

DAIRY PRODUCTION

Energy Metabolism of Dairy Cattle

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ABSTRACT

Energy metabolism research during the past 25 yr has resolved many uncertainties of energy use by lactating cows. Use of metabolizable energy for milk production essentially is unaffected by milk yield but is slightly influenced by its source. Estimates of efficiency of use for milk production (60 to 64%) are lower than earlier estimates (69 to 70%) primarily because of lower maintenance costs. Efficiency of metabolizable energy for body gain is higher in lactating (75%) than nonlactating (60%) cows. Use of body tissue energy for milk production is about 82% efficient. End products of digestion contribute to variation in efficiency of fattening and in partition of energy between milk and body gain in the lactating animal.

Energy use in the growing animal is influenced by composition of tissue gained and composition of the diet. Energetic efficiency of protein deposition is apparently much lower than that of fat deposition. A substantial part of the lower efficiency of protein deposition is related to energy costs of protein turnover.

Incomplete digestion of mixed diets at high intake by lactating cows and methods to predict energy partition are serious practical problems. In the short term, improved methods to predict intake effects on metabolizable energy of mixed diets will increase accuracy of diet formulations. In the longer term, methods to predict quantities of nutrients absorbed from the gut will permit a more flexible and accurate method of evaluating diets and predicting animal performance.

INTRODUCTION

In 1955 Blaxter and Graham (23) stated, "In the period since Kuhn and Kellner, the consolidation and extension of the net-energy principle, which might have been expected to have occurred as a result of such brilliant work, has, with several notable exceptions, not taken place. Instead, the period has been characterized by polemical argument rarely illuminated by an experiment and hardly ever by a calorimetric trial. Kellner's original work has been recalculated, re-expressed and, in short, sucked dry. . . . Clearly, in the assessment of the nutritive value of foods, the future must involve extensive experimentation and measurement rather than the almost complete dependence on pioneer evidence which has characterized the past 50 years."

Progress has been considerable in the field of energy metabolism since those words were written. Efficiency of energy use and energy requirements have been identified more precisely. Progressively more intensive experimentation has described physiological and biochemical bases for an increasing part of the variation in energy use. Although energy metabolism has been studied at many levels from specific biochemical transformations to whole populations of animals, this review will deal primarily with energy use in the whole animal. Aspects of energy metabolism that relate to the effectiveness with which dairy cattle consume a variety of diets for growth, reproduction, and production of milk will be considered.

Energy Terminology

In the discussion, terminology is that in general use. Digestible energy (DE) is gross intake of energy minus energy voided in the feces. Metabolizable energy (ME) is DE minus energy in methane and urine. Generally ME is an expression of the amount of energy available for metabolism by the animal, although ME includes some energy, e.g., heat of fermentation,

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not available for metabolism and does not include some energy, e.g., urine energy, which is a product of metabolism. The terms for the partial efficiency of ME used for maintenance, lactation, protein gain, fat gain, and gain in total tissue energy are k_m , k_l , k_p , k_f , and k_g . Heat increment (HI) is the increase in total production of heat associated with an increase in the consumption of food.

Energy units are calories (cal), kilocalories (kcal = 1000 cal), or megacalories (Mcal = 1000 kcal) for the convenience of the US reader although many of the original papers included the joule (1 cal = 4.184 J; $J = M^2 \cdot kg \cdot s^{-2}$).

The Situation 25 Years Ago

Reviews by Blaxter (14, 15) and Reid (77, 78) and major texts by Blaxter (17) and Kleiber (47) summarized much of the work on energy metabolism of dairy cattle and present the most comprehensive descriptions of the energetics of dairy cattle available in their time. Earlier studies showed that lactation was more efficient than fattening. Reid (78) summarized the available calorimetry data and concluded that ME consumed in excess of maintenance was used to the extent of 69.3% for milk production and 58.0% for body increase and that both were relatively constant. Growth was thought to be more efficient than fattening. Energy from grains or concentrate feeds generally was accepted to be used more efficiently than energy of forages, especially for growing animals. This difference appeared to be related to the crude fiber content of the forage.

Considerable disagreement existed regarding the relationship between energy intake and energy balance (EB). Workers generally accepted that this relationship was curvilinear when data both above and below maintenance were included. Blaxter (15) emphasized the curvilinear relationship between food consumed and energy retention and indicated that this effect was at least in part from a decline in ME value with increased intake.

Although work had documented reduced digestibility by lactating cows in comparison with that of cows at maintenance intake, this effect was not accepted universally. Reid (78) emphasized the importance of reduced digestibility and increased body fattening by lactating cows at high feed intakes in ex-

plaining apparent diminishing returns in feeding trials with lactating cows.

Considerable uncertainty remained with regard to the effect of diet quality or rate of milk production or rate of growth on efficiency of use of ME and whether diet effects were similar for fattening and milk production. These questions were of fundamental importance in providing accurate and useful feeding standards.

The situation in 1956 can be understood most adequately by remembering that the limited calorimetric data on lactating cows at the time had been obtained many years previously. Those results, although important and although obtained with precise methods, were inadequate to answer important questions raised about factors affecting efficiency of energy use by cattle. Those results were recalculated and debated in the light of newer knowledge. New interpretations were put forward without benefit of facilities to test their validity. New experimentation was needed.

The Last 25 Years

The 25 yr since 1956 coincides almost exactly with an exceptional burst of experimentation in animal energetics. In the late 1950's, major commitments to support energy metabolism research were made in a number of countries including the US. The increase in rate of experimentation with lactating cows can be appreciated from the fact that a total of 110 complete energy balance trials with 38 cows, including all replicates, had been completed in all of the laboratories in the world before 1961 (34). Since that time the results of 806 balance trials with lactating cows have been published from the Beltsville laboratory alone. To coordinate the increased research activity and to share research plans and results, an International Symposium on Energy Metabolism was held in Copenhagen in 1958 under the sponsorship of the European Association of Animal Production (EAAP). Succeeding symposia, held every 3 yr, have provided a continuing focus for energy metabolism research. The proceedings of these symposia, published by the EAAP, document a substantial part of the energy metabolism research with farm animals during the last 25 yr (Table 1).

The symposia in 1958 and 1961 dealt largely

TABLE 1. Symposia on energy metabolism sponsored by the European Association of Animal Production (EAAP).

1st	Symposium on Energy Metabolism. Principles, Methods, and General Aspects. Copenhagen, Denmark. 15–19 September 1958. Publ. by EAAP (Publ. No. 8) and Statens Husdyrugsudvalg, Copenhagen. Grete Thorbek and H. Aersoe, ed.
2nd	Symposium on Energy Metabolism. Methods and Results of Experiments with Animals. Wageningen, the Netherlands. 11–15 September 1961. EAAP Publ. No. 10. E. Brouwer and A.J.H. van Es, ed.
3rd	Symposium. Troon, Scotland. May 1964. Energy Metabolism. Publ. by Academic Press, New York and London. 1965. K. L. Blaxter, ed. EAAP Publ. No. 11.
4th	Symposium. Energy Metabolism of Farm Animals. Warsaw, Poland. September 1967. Publ. by Oriol Press, Newcastle upon Tyne, England. 1969. K. L. Blaxter, J. Kielanowski and Grete Thorbek, ed. EAAP Publ. No. 12.
5th	Symposium. Vitznau, Switzerland. September 1970. Energy Metabolism of Farm Animals. Juris Verlag, Zurich. A. Schurch and C. Wenk., ed. EAAP Publ. No. 13.
6th	Symposium. Hohenheim, B.D.R. September 1973. Energy Metabolism of Farm Animals. Publ. by Universitat Hohenheim Dokumentationsstelle. 1974. K. H. Menke, H. J. Lantzsck, and J. R. Reichl, ed. EAAP Publ. No. 14.
7th	Symposium. Vichy, France. September 1976. Energy Metabolism of Farm Animals. Publ. by G. de Bussac, Clermont-Ferrand. M. Vermorel, ed. EAAP Publ. No. 19.
8th	Symposium. Cambridge, England. September 1979. Energy Metabolism. Publ. by Butterworths, London. 1980. EAAP Publ. No. 26. L. E. Mount, ed.

with methodology: construction of respiration chambers, techniques of gas analysis, and potential errors in energy balance measurements. Succeeding symposia dealt increasingly with presentation of results of animal experiments, discussion of interpretations of energy balance measurements, and proposals for application of findings in practice including discussions on feed evaluation and feeding standards. More recent symposia have dealt progressively less with feed evaluation and increasingly with specific factors limiting or causing variation in energy use by farm animals including more intensive and physiological experimental approaches and newer methods of describing and interpreting data.

Major advances during this time have been in identifying undetected sources of variation in energy use, in developing quantitative descriptions of known sources of variation, and in developing recommendations for means of implementing knowledge of energetics in practical feeding systems.

Effects of Absorbed Nutrients

Energetic Efficiency. A major improvement in understanding the causes of variation in energy efficiency of animals fed different diets was the demonstration of Armstrong, Blaxter, and their coworkers (2, 3, 4, 6, 7) that the heat increment of mixtures of steam volatile fatty acids (VFA) was influenced greatly by the proportion of acetate in the fattening sheep but had less effect in sheep at maintenance. The energy of VFA infused singly into the rumen of fattening sheep was used with efficiencies of 32.9% for acetic acid, 56.3% for propionic acid, and 61.9% for butyric acid. Mixtures of VFA containing 75 and 25% acetic acid were used with 31.8 and 58.1% efficiency. Other studies showed a lower efficiency (54.5%) for glucose infused into the rumen than for that infused into the abomasum (71.5%) or jugular vein (72.8%). These studies indicated the importance of end products of digestion as opposed to nutrients consumed in influencing metabolic efficiency in ruminants.

These studies also suggested that variation in the efficiency with which specific end products of digestion are metabolized could account for a substantial part of the apparent difference between use of fibrous diets and that of diets containing large amounts of starch. The apparently low efficiency of acetate use in the fattening animal appeared to account for the depression in net energy of feeds high in fiber that had caused Kellner to introduce his "fiber correction factor" some 50 yr earlier.

More recent experiments indicated that the proportion of acetate of the rumen fermentation products may not explain fully the variation in use of ME and that in some circumstances acetate may be used efficiently for body gain. Tyrrell et al. (92) reviewed several experiments in which acetate apparently was used with relatively high efficiency for body gain and reported the results of calorimetric investigations with VFA infusion in mature cows. They found a difference from the nature of the basal diet in the partial efficiency of acetate for body gain. Use of ME from infused acetic acid was 27% for cows fed 100% hay and 69% for cows fed a diet of 30% hay.

Ørskov et al. (71) reported experiments in which lambs were sustained entirely by intragastric infusion of VFA, protein, minerals, and vitamins. For mixtures of VFA with 450 to 750 mmol acetate/mol, efficiency of use was 57 to 64%. They also recalculated the earlier data of Armstrong and Blaxter and reported that those results predicted an efficiency of 44 to 50%. Ørskov et al. (71) concluded that the effect of proportion of acetate on efficiency of energy use in growing animals was, in both instances, too small to be of practical significance.

The differences in the results of Tyrrell et al. (92) and Ørskov et al. (71) remain unresolved. A partial explanation may be found in the differing physiological state of the experimental animals. Data of Ørskov et al. (71) pertain to growing lambs depositing substantial protein whereas data of Tyrrell et al. (92) pertain to fattening in adult cows. Under some conditions acetate is used with low efficiency for fattening although some questions remain as to exactly what those conditions are. Also, acetate can be used efficiently in many instances, especially with high concentrate diets.

Partitioning of Energy. In only a relatively

few experiments has the use of individual VFA in lactation been investigated. Armstrong and Blaxter (5) in calorimetric studies infused mixtures of VFA, propionate, and acetate into the rumen of goats and found efficiencies of 71.4, 72.3, and 65.0% for lactation and 50.3, 52.3, and 44.4% for energy retention in the nonlactating body. Two particularly important findings were described in this paper. First, acetic acid infusion resulted in an increase in milk fat secretion and a decline in body fat deposition whereas with propionic acid infusion the reverse was true. Second, heat production was not changed. This second finding led them to the conclusion that energy retention in the adult ruminant is more efficient accompanied by the simultaneous process of milk secretion than in the nonlactating animal. The effect of VFA infusion on energy partition was noted with lactating cows by Ørskov et al. (70) in calorimetry experiments. Acetic acid infusion resulted in more milk energy and less gain of body energy than did propionic acid infusion. No difference in efficiency was found.

Effects on energy partition in lactation have been similar with changes in diet. Table 2 shows results of an experiment by Flatt et al. (36, 37) in which cows fed a 60:40 ratio of forage to concentrate produced more milk and lost more body tissue energy than cows fed a 20:80 ratio. The ratio of acetate to propionate in rumen VFA was also higher on the higher forage diet. In incremental studies of corn grain and beet pulp, Tyrrell et al. (89) found a greater percentage of the increase in energy balance (milk plus body tissue) was milk when beet pulp was added to the diet than when corn was added.

Sutton et al. (82) observed a reduction in proportion of acetate in rumen VFA and a reduction in milk fat yield by lactating cows when the percentage of concentrate was increased from 60 to 90%. At 90% concentrate, more starch reached the duodenum when corn grain was fed than when barley was fed. Live weight gain was also greater on the 90% corn diet, and milk yield was less. When corn replaced barley, the contribution of rumen digestion to overall digestion of energy was reduced considerably.

Effects of percentage concentrate, percentage of crude protein, and feed intake on partition of energy in lactating cows were studied by Journet et al. (44). The partition of energy into

TABLE 2. Influence of hay:grain ratio on partition of energy between milk and body tissue^a.

Item	Hay:grain ratio		
	60:40	40:60	20:80
Metabolizable energy (ME) intake, Mcal	36.12	36.42	34.87
Energy balance, Mcal	11.94	12.63	12.16
Milk energy, Mcal	13.94	13.17	10.41
Tissue energy, Mcal	-2.00	-.54	1.75
Milk fat, %	3.5	3.0	2.7
Acetic:propionic	3.32	2.57	2.00

^aData from Flatt et al. (36, 37).

milk decreased with increasing percentage of concentrate and decreasing percentage of milk fat. They also found that when energy intake varied around the requirement, about one-third of the increment of energy went into milk and two-thirds into body gain. No relationship between major VFA and milk production was found, but minor VFA (isobutyric, isovaleric, and valeric) in the rumen and crude protein in the diet were related positively to milk production.

Variation in the partial efficiency of use of the energy of VFA is considerably more important in fattening than in lactation whereas the effect in the growing animal is less certain. In the lactating cow, however, amounts of individual VFA absorbed from the gut can exert a significant effect on partition of energy between milk and body tissue. Effects of variation in amount and type of diet on energy efficiency and energy partition likely will not be explained satisfactorily without comprehensive knowledge of amounts of specific nutrients which are absorbed from the digestive tract.

Intake and Associative Effects

Intake Effects. Although intake effects on digestibility had been shown early in this century (29, 41), the practical significance of this effect by no means was accepted universally. The question was debated at a symposium in 1965 (26, 34, 76, 79). Brown (26) cited several instances in which intake effects on digestibility appeared to be conflicting. He concluded that although reduced digestibility had been detected at high intakes of diets

containing large amounts of concentrates in a number of experiments, additional information was needed. Flatt (34) reviewed the information then available on intake effects on ME value of diets and concluded that such an effect could not be documented. In a study of Beltsville data, Moe et al. (54) also found no intake effect on ME values of diets containing 40, 60, and 80% concentrate for lactating cows. Not until the 1970's did experimental results begin to appear to indicate in a relatively systematic fashion that ME values of diets for lactating cows were substantially lower than the same diets fed to nonlactating cows at a maintenance intake.

The significance of depression in digestibility of diets at high intakes by lactating cows was established firmly in extensive digestibility measurements by Moe et al. (56), Wagner and Loosli (103), and Ekern (31). Tyrrell and Moe (86) reviewed these and other studies and concluded that digestibility of normal diets by dairy cows was reduced by about 4% for each increase in intake equivalent to the amount needed for maintenance. They also concluded that the rate of reduction in digestibility was greater for diets containing larger percentages of concentrate although this effect was less pronounced for diets based on corn silage. Intake effects are as great with corn silage-based diets as with other forages when high percentages of grains are fed. At lower percentages of grain, however, intake effects are likely greater with corn silage diets than for those containing other forages.

In a more recent review, Tyrrell (85) cites evidence that the digestibility of corn silage-based diets is improved by addition of ground

limestone to the diet (109) or by increased protein content (74) and in alfalfa-based diets by increased protein content (88).

Tyrrell and Moe (87) reported a reduction in digestibility of corn silage-based diets supplemented with either corn or barley grains for lactating cows. The ME value of the barley diet was not influenced by intake whereas ME value of corn diet decreased at higher intakes. The decline in digestibility was similar for the two diets. The decline in digestibility of cellulose and hemicellulose fractions was about 8 percentage units and that of starch about 3 percentage units per unit of maintenance increase in intake.

Wheeler and Noller (110) reported that a part of the reduced digestibility of energy in lactating cows consuming corn grain and corn silage in large amounts was prevented by supplementation of the diet with 2.7% limestone. Supplementation with limestone increased fecal pH, reduced starch losses in the feces, and improved feed efficiency. They suggested that the increased fecal pH reflected a more favorable intestinal pH for activity of pancreatic alpha amylase.

Poos et al. (75) supplemented diets of lactating cows with either urea or soybean oil meal (SBOM). Urea was effective in improving digestibility of diets containing 11.6 to 13.6% crude protein when added in amounts to increase crude protein to 13 to 14.2%, but only SBOM was effective at higher percents. These results suggest that urea is effective in improving digestibility at higher crude protein in lactating cows than had been shown previously for nonproducing animals. Improved digestion of corn silage diets by lactating cows with supplemental urea also has been shown by Verite (101).

In experiments with lactating cows, Tyrrell and Moe (88) found a greater effect of intake on ME value at lower protein than at higher. When diets of alfalfa hay, corn, and SBOM were increased from 14 to 17% crude protein by substitution of corn with SBOM, both DE and ME were increased at high intakes. When protein was increased to 20%, however, only DE was increased. With corn silage diets, DE and ME were increased when crude protein was increased from 11 to 14% but not when crude protein was increased further to 17%. Addition of 2.5% limestone had no effect on digestibility

of energy in the latter experiment.

Associative Effects. Lactating cows usually are fed mixed diets rather than either all forage or all concentrate. The digestion of mixed diets at high intakes commonly is compared with digestion of the same diet at a maintenance intake to measure "intake effects". "Associative effect" refers to digestibility of a mixed diet different from that predicted from direct measurement of the forage and concentrate separately. Intake effects and associative effects are basically the same thing, the incomplete digestion of a mixed diet at a high intake. This is implicit in the established relationship between percentage of concentrate and intake effects. The importance of associative effects for lactating cows concerns additivity of the digestibility of component feeds in a mixed ration. In feed evaluation studies, the digestibility of concentrates typically is measured by difference with nonproducing animals, usually at a maintenance intake. Blaxter (20) summarized extensive studies of ME of diets containing 0 to 60% concentrate with sheep at maintenance and concluded that associated effects were not a practical problem. At higher feed intakes, however, associative effects can be real. An example is described by Joanning et al. (43), who found digestibility of a mixture of corn grain and corn silage was 11% less than that predicted from digestibility of the component feeds measured at high intakes. Intake effects on digestibility were observed on mixed diets, but not when either corn silage or corn grain was fed alone. These data are illustrated in Figure 1.

Intake effects have been expressed by Van Soest and coworkers (100) by describing "discount factors", which represent the reduction in digestibility of single feedstuffs when intake is increased by an amount equal to maintenance. They listed discounts for a large number of feeds from *in vivo* data and *in vitro* digestion rates and available passage rates. They concluded that feeds of higher cell wall content and of a low degree of lignification tend to have the largest discounts. They also stated that starch adds to the cell wall effect in cereal grains. The use of discount factors for individual feeds in computing the actual digestibility of mixed diets incorporates the susceptibility of component feeds to intake effects. Discount factors presented by Van Soest et al. (100),

RELATIONSHIP BETWEEN INTAKE EFFECT AND ASSOCIATIVE EFFECT

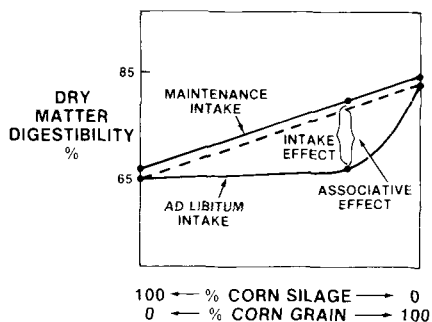
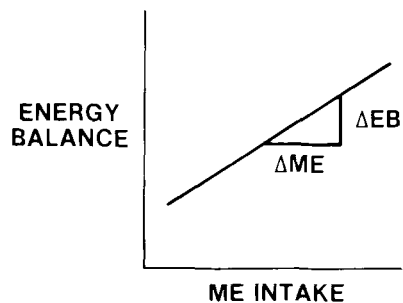


Figure 1. Data of Joanning et al. (43) show an associative effect between corn grain and corn silage at ad libitum intake but not at lower intake.

however, do not solve the problem of non-additivity or associative effects. A useful extension of the discount concept will be a procedure for estimating discounts for total mixed rations so that the interactions between fiber degradation and use of soluble carbohydrates can be incorporated.

Partial Efficiency Estimation

Efficiency is the ratio between energy in the product formed and the amount of energy



$$\text{METABOLIC EFFICIENCY} = \frac{\Delta EB}{\Delta ME} = k$$

$$k_l = \frac{\Delta \text{MILK}}{\Delta ME}$$

$$k_g = \frac{\Delta \text{GAIN}}{\Delta ME}$$

Figure 2. Partial efficiency of metabolizable energy (ME) for production.

required to produce that product as in Figure 2. With several physiological processes occurring simultaneously, however, estimates of partial efficiency for each process are clouded by experimental error and also by necessary assumptions. The most troublesome assumption concerns maintenance. Three alternatives for estimating energetic efficiency are in Figure 3. The estimate may be derived from two or more EB measurements made above maintenance in which case the estimate is by difference or regression. The precision of the estimate is determined by experimental error and by the magnitude of the difference in energy intake and production. Alternative methods involve an assumed amount of either ME or net energy (NE) required for maintenance combined with a single estimate of EB at some point above maintenance. These alternative methods yield lower errors because no error is associated with the maintenance estimate. An incorrect assumption regarding maintenance, however, will introduce a bias. Considerable variation in published estimates of partial efficiency is from differences in assumptions regarding maintenance.

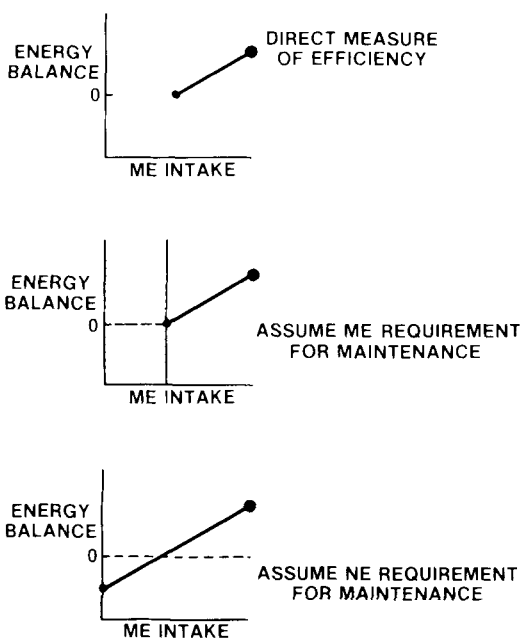


Figure 3. Partial efficiency may be estimated by regression (top) or by assumed metabolizable energy (ME) or, net energy (NE) required for maintenance.

The problems associated with mathematical estimates of partial efficiency, including the concepts of maintenance, were discussed extensively by Van Es (95). He emphasized limitations of the concept of net energy for maintenance and efficiency of energy use for maintenance. Energy required for maintenance is primarily for the production of ATP, and this energy along with the wasted energy is lost eventually as heat. Heat production at maintenance is, therefore, the total of productive and nonproductive energy. Heat produced by the fasting animal is the result of body tissue being metabolized to supply the energy needed to maintain the animal. The ratio between fasting and maintenance heat production is, therefore, an expression of the relative efficiency of body tissue energy and dietary energy in meeting the needs for maintenance. Efficiencies calculated in such a manner should be referred to as "apparent efficiency" and bear little relationship to the efficiency computed for energy use above maintenance in which a measureable end product is formed.

Van Es (95) also discussed errors associated with estimation of maintenance requirement by regression. He noted that regression analyses theoretically require that the independent variable(s) be measured without error. If not, the computed regression coefficients will be underestimated. Since ME and EB both are measured with error, including some sources of error such as fecal, methane, and urine losses that are common to both, the model selected will influence estimates of partial efficiency and the estimate of maintenance.

Cramer (28) described an orthogonal regression procedure that accommodates errors in both variables. It minimizes the perpendicular distances from the line to the points rather than the vertical distances from the line to the points as in conventional regression.

Because of the sources of error common to EB and ME, a system has been proposed in which retained energy (R) is related to gross energy intake (G) by scaling both with fasting heat production in a generalized form of the Mitscherlich equation $R = B(1 - \exp(-pG)) - 1$, where the parameters B and p are fitted by an iterative procedure (19, 21, 22). This technique avoids assumptions regarding maintenance requirements but requires direct measurement

of fasting heat production by each test animal or a tabulation of fasting heat production according to breed, size, sex, and other attributes and of the energy retentions associated with gains in body weight.

With the increased attention to the description of the maintenance component in growing animals, Webster et al. (106) computed a "basal" component of metabolism related to live weight from EB measurement with growing steers and concluded that the basal component was closely related to body weight to the exponent .734. This estimate was, however, obtained by calculating the "basal component" from assumed relationships between Q (% ME in the diet) and k_m and k_f (1) which involve maintenance of mature animals and efficiency of fattening. Because actual measurement of fasting metabolism in these animals declined with increasing weight when expressed as kcal/kg.⁷³ in accord with ARC (1), the authors concluded that these findings cast serious doubt on the validity of use of measured fasting metabolism as a baseline from which to predict efficiency of growth.

The uncertainties associated with statistical partitioning of energy cost in the producing animal into maintenance and production are considerable. Although newer mathematical techniques eventually may permit abandonment of the concept of maintenance, especially in the growing animal, it is a useful and necessary component in discussing energy use by animals of differing production rates. In the discussions that follow, the reader is reminded that assumptions regarding maintenance exert considerable effect on estimates of production efficiency.

Maintenance and Lactation

Calorimetric experiments by Brouwer et al. (25) and Van Es (94) showed that the value of a series of hays for maintenance of cows was more closely related to their ME content than to starch equivalent. Blaxter (16) summarized results of calorimetric studies with diets ranging from poor quality forage to all concentrate and concluded that efficiency of use of ME for maintenance was fairly constant. These results supported the conclusion of Ritzman and Benedict (80) from earlier calorimetric studies. Blaxter (16) concluded further that the ef-

iciency for maintenance of ME from these natural feeds was equal to that of VFA infused into the rumen when a correction was made for the heat of fermentation of the natural feeds.

These studies showed that the variation in use of ME for maintenance was low, but some variation did exist, presumably in part from losses in heat of fermentation, which was not measured in the determination of ME. Agricultural Research Council (1) described variation in efficiency of use of energy for maintenance (k_m) as a function of percentage of ME in the diet (Q_m) as follows: $k_m = 54.6 + .30 Q_m$.

A major question, unresolved in earlier calorimetric investigations, was the extent to which efficiency of ME for milk production was influenced by the source of dietary ME. Initial lactation studies at Beltsville (27) were with diets of alfalfa hay and concentrates in ratios calculated to provide 50, 75, and 100% of estimated net energy (ENE) from the alfalfa. When maintenance was assumed to be 131 kcal ME/kg^{.75}, efficiencies of use of ME in excess of maintenance were 65, 61, and 54%, respectively, for lactation.

Hashizume et al. (42) found the efficiency of ME of diets containing 45 and 71% of concentrate consumed in excess of maintenance (116.3 kcal/kg^{.75}) was used with efficiencies of 74.0 and 68.2%, respectively, for milk plus retained body tissue energy.

Van Es and Nijkamp (98) reported the results of 41 balance trials with lactating cows consuming mixed diets of concentrate, silage, and variable amounts of hay. In these studies, no effects of percentage of crude fiber or of crude protein on efficiency of milk production were detected. Also, no differences in utilization of hay and silage of equal ME and protein content were found. These workers concluded that ME was used for milk production with an efficiency (k_l) of 54 to 58% and that 10.1 to 11.7 Mcal ME was required for the maintenance of a 500 kg cow (96 to 111 kcal ME/kg^{.75}). Van Es and Nijkamp (98) discussed problems associated with mathematical descriptions of results of experiments with lactating cows in positive or negative body tissue EB. Relationships between ME intake and milk energy were studied by multiple regression with separate terms for body weight, milk energy, tissue energy gain, and tissue energy loss and by applying several methods of adjusting to zero

body tissue EB. The various methods yielded slightly different estimates of efficiency but all methods indicated a slight increase in efficiency of ME use for milk production with an increase in metabolizability of the diet.

An extensive series of EB experiments by Flatt et al. (37) with Holstein cows producing up to 49 kg of 4% fat-corrected milk (FCM) per day and consuming diets of 40, 60, and 80% concentrate plus alfalfa hay showed no significant differences among diets in efficiency of use of ME for milk production plus tissue energy gain. These studies included cows at all stages of lactation and when nonlactating and at both ad libitum and restricted feeding. The magnitude of changes in body tissue energy status was far greater than in previous experiments and varied from -20.6 to +18.3 Mcal body tissue energy per day. Differences due to diet were in body tissue balance; cows on the highest concentrate diet mobilized less fat in early lactation and deposited more fat in late lactation than cows on the highest forage diets at equal ME intake. The regression of total EB of milk plus body tissue energy on ME intake was $EB \text{ (kcal/kg}^{.75}\text{)} = -93.4 + .66 \pm .011 \text{ ME (kcal/kg}^{.75}\text{)}$. This equation indicated 66% utilization of ME and zero EB at 142 kcal ME/kg^{.75}. Extensive mathematical analyses of these data led to several conclusions: 1) use of ME for milk or body tissue gain was relatively unaffected by milk yield, amount of body tissue gain (or loss), and stage of lactation; 2) the major difference among diets as well as among individual cows was in the amount consumed and energy partition, i.e., milk production or fattening, rather than the efficiency with which ME was used; and 3) the apparently high maintenance requirement was not due to milk yield or to lactation per se but may have been influenced by pregnancy.

The ad libitum feeding of high protein (19.5%) diets in the experiment of Flatt et al. (37), although necessary to meet the objectives of that experiment, provided substantially more protein than needed for maintenance plus milk production. The effects of excess protein as well as the contribution of pregnancy were studied with all available data from Beltsville, which included 350 trials with lactating cows and 193 with nonlactating cows. The decrease in EB attributable to intake of nitrogen in excess of protein required was 7.3 kcal/g excess

nitrogen (90). The amount of ME required during pregnancy was described (57) by the equation $ME \text{ (kcal/kg}^{.75}) = 100.8 + .567e^{.0174t}$ on day t of gestation. These data indicate 11.5% efficiency of ME for fetal gain.

Multiple regression analysis were used by Moe et al. (62, 63) to derive estimates of maintenance needs and partial efficiencies of milk production and tissue gain in Tables 3 and 4. Partial efficiencies of ME used for milk production and body gain in lactating cows were 64 and 75% and efficiency of maternal body gain in nonlactating cows was 60%. The efficiency of use of body tissue energy for milk production by cows in early lactation was estimated by comparing partial regression coefficients representing the amount of ME required for milk production and the amount of dietary ME spared by body tissue loss. The estimated conversion of body tissue energy to milk energy was 82% efficient and likely reflects substantial direct incorporation of body lipids into milk fat. These results showed that temporary storage of energy as body fat in late lactation combined with use of body fat in early lactation is nearly as efficient as direct use of dietary ME for milk production ($75\% \times 82\% = 62\%$ vs. 64%).

The findings described in the preceding paragraph were used by Moe et al. (55) to identify the relationship between diet quality and efficiency of milk production. Energy of diets was expressed as net energy for lactation (NE_l). Maintenance requirements estimated by pooled linear regression within 32 diets from the 350 trials with lactating cows were 122.1 and 111.3 kcal ME or 78.9 and 67.7 kcal NE_l per kg^{.75} of body weight, depending on whether ME intake or milk energy was the dependent variable. Because the average measured fasting heat production in the Beltsville laboratory (73.5 kcal/kg^{.75}) with nonlactating, non-pregnant dairy cows following a period of maintenance feeding (35) was between the regression estimates (78.9 and 67.7) of the NE_l required for maintenance, the authors concluded that the amount of energy required for maintenance of lactating cows could be described adequately as 73 kcal NE_l (or NE_{milk})/kg^{.75} and that a separate NE term for maintenance (NE_m) was unnecessary.

With that assumption, the NE_l of individual diets was studied by relating NE_l of diet dry

matter (DM) to other expressions of energy as follow (regression coefficient \pm SE):

$$NE_l \text{ (Mcal/kg DM)} = -.19 + (.703 \pm .020) ME \text{ (Mcal/kg DM)},$$

$$NE_l \text{ (Mcal/kg DM)} = -.36 + (.677 \pm .022) DE \text{ (Mcal/kg DM)}, \text{ and}$$

$$NE_l \text{ (Mcal/kg DM)} = -.12 + (.0266 \pm .0011) TDN \text{ (\% of DM)}.$$

The ME, DE, and total digestible nutrients (TDN) in these equations were those actually observed in the lactating animal, and the authors emphasized that those relationships were not appropriate for measurements of digestibility at maintenance. These results indicate 61 to 64% efficiency of ME use for milk production from normal diets.

In a recent analysis of Beltsville data (61), results of 313 energy balance trials with lactating cows published since 1970 were used to study the same relationships. The relationships between NE_l and other expressions of energy from this separate data set were:

$$NE_l \text{ (Mcal/kg DM)} = -.21 + (.697 \pm .022) ME \text{ (Mcal/kg DM)},$$

$$NE_l \text{ (Mcal/kg DM)} = -.41 + (.673 \pm .021) DE \text{ (Mcal/kg DM)}, \text{ and}$$

$$NE_l \text{ (Mcal/kg DM)} = -.51 + (.0315 \pm .0015) TDN \text{ (\% of DM)}.$$

The ME and DE equations are virtually identical to those derived earlier with a totally different data set. The coefficient for the TDN equation is about 18% greater than in the earlier equation, indicating a greater effect of percent TDN on NE_l than in the earlier data set. The change in the TDN equation is unexplained although the more recent data set included several diets containing silage for which drying losses and ether extract analyses may have introduced errors not in ME and DE data. Greatest reliance should be placed on ME and DE equations because they are based on direct combustion of wet material. For practical use the ME equations given above can be simplified to $NE_l \text{ (Mcal/kg DM)} = -.2 + .7 ME \text{ (Mcal/kg DM)}$ in which ME has been adjusted for intake and associated effects.

Maintenance and Growth

Measurement of energy cost of growth in

TABLE 3. Multiple regression analysis of metabolizable energy (ME) intake (Mcal ME/day) during 543 energy balance measurements with dairy cows^a.

	Metabolic body size (kg ^{.75})	Milk energy (Mcal)	Body tissue gain (Mcal)	Body tissue loss (Mcal)	Constant
Lact., neg. balance (N=126, R ² =.957, Sy.x=1.886, ME=30.060 ± 9.0 Mcal)					
Coefficient	.153 ± .012	1.512 ± .034		1.270 ± .045	-2.889
Average	114.6	14.882		-5.479	
Lact., pos. balance (N=224, R ² =.950, Sy.x=2.025, ME=32.726 ± 9.0 Mcal)					
Coefficient	.135 ± .009	1.576 ± .029	1.378 ± .054		-1.889
Average	113.0	9.416	3.288		
Dry cows, neg. balance (N=75, R ² =.707, Sy.x=1.735, ME=10.401 ± 3.1 Mcal)					
Coefficient	.050 ± .015			.990 ± .091	6.781
Average	129.9			-2.904	
Dry cows, pos. balance (N=118, R ² =.897, Sy.x=1.503, ME=18.140 ± 4.6 Mcal)					
Coefficient	.089 ± .011		1.703 ± .058		1.401
Average	128.1		3.160		
Lactating cows (N=350, R ² =.952, Sy.x=1.985, ME=31.766 ± 9.0 Mcal)					
Coefficient	.141 ± .007	1.552 ± .22	1.339 ± .045	1.279 ± .034	-2.152
Average	113.6	11.366	2.101	-1.972	
Dry cows (N=193, R ² =.911, Sy.x=1.676, ME=15.133 ± 5.6 Mcal)					
Coefficient	.072 ± .009		1.677 ± .055	.933 ± .065	3.670
Average	128.8		1.932	-1.128	
All cows (N=543, R ² =.968, Sy.x=2.075, ME=25.740 ± 11.5 Mcal)					
Coefficient	.104 ± .006	1.623 ± .014	1.473 ± .036	1.234 ± .028	.622
Average	119.8	7.398	2.045	-1.937	

^aData from Moe et al. (62).

cattle is made difficult by the combined effects of apparent declining maintenance needs as the animal approaches maturity and the changes in composition of tissue deposited with age and level of feeding. Fasting heat production of cattle when expressed per unit of metabolic size declines with age as in Table 5. Various exponents of body weight have been used to describe metabolic size (47). Even small differ-

ences in exponent produce large differences in estimates as can be seen by comparing fasting heat production expressed per unit weight raised to the exponents .73 and .75 in Table 5. A sort of gentleman's agreement to express results of EB measurements by the exponent .75 was reached at the third Symposium on Energy Metabolism. This agreement was intended to facilitate comparisons of results from

TABLE 4. Estimates of maintenance requirement and partial efficiency of energy use in the dairy cow^a.

	N	ME ^b for maintenance (kcal/kg ^{.75})	Milk from ME	Tissue from ME (%)	Milk from tissue
Lactating cows	350	122	64.4	74.7	82.4
Nonlactating cows	193	100		59.6	

^aData from Moe et al. (62).

^bME is metabolizable energy.

TABLE 5. Preferred fasting heat production of cattle.

Age of animal ^a (months)	Body weight ^b (kg)	Fasting metabolism	
		(kcal/kg ^{.75 a})	(kcal/kg ^{.75 c})
1	55	140	129
3	80	135	124
6	150	125	113
12	275	110	98
18	400	100	89
24	525	95	84
36	650	90	79
48	650	85	70
48	650	80	70

^aFrom ARC (1).

^bSuggested mean body weights of growing large breed dairy cattle for corresponding ages, from NRC (66).

^cRecalculated from Columns 2 and 3.

different laboratories. The use of body weight in kg^{.75} reduces variation from mature body size in fasting heat production and presumably maintenance requirement. The use of metabolic body size to partition energy use between maintenance and production is apparently less suitable for the young growing animal than for adults. Recent work on the partition and energy cost of protein and fat gain and work on the energy cost of protein turnover, however, is helping to clarify energy transactions in young growing animals.

Several recent reviews discuss manipulation of growth (32), energy cost of growth (52), and nutrition and genetic effects on body composition (50).

Thorbek (83) computed efficiencies for body gain in growing pigs with Brierem's (24) estimate of maintenance needs, 196.3 kcal ME per kg^{.56} body weight. Decline in efficiency of ME for gain was linear with increasing percentage of total gain as protein. Using a linear function for maintenance ME (1683 + 8.1 LW for live weights (LW) between 20 and 90 kg), Thorbek (84) found partial efficiencies for protein and fat deposition of 43 and 77%. Kielanowski and Kotarbinska (46) studied several exponents of body weight in describing relationships between ME intake or heat production and protein and fat gain in growing pigs. They found the exponent .734 fit best and used .75 for simplicity. Energy cost of protein deposition was 16 kcal ME/g, and cost of fat

deposition was 13 kcal ME/g. Those estimates correspond to partial efficiencies of about 35 and 71%, respectively.

Partial efficiency of protein and fat gain in growing lambs (30 to 60 kg) was estimated from EB and fasting measurements of heat production (10). Partial efficiencies were 76% for maintenance, 35% for protein gain, and 99% for fat gain when a weight exponent of .75 was used. Recent work with calves (72) and with bulls and heifers (38) also shows a lower energetic efficiency for protein gain than for fat gain.

Millward et al. (52) emphasized that statistical identification of heat production associated with protein and fat deposition, although useful to predict growth performance in animals, is arguably misleading in mechanistic terms. Protein and fat depositions are not completely independent even though fat deposition is likely more manipulable than protein deposition. If some fat is deposited as an inseparable component of lean tissue growth, the cost of that fat deposition will be statistically identified with protein deposition and the efficiency of protein synthesis thereby will be underestimated.

The contribution of protein turnover to the apparently high cost of net protein synthesis and the higher rate of metabolism in young growing animals has been the subject of recent intense study. This topic was considered in detail by Waterlow et al. (105). They presented

evidence from rats that protein turnover declines with age and that protein degradation is greater in animals growing more slowly. Edmunds and Buttery (30) presented data showing substantial differences among specific tissues in the fractional rate (per day) in protein synthesis; .058 for lean tissue, .475 for brain, and intermediate rates for other tissues. They also indicated that the ratio of synthesis to deposition was 3:1. The clarification of the role of protein turnover in the growing animal will, hopefully, be of considerable value in partitioning energy costs in young growing cattle.

Another important factor in identifying energy needs of the growing animal is the extent to which body composition is influenced by nutritional manipulation. Many dietary effects have been summarized concisely by Black (12) for the growing lamb. His data suggest that animals grown at higher nutrition will have higher body fat than animals grown more slowly although the difference in composition becomes progressively less as the animal approaches maturity. Protein content of the body increased progressively as protein content of the diet (percent of ME) was increased from 6% to 10, 15, and 20%. This response to protein steadily declined with increasing body weight. Protein above 10% of ME had little effect on composition of lambs weighing over 30 kg.

Tyrrell et al. (91) partitioned gain of Hereford heifers into protein and fat by carbon and nitrogen balance in animals in fast and when given maintenance and *ad libitum* intake. Regression of fat deposition on total energy deposited indicated that 95% of the change in EB was from change in fat retention and only 5% from change in protein retention.

The limitation of energy retention alone as the expression of productivity in growth is apparent from results of Tyrrell and Waldo (93) and Waldo and Tyrrell (104). In calorimetric and growth studies they fed direct cut orchardgrass silage with or without a mixture of .12% formaldehyde and .14% formic acid. Each silage was fed alone and supplemented with formaldehyde-treated sodium caseinate and fed to Holstein steers. Treatment of the silage or supplementation with casein improved nitrogen retention but did not influence energetic efficiency. Increasing intake of insoluble

protein increased the proportion of gain as protein from 38 to 51% of total calories gained.

Discrete Effects on Energy Use

Many sources of energy loss are included in the discussion of energetic efficiency presented above. Many of these have been studied specifically, and the information gained has improved our understanding of total use of energy by cattle. Webster et al. (107) discussed several components of heat increment (HI) including the cost of eating and ruminating, the heat produced by rumen fermentation, and the increased heat produced by the tissues of the gut and the liver. He cited a range in energy costs of eating of 2.5 cal/kcal ME for grass pellets and 36 cal/kcal ME for fresh grass. He concluded that the energy cost of ruminating could be discounted as a contribution to HI.

Webster et al. (108) estimated heat of fermentation *in vivo* in sheep and found 68 cal heat produced per kilocalorie of digestible energy from forage diets. He found no difference due to diet source in the amount of heat produced by the tissues of the gut, but heat production increased exponentially with increasing ME intake. At an intake of 143.4 kcal ME/kg^{.75}, heat production in the tissues of the gut was 27 kcal/kg^{.75} per 24 h. Fasting heat production of gut tissues was 15 kcal/kg^{.75}. The HI due to feeding in the gut was, therefore, 12 kcal/kg^{.75} of which 7 kcal was fermentation heat and 5 kcal was aerobic metabolism in the gut tissues. Webster et al. (107) concluded that processes of *ingestion and digestion* can account for about 25 to 30% of total HI and that most of the variation in total HI must be from the nature of substrates made available by digestion as suggested by Armstrong and Blaxter (2, 3).

Environmental temperatures influence total energy use in several different ways. Young (112) reviewed effects of cold environment on energy use and emphasized that thermal stress is described too frequently in terms of temperature alone. He cites Lee's (49) compilation of environmental variables (temperature, humidity, air movement, radiation, precipitation), animal characteristics (species, age and sex, breed and type, metabolic state, coat, acclimatization, nutrition and hydration, derangement and disease, individual variability) and criteria of effect (productivity, growth, reproductivity,

physiological response, pathological patterns) to illustrate the complexity of describing or predicting environmental effects. This topic is covered extensively in a separate paper in this issue, so I will not pursue the topic here.

Most energy metabolism research has been under conditions of "thermal neutrality" so that environmental effects must be considered in applying the data to extreme conditions. One specific effect, however, should be mentioned here because it appears to operate over a wide range of environmental conditions. This effect is a reduction in digestibility with decreasing temperature. Young (112) cites several experiments in which the mean reduction in DM digestibility was 1.8 percentage units per 10° C reduction in temperature. Kennedy et al. (45) reported that decreasing temperature had the effect of increasing rate of passage of rumen ingesta, which decreased organic matter digestion but improved efficiency of synthesis of microbial protein.

Improvements in Research Techniques

Innovation or development in related fields has had a profound effect on techniques available to researchers in energy metabolism. Improved surgical techniques and development of integrated electronic circuits and inexpensive computers have had a profound effect on collection and analysis of pertinent data. Recent reviews document the development and use of several techniques.

The increased use of intestinally cannulated animals has allowed identification of site of digestion and disappearance of nutrients from specific segments of the gut (51). The increased availability and use of markers has permitted systematic study of the dynamics of food particle degradation and passage through the gut (33). Methods of measuring blood flow have been used to measure quantitatively uptake of nutrients from the gut (9, 48). Improved analytical sensitivity and automated analysis have improved the ability to identify and quantify intermediary metabolites.

As these more refined techniques increase our understanding of the metabolism of specific nutrients and individual tissues, more sophisticated mathematical techniques are needed to integrate this information into descriptions of energy use in the whole animal. Simulation and

modeling can be powerful tools in evaluating hypotheses about nutrient use and animal production (8, 13, 40).

Although calorimetry has proliferated during the past 25 yr and some novel approaches have been used, accuracy has not been improved over that in the early work of Armsby and Kellner. Indirect calorimetry provides a measurement of respiratory exchange and, indirectly, heat production. Calorimetry serves as a point of reference in characterizing energy use by the whole animal. It is one technique among many to test hypotheses regarding energy use by animals. The most effective use of calorimetry will be in experiments in which heat production is measured simultaneously with rates of metabolism of specific nutrients.

Feed Evaluation and Feeding Standards

Feeding standards in use in 1956 were the total digestible nutrients (TDN) and estimated net energy (ENE) systems in the US and starch equivalents (SE) in much of Europe. The ENE system (64, 65) was based on NE of feeds for growth and fattening in comparison with that of corn grain which was assigned 2.08 Mcal NE/kg dry matter. The starch equivalent system (111) was based on the earlier work of Kellner in which 100 lb of test feed was described in terms of pounds of starch equivalent. With a few exceptions, none of these systems provided separate values for fattening and lactation. All systems implied that relative values of feeds were similar for fattening and lactation.

As the definition of energy requirements became more precise and as factors influencing the energy value of feeds were understood better, new proposals were advanced for use in practical feeding situations. A system based on ME initially was proposed by Blaxter (17) and described in detail by ARC (1) and Blaxter (18). The main provisions of this ME system were:

- 1) Energy requirements of animals and energy value of feeds should be expressed in an energy unit, the calorie.
- 2) The basic tabulation of the energy value of feeds should be the ME, determined at maintenance nutrition.
- 3) ME required for maintenance is 1.35 times fasting heat production.

- 4) Efficiency of ME for maintenance and body gain can be expressed as a function of ME concentration.

The ME system, although nearly universally accepted as the most scientifically sound system available, was not used widely in practical feeding systems. The most common complaint was that it was too complex. Although not widely used directly, parts of the ME system were included in nearly every feeding system developed since that time. The system currently used in the United Kingdom is an ME system expressed in joules described by the Ministry of Agriculture, Fisheries, and Food (53). It is a modification of the ARC (1) system in which intake effects are ignored and ME use for milk production is assumed to be a constant 62% for all diets.

Nehring and coworkers (67, 68, 69, 81) introduced a system in which requirements for maintenance, growth, and lactation are expressed in terms of a feed unit for fattening. The energy values of diets are computed from digestible nutrients and adjusted for digestibility of the total diet.

Intake effects in the NRC (66) systems are incorporated into requirements for milk production in the DE, ME, and TDN systems and into the values of feedstuffs in the NE_l system. The NE_l at 3 × maintenance are computed from 1 × TDN by the equation (60), $NE_l \text{ (Mcal/kg DM)} = -.12 + .0245 \text{ TDN (\% of DM)}$, which assumes a reduction in TDN of 4% per multiple of maintenance.

In the Netherlands (97, 99), ME is computed from digestible nutrients and is assumed to decline by 1.8% per multiple of maintenance. The NE_l are converted to a feed unit (1 VEM = 1.65 kcal NE_l) that corresponds to the value of 1 g barley.

Vermorel (102) developed a similar system for France in which NE_l also is converted to a feed unit based on barley (1 UFL = 1.73 Mcal NE_l). The NE_l is computed from ME after adjustments for intake and associated effects according to percentage concentrate in the diet and forage quality.

In Switzerland, Bickel and Landis (11) described a system that is basically the same as those for the Netherlands and France except that energy units are expressed in joules instead of calories.

Energy systems for lactating cows have taken on a variety of outward appearances, especially with regard to the units which are used at the farm. Both calories and joules are used, although use of the joule is increasing as a result of its adoption by most European scientific journals. The ME, NE_l, NE_g, and various feed units are used. This proliferation of units of expression has occurred despite attempts to avoid confusion by trying to identify a single unit that could be used on a world wide basis for feed evaluation and formulation of diets for cattle.

A working group of the EAAP was established to develop recommendations for standardization of terminology (96). Activities of that group and a workshop sponsored by the International Union of Nutritional Sciences (73) led to emphasis on the different requirements of units for feed evaluation than for practical feeding systems. Feed must be evaluated in such a way that the potential value of that feed for animals is identified. If information about feeds is to be compiled from many sources, the measurement should be repeatable and should reflect feed quality rather than effects of the animal or technique used for the measurement. The most descriptive and reproducible measurement of feeds is ME determined at the maintenance intake, as suggested by Blaxter (17). Net energies are suited less well in measuring the value of a feed because such measurements involve animal effects, intake, associative effects, and differences in methods of measurement (58).

In contrast to the need to use a uniform term (ME at maintenance) to describe the value of feeds, units used in practical feeding systems need not and probably cannot be standardized to the same degree. The unit used, whether a feed unit, NE, or ME should be understood by the user, should be adequate to describe energy needs of the animal, and should be estimable from ME. Nearly all of the systems introduced recently are similar in that ME at maintenance is used as the starting point. The accumulated knowledge regarding intake and associated effects and efficiency of energy use by the animal then is used to develop working requirements and feed values for use in formulating rations. Working units such as NE should not be viewed as fixed attributes of feeds but must be upgraded continually as

additional information is gained about how ME of diets and ME use change with feed intake and type of animal product formed.

All major feeding standards treat efficiency of energy use primarily as a function of concentration of ME in the diet. A major gain in the usefulness of feeding systems, especially for predicting animal performance, will be possible when sufficient information is available on the relationship between amounts of specific end products of digestion and performance of animals (58, 59). A major gain in feed evaluation will come through identification of important feed attributes that influence nutrient availability either through their own inherent potential or by their influence on the environment within the digestive tract. Information on feed attributes influencing nutrient availability will allow accurate prediction of intake and associated effects and also permit strategies to minimize those effects.

The Next 25 Years

The mean milk production per cow per year in top herds has increased from about 8,000 kg to 11,000 kg in the past 25 yr. This gain has been possible through genetic improvement and application of feeding and management systems that are responsive to the cow's nutrient needs. I am aware of no evidence that precludes progressive improvements in these areas such that herds averaging 14,000 kg milk per year may be seen by the year 2006. The fact that one cow, Beecher Arlinda Ellen, actually produced over 22,800 kg of milk in 305 days indicates the biological possibility of production at sustained high daily rates.

What roadblocks must be removed to allow cows to achieve such production? I frequently have heard the comment that Ellen must have had an "unusually efficient metabolism" because she could not otherwise possibly have consumed enough feed to produce at that rate. More likely, Ellen's success was because of two factors. First is the formulation of a diet that could be consumed in sufficient amounts without overloading her physiological ability to maintain conditions within her digestive tract for maximum rate of fermentation, digestion, and absorption. Ellen is reported to have consumed up to 26 kg of top quality alfalfa hay and 25 kg of a concentrate mixture per day.

Second is that she was blessed with an extraordinary ability to synthesize milk from available nutrients at a high rate (up to 88.7 kg per day), not necessarily more efficiently but at a greater rate. In short, this cow was able to deal with the stress of high feed intake and produce milk. Much of the progress in genetic improvement in dairy cows will be through improvements in cows' ability to maintain homeostasis with regard to the environment within the digestive tract through salivary secretions, intestinal secretions, and a reduced sensitivity to those effects such as rumen fill and blood metabolites that may tend to inhibit feed intake. Ability to cope with the stress of high feed intake and to synthesize milk both will likely be improved in selecting animals for higher milk yield. The role of the nutritionist is to formulate diets that minimize the stresses that tax the cows' ability to consume and digest large amounts of feed and to effectively absorb and metabolize the needed nutrients. To formulate these diets we need to understand limitations to intake and digestion of feeds and metabolism of nutrients. Without benefit of a "crystal ball" I propose the following as areas likely to yield to research in coming years in physiological, not priority, order:

- 1) Remove current limitations to rate of microbial degradation of structural carbohydrates in the rumen. Conventional wisdom recognizes the need for substantial amounts of rapidly fermented fiber in diets of lactating cows. New chemical techniques are needed to characterize the resistance of feeds and diets to high rates of degradation. Conditions within the rumen for optimum rate of fermentation must be identified.
- 2) Improve efficiency of synthesis of microbial protein. The current limitation in use of highly degradable protein, naturally occurring nonprotein nitrogen (NPN), and supplemental NPN by lactating cows and young growing cattle is the unfavorable ratio of microbial protein to total end products of fermentation. Evidence from in vitro studies suggests that higher efficiencies of protein synthesis are feasible.
- 3) Prevent unnecessary digestive losses of energy. Identify optimum physical-chemical conditions within each segment of the gut

for maximum rate of fermentation, digestion, and absorption. Identify feed factors that influence gut environment. Identify mechanisms for homeostatic regulation of gut environment through secretory or transfer processes.

4) Identify measurable feed attributes or characteristics that, when applied to a mixed diet with unknown ingredients, permit prediction of amounts of specific nutrients likely absorbed from the gut. Such characteristics include not simply content of important nutrients but attributes that affect nutrient availability, i.e., susceptibility to high rate of fermentation and digestion, and attributes that influence gut environment or mechanism of absorption and thereby influence value of total diet.

5) Identify quantitative relationships between end products of digestion and animal performance, i.e., the role of specific nutrients or groups of nutrients in limiting milk yield or growth and influencing partition of nutrients between milk and body gain or composition of body gain. No single area of research will yield more lasting improvements in animal performance and effective use of the available feed supply than an understanding of how animals respond to variations in amounts of key nutrients absorbed from the gut.

6) Develop practical feeding systems based on information from items 4 and 5 above. Effectiveness of diet formulation and prediction of animal performance can be improved greatly by development of mathematical techniques that relate both diets and animals' performance to quantitative descriptions of nutrients absorbed from the gut. Dynamic models that accurately predict incremental changes in animal performance resulting from changes in diet are needed to replace currently used static models consisting of tables of nutritive value of feeds and nutrient requirements of animals.

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