

Dietary-induced thermogenesis and feed evaluation in ruminants

BY E. R. ØRSKOV AND N. A. MACLEOD

Rowett Research Institute, Bucksburn, Aberdeen AB2 9SB

In simple-stomached animals it is still uncertain if the composition of absorbed nutrients affects dietary-induced thermogenesis. For instance MacLeod *et al.* (1989) found no change in percentage energy retention in poultry that were given different amounts of protein, carbohydrate and fat. In ruminants, however, it is generally recognized that the heat produced from similar amounts of metabolizable energy (ME) is greater from a diet based on cellulosic roughage than from one based on concentrates. The recognition of these differences is not new and not in dispute but sometimes heated debates have taken place as to the exact cause of the differences.

HISTORICAL PERSPECTIVE

First indications of the effect of roughages on dietary-induced thermogenesis can be gleaned from early feed evaluation systems. Initially feeds in Europe were evaluated relative to straw or meadow hay (see Tyler, 1975). Morton (1855) lists several authors' estimates of the value of grain relative to good-quality meadow hay and most of the authors estimate 50–60 kg grain to be equal in nutritive value to 100 kg meadow hay. Since grain is likely to be about 80% digestible and meadow hay 50–60% digestible the greater value given to grain is apparent. When Kellner (1926) proposed a new feeding system based on pure nutrients, because of the variability in previous standards, he compared feed values relative to pure starch for fattening of steers. With use of respiration calorimetry Kellner (1926) observed differences in heat production between cellulosic roughages and starch when a similar amount of ME was given. Kellner (1926) attributed these differences to variation in work of digestion ('Verdauungsarbeit') and devised correction factors based on crude fibre.

Kellner's (1926) explanation was generally accepted, although the American feed evaluation system which was developed later simply compared feeds on the basis of total digestible nutrients and this is still largely used in the USA today.

When the team in Cambridge led by Sir John Barcroft (Barcroft *et al.* 1944) proved clearly that the main source of energy for ruminants consisted of volatile fatty acids (VFA) formed during anaerobic fermentation, not as previously thought digestible microbial polysaccharides (Baker, 1942), other reasons were put forward to explain the differences between roughage and concentrate diets. The establishment of the importance of VFA and the development of chromatographic methods to separate VFA soon led to the general finding that the proportion of acetic acid was highest on roughage diets while the proportion of propionic acid was highest on concentrates. Table 1 compares fermentation patterns from different nutrients (Ørskov & Oltjen, 1967). A hypothesis was put forward initially by McClymont (1952) that the higher heat losses with roughage diets could be associated with the higher proportion of acetic acid in the fermentation end-products. Consideration of oxidative metabolism based on Krebs citric acid cycle indicated that successful oxidation of acetyl-CoA depended on continuous regeneration

Table 1. *Effect of type of carbohydrate on molar proportion (mmol/mol) of volatile fatty acids in the rumen of two steers receiving purified diets (Ørskov & Oltjen, 1967)*

| Substrate | Acetic acids | Propionic acid | Butyric acid | Higher acids |
|------------------|--------------|----------------|--------------|--------------|
| Cellulose | 737 | 183 | 48 | 32 |
| Starch | 604 | 247 | 104 | 45 |
| Starch + glucose | 571 | 289 | 99 | 41 |
| Sucrose | 496 | 232 | 202 | 70 |
| Glucose | 380 | 223 | 258 | 139 |
| SE | 28 | 29 | 10 | — |

of oxaloacetic acid. Oxaloacetic acid, if deficient, could only be generated from glucose or glucose precursors such as propionic acid and not from acetic acid. Thus, the term futile cycling was coined in the belief that a relative glucose deficiency would lead to an inefficient capture of ATP from acetate oxidation and be responsible for the differences between roughage and concentrate diets. The development of techniques of rumen cannulation and respiration calorimetry led to a test of the hypothesis by Armstrong & Blaxter (1957*a,b*) and Armstrong *et al.* (1957, 1958). They carried out a series of experiments in which VFA singly or in mixtures were infused into the rumen of sheep. They observed that while infusion of the different VFA into the rumen of fasted sheep gave similar increases in heat production, differences were seen when fed sheep were given infusions above energy maintenance; greater increases in heat production were observed when acetic acid was infused (67 kJ/100 kJ total VFA) than with propionic and butyric acids (44 and 38 kJ/100 kJ respectively). They also postulated that there was a linear relationship between heat production and proportion of acetic acid in the rumen fluid by infusing two mixtures varying in the proportion of acetic to propionic acid. However, this assertion was based on a miscalculation between molar and energy proportions. Nonetheless, findings presented by Blaxter (1962) and Agricultural Research Council (1965) do demonstrate a general relationship between molar proportions of acetic acid and dietary utilization of ME. There were, however, a couple of problems in accepting a causal basis for this relationship. First if the problem was due to inefficient utilization of acetic acid or so-called futile cycling then a curvilinear relationship should be expected between utilization and acetic acid production, since there was no evidence for inefficient utilization when the supply of C₃ or oxaloacetate was adequate. Second since butyric acid is also utilized as C₂, a similar efficiency to acetic acid might have been expected. Following these observations a great many large-scale experiments were conducted to test these ideas. Ørskov & Allen (1966*a,b,c*) and Ørskov *et al.* (1966) conducted comparative slaughter experiments with lambs given dietary supplements of acetic, propionic and butyric acids. They found no differences at all in energy retention between the different salts added at a level of 15% of ME. In one experiment there was some evidence that when acetate was added to a low-roughage diet it was utilized better than when added to a high-roughage diet, thus providing some evidence of curvilinearity. Similar results were shown by Bull *et al.* (1970) using triacetin. Hovell *et al.* (1976), again using VFA salts, showed some evidence of curvilinearity with levels of acetate incorporation, but otherwise no consistent difference in utilization between acetate and

propionate. Ørskov *et al.* (1969) infused acetic and propionic acids into the rumen of dairy cows and found no difference in heat production but differences in the partition of energy between tissue and milk. Tyrrell *et al.* (1979) observed a slightly more efficient utilization of acetic acid when it was infused into the rumen of cows receiving a low- rather than a high-roughage diet. Jenkins & Thonney (1988) found a higher empty-body gain when a large supplement of propionate salt was given. This led to high levels of propionic acid in the peripheral circulation which is known to elicit insulin release (Bassett, 1974).

PROBLEMS OF SUPPLEMENTATION

It has generally been observed that levels of VFA infusion above 0.15 of ME created problems of inappetence in the case of VFA salts and digestive problems in the case of acid infusions. This low level of supplementation created difficulties of interpretation. First, as there is a large between-animal variability in intake it is sometimes difficult to detect the effect of a supplement providing 0.15 of energy and even more difficult when the experiment is designed to show possible differences between different VFA. Second, the assumption is made that the salt or acid infusion had no effect on the digestion or utilization of the feed to which it was added. The third difficulty is apparent particularly when acetic acid or acetate is added even at 15% of ME to diets already generating a high proportion of acetic acid. In Table 2 a series of molar proportions are converted to energy proportions and it can be seen that acetic acid due to its low energy value per mole assumes much less importance when converted to energy proportion. In general a molar percentage of 75% of acetic acid is the extreme found even with very-poor-quality roughages. It will then be understood that if 15% of ME is added in the form of acetate or acetic acid, molar proportions are soon reached which are outwith conditions occurring in practice. This criticism of supplementation, however, also applies to the original observation of Armstrong and colleagues. Intravenous infusion of acetate or propionate has also been attempted but since propionic acid is generally metabolized in the liver and elicits an insulin response if it enters the peripheral circulation it is not possible to relate such results to normal diets (Eskeland *et al.* 1973).

Table 2. *Molar proportions and equivalent energy proportions for different mixtures of volatile fatty acids and efficiency of utilization above maintenance (K_f) determined with intragastric nutrition of lambs (Ørskov *et al.* 1979)*

| | Molar proportions (mmol/mol) | | | | |
|-------------------------|------------------------------|------|------|------|------|
| Acetic acid | 850 | 750 | 650 | 550 | 450 |
| Propionic acid | 50 | 150 | 250 | 350 | 450 |
| Butyric acid | 100 | 100 | 100 | 100 | 100 |
| | Energy proportions (J/kJ) | | | | |
| Acetic acid | 720 | 590 | 480 | 390 | 300 |
| Propionic acid | 70 | 210 | 330 | 430 | 530 |
| Butyric acid | 210 | 200 | 190 | 180 | 170 |
| Determined K_f values | 0.59 | 0.61 | 0.61 | 0.57 | 0.64 |

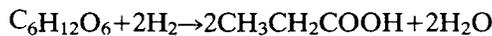
Table 3. *Effect of grain processing on proportions of volatile fatty acids (mmol/mol) and feed utilization by groups of eight early-weaned lambs (Ørskov et al. 1974)*

| Type and form of grain | Acetic acid | Propionic acid | Higher acid | Digestibility | Food conversion (kg dry matter/kg gain) | Live w gain (g/d) |
|------------------------|-------------|----------------|-------------|---------------|---|-------------------|
| Whole barley | 525 | 301 | 174 | 81.1 | 2.75 | 340 |
| Ground barley | 450 | 453 | 97 | 77.2 | 2.79 | 347 |
| Whole oats | 650 | 186 | 164 | 69.9 | 3.07 | 241 |
| Ground oats | 532 | 375 | 93 | 67.5 | 3.33 | 238 |

Although the evidence for no difference in efficiencies of utilization of the VFA is overwhelming, commercial companies competed to find products which could decrease acetate and increase the proportion of propionic acid in the rumen. Here it must be pointed out that if the assessment of ME utilization was based on a single factor of converting digestible energy to ME then some relationship between utilization and proportion of acetic acid would be found; on grounds of stoichiometry the disposal of hydrogen to produce methane is positive while acetic acid is produced



while the production of propionic acid would act as a H sink



and reduce CH_4 production. Thus, some relationship between utilization and digestible energy can be expected to relate to proportion of acetic acid due to the implication of CH_4 production (Hungate, 1966; Ørskov *et al.* 1968). Such differences are, however, small and difficult to detect. It is, for instance, possible to change the type of fermentation by cereal processing without any detectable change in feed utilization. For example, Table 3 shows the effect of feeding whole or processed oats or barley to early-weaned lambs. In spite of large changes in type of fermentation there were no significant differences in digestibility and feed utilization.

With the development of the technique of intragastric nutrition (Ørskov *et al.* 1979; MacLeod *et al.* 1982) it became possible to nourish ruminants totally on VFA infused into the rumen and protein to the abomasum. This alleviated the problems referred to earlier, on control of VFA composition absorbed with respect to basal diet. A large-scale trial involving forty-eight cannulated sheep was carried out with a wide range in VFA proportion covering almost any conceivable composition of VFA, and even unphysiological ones with molar percentages of propionic acid varying from 5 to 45% and acetic acid from 45 to 85%. The heat production was measured both at an estimated maintenance energy input (450 kJ/kg $\text{W}^{0.75}$) and at twice the maintenance energy input. The calculated efficiencies of utilization above energy maintenance (K_f) are given in Table 2. As can be seen there was no consistent difference in utilization over the large spectrum of VFA proportions tested, the average utilization of VFA being in the region of 60%. It is interesting that almost the same efficiency of utilization was observed by caecal infusion of VFA or fermentable carbohydrates in pigs reported by Gadeken *et al.* (1989) and Muller *et al.* (1989) respectively.

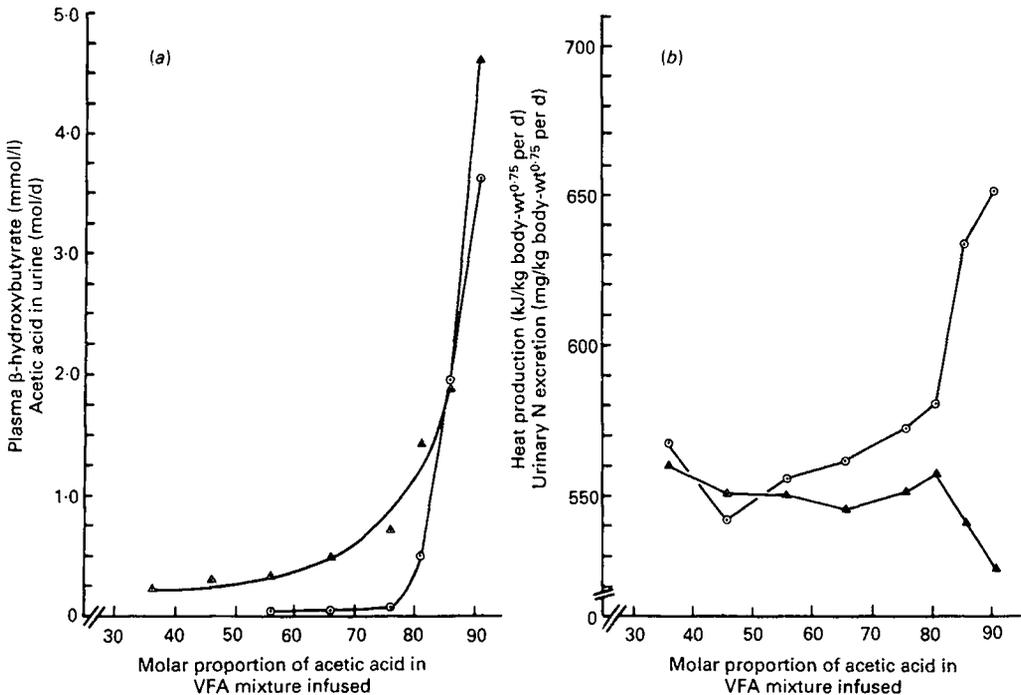


Fig. 1. The effect of molar proportions of volatile fatty acids (VFA) infused into the rumen (a) on plasma β -hydroxybutyrate (Δ) and excretion of acetic acid in the urine (\circ), and (b) on heat production (Δ) and urinary nitrogen excretion (\circ) of four Friesian steers.

Recently, trials with cattle have further substantiated the results using indirect open-circuit calorimetry to measure heat production. Here, the molar percentage of acetic acid was varied from 30 to 92. The molar percentage of butyric acid was held constant at 8. The molar percentage of propionic acid varied from 0 to 60. Still higher proportions of propionic acid resulted in several metabolic problems including haemolysis and blood in urine. The most important results are presented in Fig. 1 (E. R. Ørskov and N. A. MacLeod, unpublished results). The level of energy input was kept here at $675 \text{ kJ/kg } W^{0.75}$ or equal to an estimated 1.5 times maintenance energy expenditure. It can be seen that at about 75–80 molar % of acetic acid in the infusate there is an increase in nitrogen excretion which suggests a deficiency of gluconeogenic compound resulting in some oxidation of amino acids in the process of protein turnover. This is followed by an elevation in the blood concentration of β -hydroxybutyrate which indicates also glucose deficiency as it can be reduced to normal levels by infusion of small amounts of glucose. The metabolic crisis finally results in a reduction in heat production accompanied by an excretion of acetic acid in the urine. Thus, at the extreme acetic acid proportions, far beyond physiological levels, the animal does not resort to wasteful oxidation of acetate or futile cycling but excretes acetic acid in the urine.

The biochemical evidence for acetate cycling or cycling between acetate and acetyl-CoA which could theoretically lead to heat losses when the utilization was blocked or inhibited is also very limited. Crabtree *et al.* (1987) showed convincingly in sheep muscle that the rate of cycling was very limited. Even with a twofold increase in acetate concentration the heat produced in that reaction could account for no more than 0.5% of

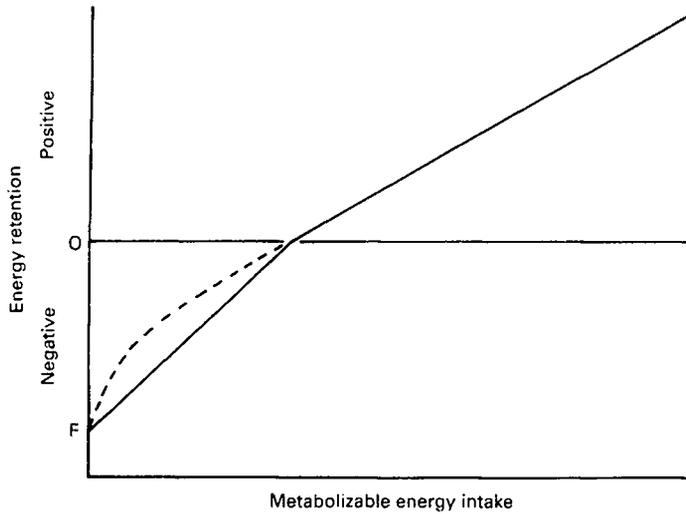


Fig. 2. The effect of energy input on efficiency of energy utilization below and above energy maintenance. (---) The probable course of events. F, fasting heat production.

basal metabolic rate. In spite of little or no evidence that a wasteful utilization of acetate was occurring in ruminant tissue, Ortigues *et al.* (1989), for instance, interpreted live weight responses to fish meal in lambs given straw-based diets as being due to glucogenic precursors from fish meal causing a 'reduction in wasteful oxidation of acetate'.

PROBLEMS OF FASTING METABOLISM

In the foregoing section it was argued that evidence for inefficient utilization of ME from roughages being a result of the high proportion of acetic acid was very sparse. Consequently one should seek an alternative explanation. First of all the concept of differences in the so-called efficiency for maintenance (K_m) and K_f efficiency for production, will be dealt with.

Determination of the efficiency for utilization of ME below energy maintenance depends on measurement of fasting metabolism in animals. This measurement has been criticized on several grounds in recent years (see Marston, 1948; Webster *et al.* 1974). In addition Koong *et al.* (1985) and Burrin *et al.* (1989) showed clearly that the numerical value of fasting metabolism depended to a large extent on the feeding level received before fasting, and that these differences could largely be attributed to differences in organ size such as liver and intestine, etc. Another problem with fasting metabolism is that it gives rise to a substantial increase in N excretion (about 40% above basal levels) indicating protein oxidation due to deficiency of glucose precursors. In addition the blood β -hydroxybutyrate is elevated. Based on these observations Ørskov (1982) suggested that it was conceptually incorrect to use fasting metabolism as this represented the metabolism of a glucose-deficient diet, i.e. body fat, to estimate the efficiency of utilization of nutritionally-balanced diets. He suggested the hypothesis depicted in Fig. 2 in which the accepted concept according to Agricultural Research Council (1965, 1980) is shown; the more likely situation is also indicated. Evidence to support this hypothesis

Table 4. *Effect of maintenance energy expenditure and total heat production in steers on the efficiency of energy retention above maintenance (K_f)*

| Diet | Metabolizable energy intake (MJ/d) | Heat production (MJ/d) | K_f assuming maintenance energy (MJ/d) of: | | |
|------------------|------------------------------------|------------------------|--|----|----|
| | | | 30 | 35 | 40 |
| High concentrate | 60 | 45 | 50 | 60 | 75 |
| High roughage | 60 | 50 | 33 | 40 | 50 |

was recently presented by KuVera *et al.* (1989). They showed that glucose infused at low levels into the abomasum of fasting steers did not result in an increase in heat production, but in some cases even a decrease, and always a decrease in urinary energy due mainly to reduction in excretion of urinary N to levels similar to basal N excretion. KuVera *et al.* (1987) also noted that a mixture of VFA given at about 0.2% of energy maintenance was sufficient to reduce fasting N excretion to that observed at energy maintenance. Thus, it seems that the concept of differences in utilization of ME below and above energy maintenance needs to be reconsidered. It can at least be postulated from the evidence that assessment of energy utilization in response to energy supply should, perhaps as a starting point, use about one-third of an estimated energy maintenance rather than fasting so that the requirement for glucose precursors is likely to be met. Similar conclusions could be drawn from the results of Gill *et al.* (1989).

PROBLEMS OF DIFFERENCES IN UTILIZATION BETWEEN FIBROUS ROUGHAGES AND CONCENTRATE

In the previous section evidence was given showing that the differences in utilization of ME from concentrate and roughage diets appeared not to be related to the composition of absorbed nutrients, and that the differences observed had been exaggerated by allocating the differences to K_f . It was also argued that differences between K_f and K_m were dubious. It follows, therefore, that the century-old realization of differences in utilization of ME between such diets still needs an explanation. Having, so to speak, disposed of differences between K_m and K_f it is necessary to consider actual differences in heat production from animals receiving roughage or concentrate diets. It will be appreciated that if the concept of K_m and K_f is maintained and if it is assumed that differences in K_m are small then differences in K_f could be very much dependent on the production level achieved and on the point determined as the maintenance energy level. For instance, if heat production in cattle is either 45 or 50 MJ/d when 60 MJ ME is given and the estimated maintenance energy need is either 30, 35 or 40 MJ energy the corresponding values for K_f can be calculated as in Table 4. It can be seen that relatively small changes in heat production, here 10%, can result in large differences in the value for K_f . It can also be seen that both K_f itself and the differences between diets depend on the maintenance level. If the maintenance need is not determined in the experiments reported it becomes possible to be somewhat subjective as to the desired results. Such problems of errors and subjectivity of interpretation was recently discussed in an interesting letter to the editor by Graham (1986) and also dealt with in some detail by Hovell *et al.* (1976).

ACTIVITY ASSOCIATED WITH FOOD CONSUMPTION

It is perhaps to be expected that if the increased heat production was associated with activity to do with eating and rumination, the differences in utilization would decrease with increasing feeding level since time spent eating and ruminating is not necessarily increased in proportion. Adam *et al.* (1984) showed that the cost of eating was related to time spent eating and not to dry matter consumed. This is, indeed, supported in work reported by Flatt *et al.* (1967) who in dairy cows did not observe differences in heat production between diets varying from 200 to 600 g roughage/kg in the form of lucerne (*Medicago sativa*) hay. Yet comparisons between roughage and concentrate diets are often made at a low level of feeding, if for no other reason than that a high level of intake of pure-roughage diets is difficult to achieve.

CAN THE DIFFERENCES BE EXPLAINED BY COST OF EATING AND RUMINATING?

If the maximum time spent eating and ruminating is assumed to be about 8 h for each activity when long roughages or grass diets are consumed, and 1 h for each activity when pelleted diets are given, the differences in energy cost can be estimated. With cattle Holmes *et al.* (1978) and Adam *et al.* (1984) observed the cost of eating to average 32 J/kg live weight per min. There is very little work reported on the cost of rumination in cattle, but KuVera *et al.* (1989) recently recorded a tentative value of 9.3 J/kg live weight per min. While the physical work associated with the two activities is likely to be similar, the blood flow etc., to the viscera is increased during eating and probably accounts for the higher observed cost of eating above rumination.

Steers weighing 300 kg and receiving long roughage would expend 6 MJ/d on the activities of eating and ruminating compared to 0.8 MJ/d for the pelleted diets. Thus, the differences in K_f for concentrates and roughage can easily be explained by these activities (Table 4). Whether standing time is also increased when longer time is spent eating is uncertain. If it is, this would further lower the apparent efficiency of roughage utilization as the cost of standing relative to laying is about 10 J/kg live weight per min (KuVera *et al.* 1989). At a low level of production (e.g. 0–600 g gain/d) such differences would contribute to substantial differences in the rate of live-weight gain. For example, if the energy value of gain is 15 MJ/kg (Agricultural Research Council, 1980) then a higher heat production with roughages of 5 MJ/d could amount to a reduced live-weight gain of almost 200 g/d.

Kellner (1926) used the term 'Verdaunungsarbeit' or work of digestion to explain differences in utilization between concentrate and fibrous roughage diets. If with this we understand cost of eating and rumination, then Kellner's (1926) observations were probably correct and all we have done during almost a century is to confirm his deduction that efficiency of utilization of absorbed energy would be increased if the 'Verdaunungsarbeit' or work of digestion were reduced, for example, by grinding and pelleting long roughages to reduce time of eating and rumination. Evidence for this can be found in the review and summary by Agricultural Research Council (1980). They showed no differences in K_f between concentrates and roughages when the roughages were ground and pelleted. However, while grinding and pelleting is costly and generally not economic for roughages. It also has the problem that outflow from the rumen would be increased

due to low particle size so that digestibility and, thus, ME concentration in the feed could be decreased.

IMPORTANCE OF VFA IN FEED EVALUATION AND ANIMAL NEED

The knowledge of VFA production in the rumen has contributed greatly to the qualitative understanding of rumen fermentation and use of energy by the host animal. To use information on VFA produced from a given feed as a contributor to feed evaluation seems of dubious value. First, the type of fermentation produced from a feed is by no means constant (see Table 3); among other aspects it varies with rumen pH and, thus, with eating and salivation behaviour of individual animals. In addition, due to different absorption rates the VFA proportions found in the rumen most often do not represent the proportions in which VFA are produced (MacLeod & Ørskov, 1984). Second, as can be seen from Table 3 and Fig. 1, over the physiological range of VFA proportions (450–750 mmol acetate/mol VFA) the animal metabolism is similar. An exception appears to be that of dairy cows which respond to acetate proportions of less than about 0.50–0.55 and propionate proportions greater than 0.35–0.45 by decreasing milk energy and increasing body energy accretion. This is particularly important when large amounts of concentrate containing starch or soluble sugars are fed twice daily and when the starchy feeds are overprocessed (see Table 3). In this instance, propionate absorption may exceed the ability of the liver to metabolize it so more enters the peripheral blood. High concentrations of propionic acid elicit an insulin response which then changes the proportion of energy for milk relative to body tissue production. Such knowledge can be used to aid general management strategies, or to identify specific problems in particular situations. However, information on the type of fermentation to expect from feeds is imprecise, subject to large between-animal variation and is so influenced by level and pattern of feeding that satisfactory prediction models currently seem unlikely. Furthermore, as the present paper has attempted to show, variation in the supply of different VFA within the normal range has no effect on net utilization so that even if it were possible to describe VFA availability to the animal, such information is unlikely to add precision to feed evaluation. On the other hand, time spent eating, rumination time, degradation rate and outflow rate are important factors in determining feed intake and feed utilization in ruminants and better knowledge of these factors is likely to offer more to animal production than concern about VFA proportions.

REFERENCES

- Adam, I., Young, B. A., Nicol, A. M. & Degen, A. A. (1984). Energy cost of eating in cattle given diets of different form. *Animal Production* **38**, 53–56.
- Agricultural Research Council (1965). *The Nutrient Requirements of Farm Livestock*. No. 2, Ruminants. London: H.M. Stationery Office.
- Agricultural Research Council (1980). *The Nutrient Requirements of Ruminant Livestock*. Slough: Commonwealth Agricultural Bureaux.
- Armstrong, D. G. & Blaxter, K. L. (1957a). The heat increment of steam volatile fatty acids in fasting sheep. *British Journal of Nutrition* **11**, 247–272.
- Armstrong, D. G. & Blaxter, K. L. (1957b). The utilization of acetic, propionic and butyric acids by fattening sheep. *British Journal of Nutrition* **11**, 413–425.
- Armstrong, D. G., Blaxter, K. L. & Graham, N. McC. (1957). The heat increment of mixtures of steam volatile fatty acids in fasting sheep. *British Journal of Nutrition* **11**, 392–408.

- Armstrong, D. G., Blaxter, K. L., Graham, N. McC. & Wainman, F. W. (1958). The utilization of the energy of two mixtures of steam volatile fatty acids by fattening sheep. *British Journal of Nutrition* **12**, 177–188.
- Baker, F. (1942). Microbial factors in the digestive assimilation of starch and cellulose in herbivora. *Nature* **150**, 479.
- Barcroft, J., McAnally, R. A. & Phillipson, A. T. (1944). Absorption of acetic, propionic and butyric acids from the alimentary canal. *Biochemical Journal* **38**, iii.
- Bassett, J. M. (1974). Diurnal patterns of plasma insulin, growth hormone, corticosteroid and metabolite concentrations in fed and fasted sheep. *Australian Journal of Biological Science* **27**, 167–181.
- Blaxter, K. L. (1962). *The Energy Metabolism of Ruminants*. London: Hutchinson.
- Bull, L. S., Reid, J. T. & Johnson, D. R. (1970). Energetics of sheep concerned with the utilization of acetic acid. *Journal of Nutrition* **100**, 262–276.
- Burrin, D. G., Ferrell, C. L. & Britton, R. A. (1989). Effect of feed intake of lambs on visceral organ growth and metabolism. In *Proceedings of the 11th Symposium on Energy Metabolism*. European Association of Animal Production Publication no. 43, pp. 103–106 [Y. van der Honing and W. H. Close, editors]. Wageningen, The Netherlands: Pudoc.
- Crabtree, B., Barr, S. A., Anderson, S. E. & MacRae, J. C. (1987). Measurement of the rate of substrate cycling between acetate and acetyl-CoA in sheep muscle *in vivo*: effects of infusion of acetate. *Biochemical Journal* **243**, 821–827.
- Eskeland, B., Pfander, W. H. & Preston, R. L. (1973). Utilization of volatile fatty acids and glucose for protein deposition in lambs. *British Journal of Nutrition* **29**, 347–355.
- Flatt, W. P., Moe, P. W., Moore, L. A., Hooven, N. W., Lehman, R. P., Ørskov, E. R. & Hemken, R. W. (1967). Experimental design, ration composition, digestibility data and animal performance during energy balance trials. In *Proceedings 4th Conference on Energy Metabolism*. European Association of Animal Production Publication no. 12, pp. 221–234 [K. L. Blaxter, J. Kielaowski and C. Thorbek, editors]. Newcastle upon Tyne: Oriol Press Ltd.
- Gadeken, D., Breves, G. & Oslage, H. J. (1989). Efficiency of energy utilization of intracaecally infused volatile fatty acids in pigs. In *Proceedings of the 11th Symposium on Energy Metabolism*. European Association of Animal Production Publication no. 43, pp. 115–118 [Y. van der Honing and W. H. Close, editors]. Wageningen, The Netherlands: Pudoc.
- Gill, M., Cammell, S. B., Haines, M. J., France, J. & Dhama, M. S. (1989). Energy balance in cattle offered a forage diet at sub-maintenance levels. In *Proceedings of the 11th Symposium on Energy Metabolism*. European Association of Animal Production Publication no. 43, pp. 300–303 [Y. van der Honing and W. H. Close, editors]. Wageningen, The Netherlands: Pudoc.
- Graham, N. McC. (1986). Energetic efficiency and amino acid supply in ruminants. *British Journal of Nutrition* **56**, 315.
- Holmes, C. W., MacLean, N. A. & Lockyer, K. J. (1978). Changes in the rate of heat production of calves during grazing and eating. *New Zealand Journal of Agricultural Research* **21**, 107–112.
- Hovell, F. D. DeB., Greenhalgh, J. F. D. & Wainman, F. G. (1976). The utilization of diets containing acetate salts by growing lambs as measured by comparative slaughter and respiration calorimetry, together with rumen fermentation. *British Journal of Nutrition* **35**, 343–363.
- Hungate, R. E. (1966). *The Rumen and its Microbes*. New York: Academic Press.
- Jenkins, T. C. & Thonney, M. L. (1988). Effect of propionate level in a volatile fatty acid salt mixture fed to lambs on weight gain, body composition and plasma metabolites. *Journal of Animal Science* **66**, 1028–1035.
- Kellner, O. (1926). *The Scientific Feeding of Animals*. London: Duckworth.
- Koong, L. J., Ferrell, C. L. & Nienaber, J. A. (1985). Assessment of interrelationships among levels of intake and production, organ size and fasting heat production in growing animals. *Journal of Nutrition* **115**, 1383–1390.
- KuVera, J. C., MacLeod, N. A. & Ørskov, E. R. (1989). Energy exchanges of cattle nourished by intragastric infusion of nutrients. In *Proceedings of the 11th Symposium on Energy Metabolism*. European Association of Animal Production Publication no. 43, pp. 271–274 [Y. van der Honing and W. H. Close, editors]. Wageningen, The Netherlands: Pudoc.
- KuVera, J. C., Ørskov, E. R., Hovell, F. D. DeB. & MacLeod, N. A. (1987). Effect of small amounts of glucose and different volatile fatty acid mixtures on fasting N excretion in lambs. *5th International Symposium on Protein Metabolism and Nutrition*. European Association of Animal Production Publication no. 35, p. 94 [S. Poppe, editor]. Rostock, DDR: Wissenschaftliche Zeitschrift der Wilhelm-Pieck Universität Rostock.
- McClymont, G. L. (1952). Specific dynamic actions of acetic acid and heat increment of feeding in ruminants. *Australian Journal of Scientific Research* **5B**, 374.

- MacLeod, M. G., Jewitt, T. S. & Anderson, J. E. M. (1989). Responses of energy expenditure and retention to wide-ranging dietary concentrations and voluntary intakes of energy and protein in growing domestic fowl. In *Proceedings of the 11th Symposium on Energy Metabolism. European Association of Animal Production Publication no. 43*, pp. 195–199. Wageningen, The Netherlands: Pudoc.
- MacLeod, N. A., Corrigan, W., Stirton, R. A. & Ørskov, E. R. (1982). Intra-gastric infusion of nutrients in cattle. *British Journal of Nutrition* **47**, 547–552.
- MacLeod, N. A. & Ørskov, E. R. (1984). Absorption and utilization of volatile fatty acids in ruminants. *Canadian Journal of Animal Science* **64**, Suppl., 354–355.
- Marston, H. R. (1948). Energy transactions in the sheep. 1. The basal heat production and heat increment. *Australian Journal of Scientific Research* **1B**, 95–123.
- Morton, J. C. (1855). *A Cyclopaedia of Agriculture*. London: Blackie & Son.
- Muller, H. L., Kirchgeszner, M. & Roth, F. X. (1989). Energy utilization of intracaecally infused carbohydrates and casein in sows. In *Proceedings of the 11th Symposium on Energy Metabolism. European Association of Animal Production Publication no. 43*, pp. 123–126 [Y. van der Honing and W. H. Close, editors]. Wageningen, The Netherlands: Pudoc.
- Ørskov, E. R. (1982). Effect of volatile fatty acid composition and protein on energy utilization and milk composition on cows sustained by intra-gastric nutrition. In *Energy Metabolism of Farm Animals*, pp. 123–126 [A. Ekern and F. Sundstøl, editors]. Aas: Agricultural University of Norway.
- Ørskov, E. R. & Allen, D. M. (1966a). Utilization of salts of volatile fatty acids by growing sheep. 1. Acetate, propionate and butyrate as sources of energy for young growing lambs. *British Journal of Nutrition* **20**, 295–305.
- Ørskov, E. R. & Allen, D. M. (1966b). Utilization of salts of volatile fatty acids by growing sheep. 2. Effect of stage of maturity and hormone implantation on the utilization of volatile fatty acid salts as sources of energy for growth and fattening. *British Journal of Nutrition* **20**, 509–517.
- Ørskov, E. R. & Allen, D. M. (1966c). Utilization of salts of volatile fatty acids by growing sheep. 4. Effects of type of rumen fermentation of the basal diet on the utilization of salts of volatile fatty acids for nitrogen retention and body gains. *British Journal of Nutrition* **20**, 519–532.
- Ørskov, E. R., Flatt, W. P. & Moe, P. W. (1968). A fermentation balance approach to estimate extent of fermentation and efficiency of volatile fatty acid formation in ruminants. *Journal of Dairy Science* **51**, 1429–1435.
- Ørskov, E. R., Flatt, W. P., Moe, P. W., Munson, A. W., Henken, R. W. & Katz, I. (1969). The influence of ruminal infusion of volatile fatty acids on milk yield and composition and energy utilization by lactating cows. *British Journal of Nutrition* **23**, 443–453.
- Ørskov, E. R., Fraser, C. & Gordon, J. G. (1974). Effect of processing of cereals on rumen fermentation, digestibility, rumination time and firmness of subcutaneous fat. *British Journal of Nutrition* **32**, 59–69.
- Ørskov, E. R., Grubb, D. A., Wenham, W. & Corrigan, W. (1979). The sustenance of growing and fattening ruminants by intra-gastric infusion of volatile fatty acids and protein. *British Journal of Nutrition* **41**, 553–558.
- Ørskov, E. R., Hovell, F. D. DeB. & Allen, D. M. (1966). Utilization of salts of volatile fatty acids by growing sheep. 2. Effect of stage of maturity and hormone implantation on the utilization of volatile fatty acid salts as sources of energy for growth and fattening. *British Journal of Nutrition* **20**, 307–315.
- Ørskov, E. R. & Oltjen, R. R. (1967). Influence of carbohydrate and nitrogen sources on the rumen volatile fatty acids and ethanol of cattle fed purified diets. *Journal of Nutrition* **93**, 222–228.
- Ortigueas, I., Smith, T., Oldham, J. D. & Gill, M. (1989). The effects of fishmeal on growth and calorimetric efficiency in heifers offered straw-based diets. In *Proceedings of the 11th Symposium on Energy Metabolism. European Association of Animal Production Publication no. 43*, pp. 65–68 [Y. van der Honing and W. H. Close, editors]. Wageningen, The Netherlands: Pudoc.
- Tyler, C. (1975). Albrecht Thae'r's hay equivalents: fact or fiction? *Nutrition Abstracts and Reviews* **45**, 1–11.
- Tyrrell, H. F., Reynolds, P. J. & Moc, P. W. (1979). Effect of diet on partial efficiency of acetate use for body tissue synthesis by mature cattle. *Journal of Animal Science* **48**, 598–606.
- Webster, A. J. F., Brockway, J. M. & Smith, J. S. (1974). Prediction of the energy requirements for growth in beef cattle. 1. The irrelevance of fasting metabolism. *Animal Production* **19**, 127–140.