The latter work gave some, tentative, indication that, provided their growth target could be achieved, sheep would avoid a feed of high rumen degradable N content (urea) rather than one containing proteins which are likely to be more slowly degraded in the rumen.

On teleological grounds it might be expected that diet selections made by ruminant animals would be influenced to a substantial extent by the consequences

for the rumen environment of selected meals. Our evidence for this stems from studies of diet selections made by pregnant and non-pregnant sheep offered feeds of different protein:energy ratio at both rumen and tissue level and from information on selections made between feeds of different (calculated) rates of fermentation in the rumen (Cooper et al. 1994, 1995). Pregnant and non-pregnant sheep appeared o make remarkably similar diet selections when offered pairs of feed which were either of high or lower energy density and where the choice variable was the N content of the diets on offer (Table 1). With a highly digestible feed pair, contemporaries - which might be seen as selection to match a difference in metabolic demand for nutrients. However, this was not the case where the foods on offer were of lower density. The choices though appear to be 'sensible' if interpreted as selection for an appropriate balance of degradable N and fermentable carbohydrate in the rumen (ERDP/ FME ratio; AFRC 1993).

In other circumstances we have found that sheep offered choices between feeds of different (estimated) fermentability will avoid an excessive intake of a very rapidly fermentable feed (Cooper et al. 1995). The extent to which this is related to the influence of feed ingredients on rumen pH, rumen osmolality or other factors has yet to be determined (Cooper et al. 1995; Engku Azahan and Forbes 1992).

It would appear from these various observations that state directed selection of feed is important within the context of the animal's overall feeding strategy. There are, of course, wider issues which govern the foraging and grazing behaviour of ruminants (Milne 199 1; Provenza 1995).

Disease also affects feeding behaviour of ruminants. Sheep, challenged with the intestinal parasite, *Trichostrongylus colubriformis*, have been found to alter their selection between feeds of different protein:energy ratio in such a way that intake of protein is maintained during the partial anorexia associated with the challenge (Kyriazakis et al. 1994, 1995). The extent to which these modifications in feeding behaviour are regulated to achieve mainte- nance of nitrogen status in response to the enhanced endogenous loss of N from parasitised animals (Mac- Rae 1993) or are stimulated by the activation of the immune response in relation to challenge is not yet known. However, the observations that sheep will redirect their diet selection in response to a diseased state is yet further evidence that animal state needs to be carefully described within systems which are designed to predict food intake and animal perform- ance (Figure 1).

## Genotype-Nutrition Interactions

Although the rates of genetic improvement of ruminant livestock have lagged behind those achieved with pigs and poultry over the last few decades, considerable progress is now being made. Progress with dairy cows is particularly striking, fuelled by the increasing international trade in semen and widespread application of AI (and to a lesser extent embryo transfer, ET) and ever more powerful quantitative techniques for the design and application of breeding schemes. Rates of increase in predicted transmitting ability (PTA) of substantial proportions of the dairy herds in the UK, and elsewhere in the world, are now around 1.5 per cent per year or around two thirds of the maximum achievable rate for current designed schemes.

This is not to say that effective strategies to improve the productive performance (growth, lean- ness, wool production) of sheep and beef cattle do not exist; they do, and the tools to make them increasingly effective, also exist (Simm et al. 1995; Villanueva and Simm 1994).

The consequences of genetic improvement in dairy cattle for feed utilisation have been considered sporadi- cally over many years. Studies of genotype x environ-

Table 1   Dietary choices made by twin pregnant or barren sheep given ad *libitum* access to a pair of feeds differing in protein content (HP or LP) but, within a pair, of the same high or low energy density

| Dietary class (MJ ME/kg DM) | High energy density (12) | | Lower energy density (9) | |
|---|---|---|---|---|
| Specification of single feeds: | | | | |
| HP feed:ERDP/FME (g/MJ) | 16 | | 13 | |
| MP/ME (g/MJ) | 12 | | 12 | |
| LP feed:ERDP/FME (g/MJ) | 7 | | 5 | |
| MP/ME (g/MJ) | 4 | | 4 | |
| Sheep | Pregnant | Barren | Pregnant | Barren |
| Proportion of HP in diet (g/kg) | 570 | 280 | 700 | 790 |
| Nutritional content of chosen diet | | | | |
| MP/ME (g/MJ) | 9.7 | 8.8 | 10 | 10.4 |
| ERDP/FME (g/MJ) | 12 | 8.8 | 10.4 | 11.1 |
| MP yield (g/d) | 183 | 193 | 212 | 262 |

ment interactions (GxE) obviously encompass factors of management, the physical environment, the thermal environment, and others, as well as nutrition. However, genotype x nutrition (GxN) interactions are often considered as a major part of GxE interactions and the majority of the literature form temperate regions on GxE is fairly specifically related to GxN.

Freeman (1967 and 1975) has reviewed much of the earlier information on GxE interactions in dairy cattle. For production of milk and milk solids, Freeman's (1975) general conclusion was that, whilst there is some evidence for GxE interactions, the magnitude of the interaction is generally small and not sufficient to give concern for making selection decision in the range of environments likely to be expected in the prevailing commercial populations. The current acceptability of that observation might be challenged on the grounds that both phenotypic performance and genotype have been improved considerably since the time of some of the earlier studies. In particular, there might be reason to think that the genetic progress which has been achieved over the last two decades in yield capacity of dairy cows has begun to outstrip the capacity of cows to eat sufficient to sustain those high yields and to remain in good health on all feeding systems which might be used in practice. Feed systems which emphasise the use of forage might cause GxN interactions which previously were small, to take an exaggerated importance with some of today's genotypes.

In comparisons between Jersey cattle and other dairy breeds, interactions between genotype and feed environment (GxN) have been found (Oldenbroek 1986, 1988). The differences applied both to feed intake and milk production traits with the difference between Jerseys and other breeds being less on a high roughage diet than on a high concentrate diet. In large part, variations in relative performance were attributed to the higher relative feed capacity of Jerseys compared with other breeds. This between-breed difference in intake capacity has been noted previously (Gibson 1986; Brigstocke *et al.* 1982). In the Oldenbroek

(1988) data scaling of liveweight to the power 0.58 (instead of 0.75) would remove the between-breed difference seen with high concentrate feeding, so it could be argued that the difference between Jersey cattle and others in feed intake is merely a question of scaling. But the difference in intake would remain for high roughage feeding, even with the alternative scale. It would therefore seem that the difference is real and perhaps accentuated with higher forage feed systems.

As well as these observations of 'feed intake capacity' between breeds, Orskov *et al.* (1988) have suggested that there are consistent and possibly important differences between cows within a breed in rumen outflow rates of fibrous particles, which may have consequences for digestibility and intake of roughages.

We have been investigating the consequences of genetic selection for milk solids yield (fat + protein) in dairy cows under UK feeding conditions (Veerkamp, Simm and Oldham 1994). The work, done at the Langhill Dairy Cattle Research Centre in Edinburgh, uses a herd of Holstein-Friesian cows in two genetic lines. The selected line is bred (AI) to proven bulls of highest possible PTA for kg fat + protein. The control line is bred (AI) to bulls with an average of zero PTA for kg fat + protein. Feeding systems are based on grass silage, brewer's grains and concentrate offered as complete mixed feeds. Half of each genetic line is managed in a high concentrate system (HC; concentrate:brewer's grains:grass silage 45:5;50 DM basis) and half in a lower concentrate system (LC; 20:5:75). The aim is to monitor the consequences of selection for high rates of yield of milk solids over the first three lactations for animals in each feed system so that long-term impacts of genetic progress can be assessed and possible genotype x feed system interactions identified.

Table 2 shows the performances of the two genetic lines of cows in the two systems of feeding at Langhill from results accumulated over the first five years of the study. The data are for performance over the first 26 weeks of lactation. Selected line animals yield more

**Table 2**  performance of selection and control line dairy cattle in the HC and LC feed systems at Langhill. Combined data (1988/89-1992/93)

|  | HC | | LC | |
|  | Selection | Control | Selection | Control |
| --- | --- | --- | --- | --- |
| Number of animals | 129 | 105 | 143 | 98 |
| Milk (kg/d) | 32.0 | 27.5 | 26.3 | 22.7 |
| Fat yield (g/d) | 1301 | 1125 | 1167 | 1006 |
| Protein yield (g/d) | 982 | 862 | 786 | 694 |
| Fat % | 4.08 | 4.12 | 4.49 | 4.48 |
| Protein % | 3.08 | 3.16 | 2.99 | 3.08 |
| Dry matter intake (kg/d) | 18.3 | 17.6 | 15.7 | 15.2 |
| Average liveweight (kg) | 611 | 602 | 596 | 594 |
| Condition score (0-5) | 2.40 | 2.54 | 2.28 | 2.51 |

milk and milk solids than control in contemporaries in each of the feeding systems. The advantage in milk solids yield (fat + protein kg) is a little greater in the HC system than in the LC system, with a difference also in the ratio of fat:protein in the extra combined fat plus protein yield. The effects of diet on milk yield and composition are very much in line with normal expectations. A striking contrast is the one between control line animals in the HC system of feeding and selected line animals in the LC system. The combined fat plus protein yields of these two groups is essentially the same, although the ratio of fat:protein yields differs somewhat. A defined level of milk yield can be achieved more efficiently with high genetic index cows in a lower input system than with average genetic index cows and high inputs of feed.

Regression of milk output and of DM intake on PTA (Veerkamp *et al.* 1995) shows that, in the HC system of feeding, increases in PTA bring with them positive and significant increases in both milk solids yield and DM intake. In the LC system, increasing PTA brings with it increases in milk solids yield (albeit at a slightly lower rate than for the HC system), but the effect son DM intake are small and non-significant. This might suggest that, in a system of feeding which relies on quite highly digestible feeds (HC) the rising food intake with milk solids yield, as PTA increases, is a reflection of food intake being substantially a function of the ability of the animal to produce milk. With reference to Figure 1, the cow is striving to achieve a desired food intake and can overcome at least some of the constraining factors associated with food and environment. By contrast, with the less digestible foods used in system LC, food DM intake does not increase much (if at all) as milk solids yield rises with PTA, reflecting limiting properties of the food as the chief constraints to intake.

Even in the higher concentrate feed system the increase in milk solids yield with PTA represents an increase in demand for metabolisable energy (ME) which is greater than the increase in DM intake with PTA will provide. The difference between enhanced ME demand with increasing PTA and change in ME intake with PTA is remarkably similar in each of the two systems at just over 0.5 MJ extra ME per day relative energy deficit per unit increase in PTA for kg fat plus protein. This might suggest that selection for increased milk solids yield is, to a large extent, also selection for cows which are 'capable" of enhanced mobilisation of body tissue. In physiological terms, this might be a reflection of enhanced pituitary activity.

As genetic selection continues over the next generations, one might query whether ever-increasing capabilities to mobilise body tissue can be maintained whilst allowing cows to remain 'fit'. Future selection criteria might need to be adjusted to favour increases in intake which are more in line with the support needs for milk. However, we must remember that the sires used in our studies have been evaluated largely (if not entirely) in management systems which are designed to support high rates of milk production and where feed is generally of high quality and abundant. Under these conditions the negative consequences of excessive tissue mobilisation may not be so obvious. The appearance of variation in the traits which are important for the effective use of high forage feeds may have been subdued. Amongst options for the future therefore are the possibilities to tailor selection criteria to avoid excessive tissue mobilisation or to make greater use of records which will help to identify animals which perform well in lower input systems. The results of the CANZ trial (Peterson, R. 1988; see Oldham *et al.* 1992) have shown that there can be some degree of re-ranking of sires when evaluations are made in different systems. (The CANZ trial wa designed to evaluate the relative performances of progeny fro Canadian (CA) or New Zealand (NA) sires evaluated either in their country of origin or in the alternate country.) There are important questions to be asked about the possibility of differences in food, especially forage intake capacity, amongst cattle which might lead to certain individuals having a competitive advantage in lower input feeding regimes. Such differences may be subdued in feed systems which rely more on high nutrient density feeds - but become important in feed systems which rely more heavily on forages.

## Partition Rules

It ha already been said that the normal nutritional state of an animal is to be undernourished, malnourished (or possibly both). Whilst prediction of food intake is likely to depend very substantially on a combination of knowledge about the performance targets of the animal, and qualities of feed (Figure 1) prediction of performance from a knowledge of intake must depend on having a set of rules about the ways in which limited or imbalanced amounts of nutrients and energy are partitioned amongst alternative pathways of use. Well-founded frameworks to address this issue are needed. Whilst attempts have been made to describe nutrient utilisation at a quasi-biochemical level in various kinds of simulation model (Baldwin *wet al.* 1987; and others) convincing evidence that this is the right level to approach the questions for purposes of describing the behaviour of the whole animal system, is perhaps lacking. There is not room here to explore the issue in any detail. However, it is obvious that success in the prediction of responses to nutrition depends heavily on getting knowledge of the rules, or regulating processes, which govern the use of nutrients for alternative anabolic processes and in catabolism. Despite a plentiful literature on elemental processes, application of that knowledge to the reliable prediction of partition in practice has yet to be realised.

## Conclusion

A very high proportion or research in ruminant nutrition over the last three decades or so has been designed to get understanding of processes of digestion and metabolism. The rewards in understanding have been enormous. However, it might be argued that the use of hat understanding to improve the predictability and control of ruminant animal performance has not been as great as one might have expected from the magnitude of the research investment. Arguably, t his might have been because developments in understanding about the nature of the whole animal and its feeding behaviour have not kept pace with the elemental sciences.

The framework presented here (Figure 1) is really very simple and straightforward. However, it has served to remind our research group that there is an important whole animal context within which advances in nutrition need to be viewed. By re-emphasising the importance of genotype and feeding behaviour, some important biological issues have been addressed. As future opportunities are exploited to enhance genetic selection or modify genetic control it will continue to be important that whole animal, as well a elemental aspects of ruminant nutritional science, are developed in concert. For purposes of predicting and controlling ruminant animal performance, development of understanding which will provide useful rules to define the partition of available nutrients between alternative pathways of use is an important immediate challenge.

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