Nutritional Energetics of Livestock: Some Present Boundaries of Knowledge and Future Research Needs

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NUTRITIONAL ENERGETICS OF LIVESTOCK: SOME PRESENT
BOUNDARIES OF KNOWLEDGE AND FUTURE
RESEARCH NEEDS\textsuperscript{1,2}

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Summary

An overview of the nutritional energetics of animals is presented to indicate with a few examples the present state of knowledge and to identify several problems needing research attention. Animals differ from each other in:

1. gastrointestinal architecture, 
2. nature and location of digestive agents and 
3. major digestive and absorptive sites.

These characteristics determine:

1. the chemical and physical nature of the usual diet ingested by a given animal, 
2. the rate and extent of digestion and 
3. the chemical nature of the absorbed products of digestion; they also influence the efficiency of energy utilization.

Both the digestible energy (DE) and the metabolizable energy (ME) values of the usual diets fed in practice and the net utilization of ME for body functions are highest in pigs and fowl, intermediate in horses and rabbits and lowest in ruminants. As the level of input of forage-concentrate diets or finely ground forage increases, the digestibility of energy by herbivores declines progressively. The rate of digestibility depression is especially pronounced in ruminants ingesting high energy diets; this effect seems attributable chiefly to a reduction in gastrointestinal pH, which results in a reduction in the digestibility of starch and cell wall carbohydrates. Improving the DE and ME values of ruminant diets is a major research challenge. The various body functions which utilize ME by mammals within species are, in order of net efficiency, maintenance > lactation > body gain > reproduction. In fowl, the net efficiency of maintenance is a little higher than that of egg production or body gain. A brief summary is made of the influences of nutritional and other environmental conditions and of animal characteristics on the utilization of ME. Evidence indicates that the relation of glucose to acetic acid utilization more nearly explains differences in the net utilization for body gain of ME supplied by different diets to ruminants than does the ruminal ratio of acetic to propionic acid, \textit{per se}.

Among continuously growing animals, the net efficiency with which ME is utilized is high in those gaining fat at a rapid rate and protein at a low rate, and vice versa. The efficiency of the \textit{in vivo} net synthesis of protein is lower than that of fat, and lower than extant estimates of the theoretical biochemical efficiency of protein synthesis. Research is needed to find a means to divert energy from the synthesis of fat to the synthesis of protein, and yet to improve the energetic efficiency of animals. Under average animal production conditions in the United States, the estimated efficiency with which protein (grams) is produced per megacalorie of DE ingested is as follows for various food products: fish, 40; eggs, 12.6; milk, 12.4; broiler, 11.9; pork, 6.1, and beef, 2.3. These estimates have taken into account the overhead DE costs, such as those of rearing and maintaining the breeding herd or flock, nonlactation periods and the reproductive and mortality periods and the reproductive production itself. The protein outputs increase...
as the intensity of production (chiefly energy input per unit of time) increases, because the energy cost of maintenance becomes a gradually smaller proportion of the total DE input. Research is needed to identify management components of production systems that have the greatest impact on nutritional efficiency of livestock. (Key Words: Nutritional Energetics, Energy Utilization, Energetic Efficiency, Body Composition, Net Protein Synthesis, Net Fat Synthesis.)

Introduction

In this paper, it is our intention to provide an overview establishing the present state of knowledge of certain aspects of the nutritional energetics of the whole animal. This coverage will also focus on certain research needs which, if fulfilled, are expected to lead to the improvement of the energetic efficiency of farm animals. In addition, the dietary energy costs of protein production by various animal production enterprises will be examined. This study will demonstrate the overwhelming opportunity for improving the nutritional energetic efficiency of ruminants as compared with that of simple-gutted animals.

Conditions Affecting the Digestible Energy (DE) and Metabolizable Energy (ME) Values of Diets

Ranges of DE and ME Concentrations in the Diets of Farm Animals. The significance of DE and ME is that they serve universally as the major rationing units or as the bases for computing rationing units, and they represent biological indices of the potential nutritive value of the diet. In the study conducted by Moe et al. (1972), 86% of the variation in net energy for milk production among diets consumed by lactating cows was attributable to the concentration of DE in the diets. The ranges of DE and ME values summarized in table 1 from many literature sources reflect chiefly animal peculiarities and the influence of the quality of diet sometimes ingested by animals. The interspecific peculiarities of animals are attributable to: (1) the chemical and physical nature of the usual diet, e.g., the ratio of concentrates to forage and the quality of forage (especially cell wall content and the extent of lignification); (2) the architecture of the gut, e.g., location of the major sites of fermentative digestion relative to the major sites of absorption, and (3) the relative degree of dependency on digestion effected by tissue-elaborated enzymes and microorganismal enzymes, and their locations (Reid, 1974). Within species, the differences in the magnitude of DE and ME values are mainly the result of quality of the diet, especially the proportions of soluble cell contents and cell wall substances, and the degree of lignification of cellulose. Extremes in nutrient balance such as very low concentrations of vitamin A or low or high concentrations of dietary protein also may affect the digestibility or metabolizability of energy.

As shown in table 1, the ME/DE values are highest for pigs, chickens and ruminants fed milk, intermediate for nonruminant herbivores and lowest for ruminants. The difference between 100 and these values represents the magnitude of the energy loss from DE in the urine of simple-gutted animals and in the urine and methane of herbivorous animals. The ME values in parentheses represent those of diets usually fed in good commercial practice. Thus, the ME values of usual practical diets are highest for simple-gutted animals, intermediate for nonruminant herbivores and lowest for ruminants.

As the magnitude of the inter- and intraspecific ranges in the DE and ME values indicates, potentially the greatest impact to be made on the overall energetic efficiency of animals lies in research that will lead to improvements in the metabolizability, especially the digestibility, of dietary energy. The opportunity for improvement is particularly great in ruminants.

Effect of Level of Energy Input on the DE Value. As the level of energy input provided by a diet of constant composition is increased
per unit of time (e.g., per day), the digestibility of energy varies in a manner that is associated with the gastrointestinal architecture of animals and, within kind of animal, with the chemical and physical nature of the diet (Reid and Tyrrell, 1964). Figure 1 represents a generalization of the influence of the level of intake on the DE value of certain kinds of diets ingested by various farm animals. It is cautioned that the DE values (figure 1) employed, though typical of those found in practice, are merely illustrative and are not constants.

In the simple-gutted animals, the level of input has little effect upon the digestibility of energy. Typical of many studies demonstrating this fact is the experiment conducted by Parker and Clawson (1967), in which lactating sows were fed one of two diets at levels of approximately two, four and six times the maintenance intake. However, increasing intakes of highly refined diets, such as one of whole milk that was fed to nonruminating calves (Blaxter, 1952), are accompanied by slightly increasing rates of digestibility. This response probably reflects a diminishing contribution of endogenous products to the total fecal matter as the intake level increases.

As the level of intake of concentrate-forage diets by nonruminant herbivores and ruminants increases, the DE value of the diet progressively declines. The influence of the level of input upon the digestibility of energy provided to ruminants by all-forage diets is associated with the particle size of the forage (Blaxter and Graham, 1956). The digestibility is unaffected or affected only slightly when the forage is ingested in long or chopped form (i.e., with a particle size of 1 cm or longer); however, the DE value diminishes with increasing inputs when finely ground forage is consumed by ruminants as pellets, meal or gruel. These conclusions are documented by the literature analyzed by Andersen et al. (1959).

The effect of level of intake on the DE value of the diet is especially marked in the high producing dairy cow because of her requisite high intake of feed. Among cows ingesting seven different forage-concentrate diets at levels up to five times the maintenance intake, the digestibility of energy was depressed by 2.1 to 6.2% (average rate 4%) per increment of intake equivalent to maintenance (Moe et al., 1965; Reid et al., 1966). The total digestible nutrient (TDN) values of corn meal (77%) and ground oats (69%) determined by difference in mixed diets fed to milking cows at approximately 2.5 times the maintenance level were considerably lower than those (91 and 76%, respectively) recorded in tables of feed composition and presumably determined at about the maintenance level with non-lactating ruminants (Moe et al., 1973). If these differences are attributable to the intake level, the depressions in TDN per multiple of maintenance were 5% for the corn diet and 2.2% for the oat diet.

Reid and Tyrrell (1964) called attention to the observation that the rate of decrease in digestibility that accompanies increasing intakes, though variable, is more marked for high concentrate diets than for diets containing less concentrates. They also suggested that the rate of depression in digestibility generally increases as the ratio of propionic acid to acetic acid produced in the rumen increases. Recently, Tyrrell and Moe (1975) examined the interaction between the intake level and the proportion of concentrates in the diet and confirmed that the rate of depression in digestibility is greater for high concentrate diets than for diets high in forage. In their generalized relationship, the rate of digestibility depression was .052% for each 1% increase in grain content of the total diet.

Although much more research is needed to determine the fundamental causes of the depression in digestibility associated with the intake level and to quantify their effects, present information indicates that digestibility depression is influenced by certain conditions associated with the environment, particularly...
the pH, of the gastrointestinal tract. For example, in lactating cows fed mixed diets containing 50% of ground corn or ground barley, the reductions in digestibility (per multiple of maintenance energy intake) of certain dietary fractions were: hemicellulose, 8.2%; cellulose, 8.1%, and soluble cell contents, 3.2% (Tyrrell and Moe, 1972). In studies of the effect upon the DE in diets of various concentrate-forage ratios fed at various levels of input, Wheeler et al. (1975) observed that the digestibility of starch ranged from 84.7 to 88.1% at intakes of 2.5 to 3.2 times maintenance, but that it was 96.2 to 96.8% at the maintenance intake level. In subsequent studies, Wheeler and Noller (1977) found that the pH of the ingesta from the rumen to the rectum (except in the abomasum) and that of the feces are on the order of 5.6 to 5.8 in cattle fed high energy diets. The correlation coefficients between fecal pH and the amount of fecal starch were ~.82 and ~.94 for two different diets. The addition of limestone or magnesium limestone to the same diets increased the pH of the intestine by about 1 unit and reduced the amount of starch in the fecal dry matter from about 32 to 9%. These workers suggested that the improved digestibility of starch might have occurred because the increased pH of the small intestine provided a more favorable environment for the action of pancreatic a-amylase, although increased pH may also have improved ruminal digestibility.

Wheeler (1977) reported that the addition of 2.17% of limestone to a complete diet fed to milking cows at 3.5% of live weight improved the digestibility of the following fractions: energy (from 65.7 to 69.0%), starch (from 85.9 to 94.6%), cell wall constituents (from 51.3 to 55.1%) and crude protein (from 65.7 to 67.8%). In generalizing the data from Purdue on the depression in digestibility associated with increased intakes of high energy diets, Noller (1978) indicated that the following proportions of the total reduction in digestibility are attributable to decreases in the digestibilities of these dietary components: starch, 45%; cell wall components, 45%; protein, 8%, and others, 2%. However, the contribution of each to the total depression in digestibility depends on the nature of the diet.

Ruminants performing high demand functions, such as high milk production or rapid body gain, require large energy inputs per unit of time. Generally, these inputs are achieved through the feeding of high concentrate diets. With increasing inputs of such diets, the digestibility of energy declines progressively. As intake increases, the rate of ingested passage increases. Since fermentative digestion is relatively slow, the extent of cell wall digestion is reduced. High concentrate diets result in the production of large amounts of volatile fatty acids, which may reduce the pH of the rumen and small intestine to within 5.0 to 6.0. (Yet, in ruminants on all-forage diets, the pH may range up to 7.0.) At a pH of less than 6.0, the growth of cellulolytic bacteria is inhibited (Hugnate, 1966; Slyter et al., 1970). Hemicellulose prepared from rumen liquor of sheep fed a hay diet reached maximum activity 5 hr after feeding; the enzyme complex was most active at pH 7.0 (Morrison, 1976). The pH optima for the following carbohydrases are: pancreatic a-amylase, 6.9; intestinal maltase, 6.8 to 7.0, and oligo-1-6 glucosidase, 6.2 to 6.4 (data from various sources summarized by Armstrong and Beever, 1969). Thus, it is indicated that the gastrointestinal environment of ruminants ingesting high levels of high concentrate diets would impair the activity of enzymes responsible for the digestion of cellulose, starch and other nutrients. This could account for most of the depression in the digestibility of energy that accompanies increased energy intake.

Other Research Needs Associated with Energy Digestibility and Metabolizability. Methods and criteria of chemical and physical definition are needed to refine the prediction of the DE and ME values of diets at different levels of input. Also, methods of estimating the net nutritive effects of the DE and ME of various diets are needed as rationing aids.

Depending on the nature of the diet and the level of feeding, ruminants lose as combustible gases 5 to 12% of the dietary energy ingested (Blaxter and Clapperton, 1965). Although methanogenesis is a wasteful process, its inhibition would be beneficial only if other processes such as digestibility of energy, synthesis of microbial protein and accumulation of hydrogen were not inhibited to the same extent (Czerkawski, 1971, 1972, 1974). Many compounds (e.g., chloroform, methylene chloride, carbon tetrachloride, long-chain fatty acids, bromochloromethane, hemiacetyl of chloral hydrate, 2,2,2-trichloroacetamide, trichloro-l-adipate and others) are known to suppress l-anine production (Bauchop, 1967; Clapper-
heat production was 109 kcal/day greater for maintenance or body gain. Clapperton and Czerkawski (1972) infused 440 mg of chloroform into the rumens of sheep as the animals ate 1,000 g/day of hay in two equal meals. In control periods, only the hay was fed. Chloroform did not affect the energy loss in the feces or urine, but it reduced the CH₄ production from 23.8 to .9 liters/day and increased the production of H₂ from 0 to 17.7 liters/day. The net intake of ME by the sheep receiving the chloroform was 163 kcal/day greater than that of the sheep not given chloroform. Since heat production was 109 kcal/day greater for the chloroform-treated sheep, indicating a Kᵢ value of .33, it is unlikely that suppression of methane production improved the efficiency of utilization of the ME.

In feeding trials, methane depressants have resulted in both negative and positive responses. Sheep given 2,2,2-trichloroacetamide (Trei et al., 1971) or HCS (Trei et al., 1972) grew more rapidly and converted feed 3 to 7% more efficiently than did the controls. Opposite effects were observed in sheep given bromochloromethane (Sawyer et al., 1974) or trichloroethyl adipate (Clapperton, 1977). Also, no improvement in rate of body weight gain or feed efficiency of cattle was effected by bromochloromethane (Johnson et al., 1972). Chloroform administered by rumen cannula to lactating goats did not affect the milk yield; however, it reduced the fat concentration and increased the protein content of the milk (Clapperton and Basmaeil, 1976).

Although the suppression of methane production and the conversion of hydrogen to energy-conserving substances would represent a substantial gain in ME, little gain of practical value has been effected to date. In some studies, methane suppressants have reduced feed intake. Animals adapt to some antimethanogenic agents by returning to normal methane outputs a few weeks after the initial suppression (Clapperton, 1977). The benefits of methane suppressants for growing-fattening animals may be different from those for lactating animals.

Dry matter digestibility by ruminants is somewhat lower under cold ambient temperatures than it is under higher temperatures. In a summary of 11 experiments carried out in cold regions of Western Canada, Young (1976) reported an average decline in digestibility of .18 percentage units per degree decrease in temperature below 20°C at the same level of feed input. In some experiments, there was little or no effect. The reduction in digestibility was attributed to an increased rate of ingesta passage through the gastrointestinal tract, and Kennedy et al. (1976) observed that digestibility of dry matter in the intestines accounted for more of the apparent digestion in the whole gastrointestinal tract of sheep kept in the cold than it did in sheep kept at higher temperatures. Also, the reduced time of retention of ingesta in the rumen and the decreased digestibility of energy observed at low temperatures are associated with increases in the concentration of thyroid hormone in the blood plasma (Kennedy et al., 1977). Wöhlbier and Schneider (1965) observed no effect of temperature on the digestibility of energy by steers over a range of 10 to 30°C.

Efficiency of Utilization of ME by Farm Animals

General Model of Examination. The model by which certain kinds of influences on the utilization of ME will be examined is represented in figure 2. This examination of animal energetics employs the well-established linearity of the relationship between the ME intake (X) above maintenance and the resulting energy balance (Y), i.e., energy gained by the body or put into other products. Both of these variables will be expressed in kilocalories per kilogram of body weight raised to the power .73 or .75, and will sometimes be referred to as...
metabolic body size (MBS). The relationship between these two variables provides: (1) the slope, which is the index of the efficiency with which ME is utilized to support a given function such as body gain, lactation, egg production or reproduction, and (2) the ME-intake intercept at zero energy storage; this value is the ME requirement of maintenance. In using this scheme to partition the net efficiency of one body function when several body functions are being performed simultaneously, it is necessary to deduct from the total energy balance the energy gain represented by the functions not being examined and to subtract the ME input associated with the functions not being investigated from the total ME input. However, much further research is needed to refine requisite coefficients for partitioning partial efficiencies in animals performing two or more functions.

Requirement of ME for Maintenance and the Net Utilization of ME for Certain Production Functions. The efficiency with which ME is utilized is influenced by, or associated with: (1) environmental conditions, especially temperature, humidity and wind movement; (2) extent of physical activity; (3) sex; (4) gastrointestinal architecture and major digestive agents; (5) the nature of the absorbed products of digestion; (6) the body functions being performed, and (7) a variety of dietary characteristics. For example, insufficient amounts of protein and of certain vitamins and mineral elements in the diet, along with an imbalanced assortment of absorbed amino acids, reduce the efficiency with which ME is utilized by animals for maintenance and production.

Since a detailed account of some of these influences and associations is given elsewhere (Reid, 1974; Reid and White, 1978a), only a few examples will be cited here to indicate the present boundaries of progress.

The partial efficiencies with which ME is utilized to support the individual body functions, in combination with the ME value of the diet, provide the means to derive by the factorial method feeding guides that might be applied under different practical conditions. In table 2, a summary is given of the maintenance requirements and the efficiency with which ME is utilized to support certain production functions of several animals fed diets commonly used in practice. The summary includes values rounded from those reported by Reid (1974) and Reid and White (1978a), but also contains data for immature mink (Harper et al., 1978), 10- to 25-day-old chicks (Thomas, 1966), 4- to 10-kg pigs (Close et al., 1979) and laying hens (Waring and Brown, 1967). These data reflect a higher maintenance requirement of very young animals than of older animals (e.g., among mink, chickens, pigs and calves), of milking cows than of nonlactating cows and of laying hens than of mature, fattening cockerels. Differences attributable to degree of maturity also exist in other species.

The maintenance requirement of ME increases with: (1) increasing physical activity, e.g., grazing animals require 10 to 90% more ME than do ruminants confined to stalls (Reid et al., 1958; Graham, 1964a,b; Young and Corbett, 1972), and increasing gradients increase the energy cost of locomotion (Clapperton, 1964; Ribeiro et al., 1977); (2) ambient temperature below or above the zone of thermal comfort (Joyce and Blaxter, 1964; Shannon and Brown, 1969; Nehring, 1958); (3) increasing amounts of dietary protein above the requirement (Garrett, 1970; Tyrrell et al., 1970), e.g., in dairy cows, ME expense of metabolizing amino acids ingested in excess of the protein requirement is 7.2 kcal/g of digestible nitrogen (Tyrrell et al., 1970); and (4) decreasing metabolizability of dietary energy (van Es and Nijkamp, 1967a,b; Moe et al., 1970). The range in ME requirements for each kind of animal listed in table 2 reflects both the quality of the diet ingested and the productive function being performed.

The data in table 2 also indicate that the net efficiency with which ME is utilized for various
TABLE 2. REQUIREMENT OF METABOLIZABLE ENERGY (ME) FOR MAINTENANCE AND THE NET UTILIZATION OF ME FOR CERTAIN PRODUCTION FUNCTIONS BY VARIOUS ANIMALS

<table>
<thead>
<tr>
<th>Animal</th>
<th>Maintenance requirement of ME, kcal/MBSa/day</th>
<th>Net utilization of ME above maintenance for:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Body gain, %</td>
</tr>
<tr>
<td>Mink, 20% mature</td>
<td>148</td>
<td>71</td>
</tr>
<tr>
<td>Pigs, 4 to 10 kg</td>
<td>148</td>
<td>83</td>
</tr>
<tr>
<td>Pigs, 100 to 180 kg</td>
<td>85 to 120</td>
<td>75 to 85</td>
</tr>
<tr>
<td>Chickens, 10 to 25 days old</td>
<td>170</td>
<td>80</td>
</tr>
<tr>
<td>Chickens, older</td>
<td>85b to 120e</td>
<td>75 to 85</td>
</tr>
<tr>
<td>Calves, 16 to 50 days old, milk-fed</td>
<td>145</td>
<td>85</td>
</tr>
<tr>
<td>Guinea pigs</td>
<td>85 to 90</td>
<td>60 to 70</td>
</tr>
<tr>
<td>Rabbits</td>
<td>85 to 110</td>
<td>60 to 70</td>
</tr>
<tr>
<td>Horses</td>
<td>85 to 110</td>
<td>60 to 70</td>
</tr>
<tr>
<td>Sheep, growing or milking</td>
<td>75 to 100</td>
<td>60 to 70</td>
</tr>
<tr>
<td>Cattle, growing</td>
<td>100 to 125</td>
<td>30 to 65e</td>
</tr>
<tr>
<td>Cows, milking</td>
<td>125</td>
<td>30 to 65e</td>
</tr>
<tr>
<td>Cows, nonlactating</td>
<td>100</td>
<td>30 to 65</td>
</tr>
</tbody>
</table>

aMBS = metabolic body size; body weight in kilograms raised to .73 or .75 power.

bMature (3.5 to 4.8 kg) fattening cockerals.
cLaying hens.
dEstimated values.
eHigher values were obtained for females; lower values were found for males fed the same diets.

The partial efficiency of ME utilization is associated with the body function being performed; that of lactation is greater than that of body gain except when fattening accompanies lactation (table 2). Although not shown in table 2, the apparent partial efficiency of maintenance is greater than that of production functions. The net efficiency of utilization of the available ME for repro-
duction (i.e., energy retention in the conceptus) in the cow and ewe ranges from 10 to 25% (van Es, 1961; Brockway et al., 1963; Graham, 1964c; Hashizume et al., 1964; Moe et al., 1970; Moe and Tyrrell, 1972; Garrett et al., 1976).

Although the ambient temperature and the extent of physical exercise have pronounced effects on the amount of ME required for maintenance, they do not influence the degree to which ME ingested above maintenance is used for production functions.

As the data in tables 1 and 2 show, both the ME values of the usual diets and the efficiency with which ME is utilized for productive functions are lowest in ruminants. Accordingly, there is much greater opportunity to improve the energetic efficiency of ruminants than of other animals, particularly the simple-gutted ones. Therefore, the ensuing paragraphs of this review will concern subjects that are significant especially to the energetics of ruminants.

Relation of Metabolizability of Energy to the Net Utilization of ME. The proportion of the dietary GE that is ME (i.e., ME/GE, sometimes denoted as “q,” the quality factor) influences the net efficiency with which ME is utilized for various body functions. Figure 3 depicts this effect. Although the effect of the metabolizability of energy on net utilization is probably different for the individual body functions (Moe and Tyrrell, 1975), van Es (1976) proposed as a compromise that, as the ratio of ME/GE increases by 1 percentage unit, the requirement of ME for maintenance, milk production and body gain in cattle decreases by about .4%.

End Products of Digestion. For 80 years preceding 1957, the cause of the lower energetic efficiency of ruminants than of simple-gutted animals remained a mystery, and it is not wholly settled even yet. von Mering and Zuntz (1877) and others attributed the ruminant’s high heat increment to the “work of digestion.” Since the early 1900’s, it has been recognized that the productive value of the ME provided by starch is considerably higher in the simple-gutted animals than in the ruminants. Data illustrating this difference are summarized in table 3.

Eventually, the viewpoint developed that the high heat increment of ruminants is associated with the volatile fatty acids (VFA) produced in the rumen. In experiments dealing with lipogenesis, Armstrong and Blaxter (1957, 1961) and Armstrong et al. (1958) infused acetic acid, propionic acid and butyric acid, singly or in mixtures, into the rumen of sheep fed a maintenance diet of hay. The net efficiencies with which the ME of the VFA infused singly was utilized for body energy gain were: acetic acid, 32.9%; propionic acid, 56.3%, and n-butyric acid, 61.9%. The ME of mixtures of the VFA containing molar proportions of 75 and 25% acetic acid (and of 15 and 45% propionic acid, respectively) was utilized with a net efficiency of 31.8 and 58.1%, respectively. When glucose was infused into the rumen, abomasum or a jugular vein, Armstrong and Blaxter (1961) found the net efficiencies to be 54.5, 71.5 and 72.8%, respectively. Thus, fermentation in the rumen reduced the net efficiency of glucose utilization. When its fermentation was circumvented by administration into the abomasum or jugular vein, the net utilization for energy gain in sheep was similar to that (73.7%) observed by Nehring (1961) in rats fed glucose. As a consequence of such observations, the viewpoint developed that increased proportions of propionic acid in relation to those of acetic acid in the ruminal mixture of VFA result in increased efficiency of ME utilization for body gain. Also, it seemed that the difference in resultant VFA mixtures might explain the greater net efficiency of ME provided by concentrates than of ME supplied by forages.

However, many experiments conducted since 1965 have failed to confirm that the ruminal ratio of acetic to propionic acid per se influences the net utilization of ME for body energy gain. The results of one such experiment...
TABLE 3. UTILIZATION OF METABOLIZABLE ENERGY OF STARCH FOR BODY GAIN BY VARIOUS ANIMALS\textsuperscript{a}

<table>
<thead>
<tr>
<th>Species</th>
<th>Utilization of ME for body gain, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rat</td>
<td>75.5 ± 1.2</td>
</tr>
<tr>
<td>Pig</td>
<td>75.5 ± 1.6</td>
</tr>
<tr>
<td>Rabbit</td>
<td>67.0 ± 1.2</td>
</tr>
<tr>
<td>Sheep</td>
<td>64.1 ± 1.6</td>
</tr>
<tr>
<td>Cattle</td>
<td>64.1 ± 1.7</td>
</tr>
</tbody>
</table>

\textsuperscript{a}Data of Nehring \textit{et al.} (1961) and Jentsch (1967).

(Bull \textit{et al.}, 1970) are summarized in table 4. It should be noted that neither the net utilization of ME for body gain nor the maintenance requirement was different at two different acetic to propionic acid ratios with each of two basal diets ingested by sheep. Certain characteristics of that experiment (Bull \textit{et al.}, 1970) were different from those of some of the other studies: (1) the hay was of very high quality (74% DE); (2) both diets were finely ground and pelleted, and (3) acetic acid was administered as triacetin, thus providing glycerol, and glucose precursor. In a recent study, Ørskov \textit{et al.} (1978) infused two levels of each of six mixtures of VFA into the rumen and administered protein into the abomasum of sheep receiving no basal feed. On a molar basis, each VFA mixture contained 10% butyric acid. The molar ratios of acetic to propionic acid ranged from 0.64:1 to 17:1. The net utilization of ME for body gain ranged from 60 to 65% for ratios ranging from 1:1 to 17:1. At the lowest acetic acid concentration, the net efficiency was 75%. The maintenance requirement of ME did not differ between treatments, and the mean value for all treatments was 103 kcal/kg\textsuperscript{75}/day. It was concluded (Ørskov \textit{et al.}, 1978) that since the VFA proportions resulting from practical diets are not outside the range of 1:1 to 17:1 ratios of acetic to propionic acid, differences in the utilization of ME cannot be explained by differences in the efficiency with which VFA are utilized.

It is well established that the net utilization for body gain of ME from pelleted, finely ground forage is higher than that of ME provided by forage of the same source fed in chopped or long form. Also, the ME requirement for maintenance is somewhat lower for animals ingesting forage of small particle size than it is for those fed chopped or long forage. Some typical results demonstrating these effects, as reported by Paladines \textit{et al.} (1964), are summarized in table 5. Since it is well established that the feeding of forages of small particle size results in a ruminal mixture that contains a higher proportion of propionic acid and a lower proportion of acetic acid than do mixtures resulting from the feeding of forages in chopped or long form, it had seemed that the mixture of VFA produced might be accountable. However, Thomson \textit{et al.} (1972) and Beever \textit{et al.} (1972) observed that 23 to 51% more of the energy of finely ground forage than of chopped forage of three sources escaped from the rumen and was digested in the small intestine. These observations imply that more carbohydrate might be absorbed as

TABLE 4. UTILIZATION OF ACETIC ACID FOR BODY GAIN BY SHEEP\textsuperscript{a}

<table>
<thead>
<tr>
<th>Basal diet</th>
<th>Additive</th>
<th>Ruminal C\textsubscript{2} : C\textsubscript{3} ratio\textsuperscript{b}</th>
<th>Maintenance requirement, kcal/MBS/day</th>
<th>Net utilization of ME, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hay, pelleted\textsuperscript{c}</td>
<td>Triacetin\textsuperscript{d}</td>
<td>5.4:1</td>
<td>88</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td>Glycerol\textsuperscript{e}</td>
<td>3.2:1</td>
<td>86</td>
<td>60</td>
</tr>
<tr>
<td>Hay and corn, pelleted\textsuperscript{c}</td>
<td>Triacetin\textsuperscript{d}</td>
<td>5.2:1</td>
<td>88</td>
<td>64</td>
</tr>
<tr>
<td></td>
<td>Glycerol\textsuperscript{e}</td>
<td>2.9:1</td>
<td>85</td>
<td>62</td>
</tr>
</tbody>
</table>

\textsuperscript{a}Data of Bull \textit{et al.} (1970).
\textsuperscript{b}C\textsubscript{2} = acetic acid and C\textsubscript{3} = propionic acid.
\textsuperscript{c}Early-cut alfalfa; DE value was 74% at the maintenance level of intake.
\textsuperscript{d}Triacetin provided 10.2% of dietary GE.
\textsuperscript{e}Glycerol provided 1.8% of dietary GE.
TABLE 5. EFFECT OF PHYSICAL FORM OF FORAGE AND DIET COMPOSITION ON THE ENERGETIC EFFICIENCY OF GROWING SHEEP

<table>
<thead>
<tr>
<th>Diet</th>
<th>DE at maintenance, %</th>
<th>Maintenance requirement, kcal/MBS/day</th>
<th>Net utilization of ME, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hay b, chopped</td>
<td>60</td>
<td>92</td>
<td>31</td>
</tr>
<tr>
<td>Hay b, ground and pelleted</td>
<td>58</td>
<td>87</td>
<td>43</td>
</tr>
<tr>
<td>50% hay b + 50% corn, ground and pelleted</td>
<td>73</td>
<td>82</td>
<td>57</td>
</tr>
</tbody>
</table>

aData of Paladines et al. (1964).
bHay of same source in all diets.

simple sugars rather than as VFA from ground forage than from chopped or long form.

It is difficult to assess the proportion of the heat increment that is ascribable to fibrousness or physical form of the diet. However, Osuji et al. (1975) observed that the energy costs of eating (kilocalories/kilogram of dry matter ingested) were, 57 for chopped, dried grass and 5.7 for pelleted, dried grass. Some of the same workers (Webster et al., 1976) showed that the total costs of eating, comminuting, fermenting and processing the ingesta in the gut constitute 25 to 30% of the total heat increment, but that the energy costs of work by gut tissue are not different for the two physical forms. Earlier, Webster et al. (1974) had found that the “work of digestion” is high for long or chopped forages.

Tyrrell et al. (1976) conducted a study to determine the effect of the nature of the basal diet on the utilization for lipogenesis of acetic acid infused intraruminally into mature, nonlactating cows. Two basal diets, consisting of hay alone and 30% hay with 70% concentrates, were used. In one experiment, both basal diets were fed in ground, pelleted form, and in another, the hay was fed in long form and the concentrates in meal form. The efficiencies with which the ME provided as acetic acid was utilized for body gain are summarized in table 6. These data show a markedly higher utilization of the ME of the acetic acid increment for the high concentrate basal diet than for the medium quality hay basal diet. Qualitatively similar observations had been made previously in a study of growing lambs fed high and low concentrate diets (Poole and Allen, 1970).

In another experiment with growing heifers and nonlactating cows fed high forage diets (Tyrrell et al., 1977a), acetic acid was infused into the rumen or glucose was infused into the abomasum, or both were infused simultaneously. The simultaneous addition of glucose into the abomasum effected a marked improvement in the utilization of the ME provided by the acetic acid. When no glucose was administered, the utilization of acetic acid infused intraruminally was essentially nil. Stokes and Thomas (1977) also indicated that the difference in the net utilization of ME for fattening is linked with a greater uptake of glucose from the small intestine of sheep fed high concentrate diets than from that of sheep fed a high forage diet.

The results of these studies are consistent with the hypothesis that glucose is required for the efficient utilization of acetate for lipogenesis as the result of glucose oxidation via the pentose phosphate cycle to yield reduced nicotinamide adenine dinucleotide, which is required to lengthen fatty acid chains. Although the observations of Tyrrell et al. (1976, 1977a) and Stokes and Thomas (1977) clarify the disparate results of many of the experiments conducted since 1957, those of Ørskov et al. (1978) seem enigmatic unless sufficient glucose was produced from certain amino acids, butyrate and propionate to maintain a high level of acetate utilization.

Association of Sex of Ruminants with Energetic Efficiency. In the study by Bull et al. (1970), in which rams and ewes were fed each of two diets, the maintenance requirement of ME did not differ between sexes, but the net efficiency with which ME was utilized for body energy gain was decidedly higher for ewes (67%) than for rams (57%, table 7). From 20,
TABLE 6. EFFECT OF BASAL DIET UPON THE UTILIZATION OF ACETIC ACID FOR BODY GAIN BY NONLACTATING COWS a

<table>
<thead>
<tr>
<th>Exp. no.</th>
<th>Basal diet of:</th>
<th>Utilization (%) of ME from acetic acid</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>30% hay + 70% concentrates</td>
<td></td>
</tr>
<tr>
<td>1 b</td>
<td>Hay</td>
<td>24.2</td>
</tr>
<tr>
<td>2 c</td>
<td></td>
<td>28.1</td>
</tr>
<tr>
<td>Mean, weighted</td>
<td></td>
<td>26.6</td>
</tr>
</tbody>
</table>

aData of Tyrrell et al. (1976).
bBoth basal diets fed in pelleted, ground form.
cHay fed in long form and concentrates in meal form.

to 50 kg, ewes contained 30 to 35% more fat and 3 to 17% less protein than did rams. During the 175-day feeding period, ewes gained 30% more fat and 31% less protein than did rams. Similar results were obtained in studies with heifers, bulls and steers of two breeds of cattle (R. Anrique, H. Ayala, S. Simpfendorfer, A. Fortin, A. F. Kertz, J. T. Reid and G. H. Wellington, unpublished data). The greater leanness of bulls than steers was associated with a significant increase in daily loss of ME as heat, even though the bulls and steers were pair-fed (Webster, 1977).

The energetic efficiency and carcass composition of steers pair-fed a basal diet or a diet containing diethylstilbestrol (DES) were examined by Rumsey et al. (1977) and Tyrrell et al. (1977b). At the end of the 27-week feeding period, they observed that the gain in carcass of the DES-fed steers consisted of 33% more protein, 76% more ash, 4% more energy, but 1% less fat than that of the controls. As shown in table 8, despite the larger carcasses and protein gain of the DES-fed steers, the utilization of ME for body energy storage by the DES-fed steers (40.8%) was lower than that by the controls (50.6%).

Some Research Needs Concerning Whole-body Energetics of Animals. Continued examination is needed to determine the exponents of body weight that are most effective to express energetic data for various ages and kinds of animals and conditions. The literature cites exponents ranging from .5 to 1.0. In 1964, the Energy Metabolism Symposium (Kleiber, 1964) adopted body weight .75 as the reference base for comparing the metabolism of various animals. This practical compromise was based on the proposals of Kleiber (1932) and Brody and Procter (1932), who computed the exponents of best fit between the interspecific basal metabolic rate of mature animals and their body weights to be .75 and .734, respectively. However, it is recognized that a value approaching .5 may be more precise for growing animals, group-confined animals and animals with little thermal insulation. Also, the body weight value employed and the maintenance of conditions under which basal metabolic rate may be determined are fraught with many problems relative to interspecific uniformity. Ideally, although seldom practical, the power function would need to be determined for each experimental situation, especially if the size of the subjects were appreciably different.

Thonney et al. (1976) showed that weight exponents are not equal for species-sex-source, sex-source within species or species-source within subclasses. Thus, a universal equation relating basal heat production to body weight cannot be considered the best fit for species-
TABLE 8. EFFECT OF DIETHYLSTILBESTROL (DES) ON THE CARCASS COMPOSITION AND ENERGETIC EFFICIENCY OF STEERS

<table>
<thead>
<tr>
<th>Treatment of ME for gain, %</th>
<th>Carcass (g)</th>
<th>Weight</th>
<th>Protein</th>
<th>Fat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>50.6</td>
<td>240</td>
<td>37.6</td>
<td>73.8</td>
</tr>
<tr>
<td>DES</td>
<td>40.8</td>
<td>258</td>
<td>42.2</td>
<td>73.4</td>
</tr>
</tbody>
</table>

aData of Rumsey et al. (1977) and Tyrrell et al. (1977b).

bDiet contained 70% concentrates and 30% forage; DES-treated group was fed 20 mg of DES per day; animals in the two groups were pair-fed to gain about 1 kg/day for 27 weeks.

cCarcass characteristics at end of feeding period; the gain in the carcass of the DES steers consisted of 33% more protein, 76% more ash, 4% more energy, but 1% less fat than in that of the controls.

Relation of Body Composition to Energetic Efficiency

Among animals undergoing sustained, uninterrupted growth, those that are depositing fat at the most rapid rate have the highest efficiency of body energy storage and the lowest efficiency of weight gain per unit of ME input. Within species, the amounts of body fat and protein at a given body weight vary among breeds depending on their maturation rates. Early-maturing breeds of ruminants have more fat and less protein than do late-maturing breeds of the same body weight. Within breeds, the propensity to fatten is associated with sex (table 7; figure 4), which is probably a reflection of the kinds of hormones and the synchrony of hormonal action that influence the maturing rate. Among ruminants, the female matures earlier and contains more fat at the same body weight than does the male with intact gonads. The male castrate is intermediate in these characteristics. Other animals, such as fowl and pigs, are different from ruminants. For example, body compositions of young male and female pigs (.9 to 30 kg of body weight) with intact gonads were not different at the same weights (Wood and Groves, 1964). Although the differences are not large beyond 30 kg, male castrate pigs have a little less fat at body weights below 70 kg and a little more fat above 70 kg than do females of the same body weights (Reid et al., 1968). At 100 kg, barrows contain about 2.2 kg more fat than do gilts.

Many reports have been published claiming that body composition has been influenced by certain nutritional treatments. In some instances, the conclusions have been correct; however, in others, it is clear that the effects of
Figure 4. Relationship of sex and level of energy input to the body composition of Holstein cattle.
the dietary treatments on body composition have not been independent of the effects of the treatments on total body weight. In some experiments, animals were fatter, and thus contained different quantities of other chemical components, chiefly because they were larger than the animals with which they were compared.

In the following paragraphs, evidence will be presented that indicates that rapid fattening and low protein storage are associated with a high energetic efficiency in animals growing uninterrupted. Also, an anomaly to this generalization that occurs in compensatory growth will be considered.

Rate of Fattening and Protein Deposition, and Energetic Efficiency. Data in table 7 show that the energetic efficiency and rate of fat gain is lower in ewes than in intact rams. In Holstein cattle fed the same diet ad libitum or at about 65% of ad libitum, the order by sex of the amounts of body fat at the same body weights and feeding levels was heifers > steers > bulls, as shown in figure 4 (R. Anrique, H. Ayala, S. Simpfordorfer, A. Fortin, A. F. Kertz, J. T. Reid and G. H. Wellington, unpublished data). The order of the efficiency of body energy gain was the same, but the order of the amounts of body protein was opposite to that of body fat. In that study, the disconcerting observation was made that the dietary energy input influenced the body composition at the same body weights; i.e., more fat and less protein were stored in animals ingesting the higher level of energy than in those receiving the lower level. This observation is different from those made by Guenther et al. (1965), Stuedemann et al. (1968), Murray et al. (1975), Swan and Lamming (1975) and Jesse et al. (1976). Those authors concluded that the level of energy intake above maintenance has little effect on body composition of cattle. However, Andersen (1975) reported that cattle of the same body size fed ad libitum contained progressively more separable fat and less muscle than did their mates fed at 85, 70 or 55% of ad libitum.

As the result of slaughter experiments that we and our co-workers conducted with over 1,200 sheep, we concluded that the body composition within breed and sex of sheep which had been maintained in continuously positive energy balance was rigidly related to body weight, irrespective of feeding level and age of animal (Reid and White, 1978b). For example, Burton and Reid (1969) reported that despite differences in the plane of nutrition imposed and in the body weights of sheep attained at given ages, weights of the chemical components of the whole, empty body were closely associated with body weight.

In most of the studies with cattle cited above, the energetic efficiency was not determined. As demonstrated in table 8, steers fed the anabolic agent, DES, had a greater rate of protein deposition but a lower energetic efficiency than their pair-fed mates that did not receive DES.

Rats fed by stomach tube in two meals a day the same amount of a high carbohydrate diet ingested by their ad libitum-fed mates gained the same amount of body weight, considerably more body fat and energy and less body protein and had a decidedly higher gross energetic efficiency (I. K. Han and J. T. Reid, unpublished data). Some of the observations made in that study are summarized in table 9.

The data cited, as well as other data (Pullar and Webster, 1972), imply that in the usual growth of animals, ME is utilized more efficiently in the net synthesis of fat than it is in the net synthesis of protein, and that the energetic efficiency is inversely related to the proportion of ME that is utilized for protein synthesis. A major future challenge is finding some means of reducing fat and increasing protein storage in meat-producing animals, yet improving their energy economy. Whether, for example, animals might be re-engineered hormonally by immunological or other means to ply usual biological events needs to be examined.

Relative Efficiency of Protein and Fat Synthesis. Attempts have been made by two methods to partition the amount of ME ingested above maintenance between body protein and fat. The methods are:

1. Total ME intake = a + b1 fat + b2 protein, where ME intake is expressed as kilocalories/MBS/day, and fat and protein are expressed as grams/MBS/day or kilocalories/MBS/day; and

2. Total ME intake-ME for maintenance = a fat + b protein, where ME is expressed as kilocalories/MBS/day, the quantities of protein and fat are expressed as kilocalories/MBS/day and the reciprocals of a and b represent the respective energetic efficiencies.
TABLE 9. EFFECT OF FREQUENCY OF MEALS ON BODY COMPOSITION AND GROSS EFFICIENCY OF RATS

<table>
<thead>
<tr>
<th>Intake</th>
<th>Body weight, g</th>
<th>Fat, g</th>
<th>Protein, g</th>
<th>Energy, kcal</th>
<th>Gross efficiency, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ad libitum</td>
<td>85.6</td>
<td>13.8</td>
<td>19.0</td>
<td>237</td>
<td>16.6</td>
</tr>
<tr>
<td>2 meals/day</td>
<td>83.5</td>
<td>30.5</td>
<td>12.8</td>
<td>359</td>
<td>25.9</td>
</tr>
</tbody>
</table>

*aFrom I. K. Han and J. T. Reid (unpublished data).  
*bGross efficiency (%) = (body energy storage/dietary GE) × 100.

Table 10 presents a summary of estimates of the efficiency with which ME is utilized for the net synthesis of protein and fat in various animals, and it also itemizes several estimates of the theoretical efficiencies. In the estimation of theoretical efficiencies, the bases are that known biochemical pathways and substrates are operating, and it is assumed that nutrients replace each other in proportion to their free-energy yield computed as the pyrophosphate-bond energy of ATP. The hypothetical value for protein synthesis assumes that body protein is produced from dietary protein that has a biological value of 100%, i.e., protein containing essential and nonessential amino acids in the same proportions as those of the synthesized protein. However, if nonessential amino acids were synthesized from carbon fragments and ammonia, the efficiency would be lower than that in the ideal situation. If an essential amino acid were lacking, other essential amino acids in excess of the required complement would be deaminated and the residue would be utilized to synthesize fat, resulting in a lower efficiency. In the synthesis of fat, the theoretical computations assume that glucose gives rise to acetyl coenzyme A by glycolysis. If glucose were produced from simpler compounds by gluconeogenesis, which to a great degree is the case with ruminants, the derived efficiency of fat synthesis would be lower.

As indicated in table 10, the estimated
calorimetric efficiency of fat synthesis in animals is about the same as, or a little higher than, the hypothetical efficiency. However, the estimated calorimetric efficiency of protein synthesis in animals is considerably lower than the hypothetical value. This suggests that protein synthetic transactions in the whole animal are different from those theoretically expected to occur or that the energy costs of such ancillary events as protein turnover and resynthesis are not appropriately accounted for.

The existing data (table 10) indicate that the efficiency of protein synthesis in the very young pig, lamb and calf is considerably higher than that in older animals of the same species. Whether such trends are real or partly the result of the method of estimation is not known. Most data are based upon partitioning of the ME intake among maintenance and protein and fat storage by multiple regression analysis. The requirement for maintenance is usually large relative to that for growth, and changes in the maintenance requirement and in the proportion of energy partitioned into protein and fat are related to the degree of physiological maturity of the animal. Thus, maintenance and the storage of fat and protein are not genuinely independent variables. In a study designed to overcome to some degree autocorrelation among the measured variables, Pullar and Webster (1974) estimated efficiencies of protein and fat synthesis in lean and obese rats. Their estimates were similar to those determined by Schiemann et al. (1969), who used the partition method.

The amount of ME charged to maintenance has a pronounced effect on the estimated efficiency of protein and fat synthesis. In the experiment of Burlacu et al. (1976), the mean maintenance requirement of ME of pigs weighing 9 to 58 kg was 151 kcal/MBS/day, and the efficiencies of utilization of ME for protein and fat synthesis were 62 to 100%, respectively. The maintenance requirement is similar to that (148 kcal/MBS/day) determined for pigs under a body weight of 10 kg (Close et al., 1979), but it appears to be considerably higher than that of larger pigs (table 2). Accordingly, the estimated efficiencies of protein and fat storage are probably overestimated.

The evidence is overwhelming that the efficiency with which ME is utilized for net protein storage is considerably lower than that with which it is used for net fat storage (table 10), and that it is also much lower than the theoretical efficiency of net synthesis. In the growing animal, the rate of accretion of muscle protein is small in relation to the turnover of protein. Other proteins turn over even more rapidly than muscle protein. According to Milligan (1971), the efficiency of peptide bond synthesis is only 3.9%, and because of turnover, the same protein would have to be resynthesized a number of times. Thus, the cost of turnover, resynthesis, synthesis of nonessential amino acids and transport of nutrients contributes greatly to the low energetic efficiency of net protein synthesis as estimated in the whole animal.

**Body Composition and Energetic Efficiency in Compensatory Growth.** The body composition of growing sheep maintained in continuously positive energy balance is quite different from that of similar animals that have undergone a period of compensatory growth to reach the same body weights. Figure 5 shows the growth patterns of sheep that were continuously fed and of those that were deprived so that they would lose about 30% of their body weight and then realimented in one study (Burton et al., 1974) of compensatory growth. Points 1, 2, 3 and 4 in the figure designate the weights and times at slaughter. The weights of chemical components and the amounts of energy in the sheep continuously fed and in those deprived or deprived and refeed are summarized in table 11. It will be noted that sheep at 50 kg (group 1) that had been grown continuously from 40 kg had the same composition as those which had been grown continuously to 70 kg and then deprived of

![Figure 5: Growth patterns of continuously fed and of deprived-refed sheep.](image-url)
TABLE 11. CHEMICAL COMPOSITION AND ENERGY VALUE OF EWES GROWN BY DIFFERENT PATTERNS

<table>
<thead>
<tr>
<th>Growth group&lt;sup&gt;c&lt;/sup&gt;</th>
<th>EBW&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Water (kg)</th>
<th>Protein (kg)</th>
<th>Fat (kg)</th>
<th>Ash (kg)</th>
<th>Energy, Mcal</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>45.6</td>
<td>21.4</td>
<td>6.2</td>
<td>16.3</td>
<td>1.5</td>
<td>190.9</td>
</tr>
<tr>
<td>3</td>
<td>46.8</td>
<td>22.1</td>
<td>6.3</td>
<td>16.4</td>
<td>1.8</td>
<td>190.9</td>
</tr>
<tr>
<td>2</td>
<td>65.6*</td>
<td>26.0</td>
<td>7.5*</td>
<td>29.7*</td>
<td>2.0</td>
<td>327.3*</td>
</tr>
<tr>
<td>4</td>
<td>63.5*</td>
<td>29.6</td>
<td>8.3*</td>
<td>22.9*</td>
<td>2.0</td>
<td>265.9*</td>
</tr>
</tbody>
</table>

<sup>a</sup>Data adapted from those of Burton et al. (1974).
<sup>b</sup>EBW = empty body weight, i.e., body weight minus ingesta.
<sup>c</sup>1,2 = grown continuously from 40 kg;
3 = grown continuously from 40 to 70 μg, starved to 50 kg;
4 = grown continuously from 40 to 70 μg, starved to 50 kg, then grown to 70 kilograms.

*Differences within components between groups 2 and 4 (P<.01).

Energy to lose body weight and return to 50 kg (group 3). Some sheep in the latter group (group 3) were fed to reach 70 kg (group 4). They contained more water and protein but less fat and energy than their mates (group 1) that were continuously fed to reach 70 kg (group 2).

In a similar experiment, Drew and Reid (1975a,b) studied sheep over the range of 30 to 50 kg body weight and obtained similar results. In addition, they studied the energetic efficiency of continuously fed and deprived-reared sheep over the same range of body weight (Drew and Reid, 1975b). Although the maintenance requirements (90 and 89 kcal/MBS/day) were not different, the efficiency with which ME was utilized for body gain was 43% over the range of growth pattern 1 to 2 (figure 5) and 57% over the range of growth pattern 3 to 4 (figure 5). Because of the longer period and consequent greater maintenance needs, sheep grown over the pattern 1-2-3-4 (figure 5) required 27% more energy per unit of body energy gain than did those grown continuously (pattern 1 to 2) to reach 50 kilograms.

Despite the reduced storage of fat and the increased accretion of protein in sheep undergoing compensatory growth, the efficiency of energy utilization was not reduced. This is an anomaly to the conclusions made previously that a high energetic efficiency of continuously growing animals is associated with a large deposition of fat and a low accretion of protein, and vice versa, and that the synthesis of fat is more efficient energetically than is that of protein.

**Overall Efficiency with Which Food Protein Is Produced by Animal Enterprises**

The energetic efficiency of a given animal as considered in the above sections is a good index of the efficiency with which that animal will produce human food during a brief time period, such as the usual feeding period. However, this measure of efficiency represents only the food energy output in relation to the dietary energy input. It does not indicate the degree of quality (e.g., the protein content) of the food product yielded. Also, the energetic efficiency of a given food production function, such as growth or milk production, is not a good index of the overall efficiency with which a livestock enterprise produces food, because it does not include the energy cost of rearing and maintaining the breeding stock that generate and nurture (in mammals) the food-producing offspring. Nor does it account for the energy costs of reproduction, nonproductive periods (e.g., dry periods of dairy cows), and losses resulting from infertility or mortality. Nevertheless, a summation of the products of the energetic efficiencies and dietary energy inputs for the various body functions, one including the appropriate respective time periods involved and the overhead losses, would provide an index of the overall efficiency of a given food-production enterprise. This kind of
accounting is impaired, however, by the lack of knowledge of the energetic efficiency of some of the body functions of certain animals. Accordingly, the following section will concern the efficiency of protein production in various food products of animal origin expressed per unit of DE input.

DE Cost of Protein Production. Since the chemical nature, the degree of refinement and, therefore, the DE value of the usual diet vary greatly among different kinds of animals, DE serves as a biologically equating parameter of dietary energy for all kinds of animals.

The data in table 12 represent the outputs (grams) of protein in various food products of animal origin per megacalorie of DE ingested. The values for fish (Rainbow trout) were estimated by Smith et al. (1978) and those for other animals were estimated by Reid and White (1978a). Since the efficiency of animal production increases with increasing inputs of DE per unit of time, the efficiency of protein production is shown for each of several rates of egg, broiler, pork, milk and beef production. The DE requirement of maintenance is constant per unit of metabolic size per day. Thus, with increasing inputs of DE, the proportion of the total input available for production increases. Accordingly, the efficiency of protein production increases with increasing production intensity.

The values in table 12 take into account the reproductive life span and the rates of sterility and mortality found in average to good practice in the United States. The last value for pork and beef is based on the assumption that sterility and mortality losses are nil. The protein represented by the carcass of the dams (mothers) was credited to the protein of their meat-producing offspring, milk or eggs; it was assumed that one of the offspring would replace the mother at the end of her productive life.

Because of the space needed to outline the conditions taken into account for all of the farm animal enterprises represented in table 12, only the considerations and assumptions concerning pork production will be cited here as examples of analogous considerations taken into account for the other animal enterprises. These are that: (1) the level of input, and therefore the rate of animal output, is correlated with the gross efficiency; (2) the production of 91-kg pigs at 6 months with a feed

### Table 12. Overall Efficiency With Which Animals Produce Food Protein

<table>
<thead>
<tr>
<th>Food product</th>
<th>Level of output and/or intensivity of production</th>
<th>Protein production efficiency, g protein/Mcal DE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish (salmonids)</td>
<td>1.5 kg feed/kg gain</td>
<td>40</td>
</tr>
<tr>
<td>Eggs</td>
<td>200 eggs/year</td>
<td>10.1</td>
</tr>
<tr>
<td></td>
<td>236 eggs/year(^a)</td>
<td>12.6</td>
</tr>
<tr>
<td></td>
<td>250 eggs/year</td>
<td>13.7</td>
</tr>
<tr>
<td>Broiler</td>
<td>1.6 kg/12 weeks; 3.0 kg feed/1 kg gain(^a)</td>
<td>11.9</td>
</tr>
<tr>
<td></td>
<td>1.6 kg/10 weeks; 2.5 kg feed/1 kg gain</td>
<td>13.7</td>
</tr>
<tr>
<td></td>
<td>1.6 kg/8 weeks; 2.1 kg feed/1 kg gain</td>
<td>15.9</td>
</tr>
<tr>
<td>Pork</td>
<td>91 kg/month; 6 kg feed/1 kg gain</td>
<td>5.0</td>
</tr>
<tr>
<td></td>
<td>91 kg/6 months; 4 kg feed/1 kg gain(^a)</td>
<td>6.1</td>
</tr>
<tr>
<td></td>
<td>91 kg/month; 2.5 kg feed/1 kg gain</td>
<td>8.7</td>
</tr>
<tr>
<td></td>
<td>Biological limit (?); 2 kg feed/1 kg gain; no losses</td>
<td>12.1</td>
</tr>
<tr>
<td>Milk</td>
<td>3,600 kg/year; no concentrates</td>
<td>10.5</td>
</tr>
<tr>
<td></td>
<td>4,944 kg/year; 22% of energy as concentrates(^a)</td>
<td>12.4</td>
</tr>
<tr>
<td></td>
<td>5,400 kg/year; 25% of energy as concentrates</td>
<td>12.8</td>
</tr>
<tr>
<td></td>
<td>9,072 kg/year; 50% of energy as concentrates</td>
<td>16.3</td>
</tr>
<tr>
<td></td>
<td>13,608 kg/year; 65% of energy as concentrates</td>
<td>20.5</td>
</tr>
<tr>
<td>Beef</td>
<td>500 kg/15 months; 8 kg feed/1 kg gain(^a)</td>
<td>2.3</td>
</tr>
<tr>
<td></td>
<td>500 kg/12 months; 5 kg feed/1 kg gain</td>
<td>3.2</td>
</tr>
<tr>
<td></td>
<td>Highly intensive system; no losses</td>
<td>4.1</td>
</tr>
</tbody>
</table>

\(^a\)Data represent approximately average USA management conditions.
conversion rate of 4:1 represents the production rate under conditions of good practice; (3) the sow has the potential to produce five litters, each of 12 pigs, in 2½ breeding years (assumption); (4) the amounts of feed ingested by the sow during rearing, gestation and lactation and those ingested by her meat-producing offspring during growth to a live weight of 91 kg constitute the total amount of feed chargeable to the carcasses produced; (5) the net production of protein includes that represented by the carcasses of the sow and her meat-producing offspring; (6) one of the sow’s offspring would replace her in the herd (assumption); (7) at the first three rates of pork production listed, the rates of sterility and mortality are 12 and 25%, respectively (assumption); and (8) at the assumed biological limit, 12 ova would be fertilized and the sterility and mortality losses would be nil (assumption). (NOTE: Analogous assumptions and considerations underlie the data in table 12 for other animal enterprises.)

It is clear that salmonids are much more efficient producers of protein than are livestock; however, they require a highly refined diet. The high efficiency of Rainbow trout seems attributable to their low energy cost of: (1) temperature maintenance, (2) locomotion, (3) reproduction (a 1- to 2-kg trout yields 3,000 to 6,000 offspring annually), (4) protein catabolism (ammonia, rather than urea or uric acid, is the principal end product of protein catabolism, and it is excreted chiefly through the gills), and (5) utilization of protein as an energy source.

Among the food products yielded by the common farm animals (table 12), efficiency is greatest for protein produced as milk, broiler meat and eggs; intermediate for that produced as pork, and lowest for that produced as beef. Within a given enterprise, protein-production efficiency increases with increasing intensity of DE input. As the losses from infertility and mortality are reduced, the efficiency increases; however, these effects have considerably less impact than does the level of energy input.

For a considerable part of their diets, or at least for land on which to grow their diets, chickens and pigs compete with humans. On the other hand, dairy cows can produce as much as 4,990 kg of milk on an all-forage diet, with an efficiency of about 12 g protein/Mcal DE. This yield is probably close to the upper limit possible on forages alone. Under the conditions of good commercial practice, pigs yield 6.1 g protein/Mcal DE. Even at the extreme biological limit, the pig would produce only 12 g protein/Mcal DE at current rates of reproduction. As a producer of protein for human consumption, the pig occupies the most precarious position of all farm animals. This is because the pig produces a relatively low protein (about 13.5%) product at usual slaughter weights, it competes almost directly with humans for food or for land on which to grow it and the swine enterprise requires a high fossil energy subsidy. Nevertheless, the pig is an important scavenger animal in many parts of the world. Also, in some parts of the world, especially in the Far East, pigs are managed much less intensively than they are in the United States.

With the human population of the world increasing rapidly, the degree of competition between humans and animals for foodstuffs of plant origin is increasing steadily. Should foodstuffs of plant origin be available in excess of man’s need, but not in sufficient amounts to produce the quantities of animal protein needed to satisfy man’s present food consumption pattern, it will be necessary to decide which kinds of animals will be hused in the future to produce man’s food.

Protein production by the milking cow is at least as efficient as that by any other farm animal, excluding fish. Under most conditions, but especially when the milking cow eats at least enough forage to satisfy her energy requirements for maintenance, she will yield a greater gain in protein output per unit of concentrates (i.e., cereal grains and oilseeds) ingested than will any other farm animal. However, in some circumstances, the surplus concentrates might be fed more effectively to fowls for meat production. For example, in some societies, milk is not used or it is not an important food, and in some peoples there is a congenital lack of lactase, which is essential to the digestion of milk carbohydrates. Also, under certain environmental conditions, or because of management problems involving disease or insect control, it may be more productive to feed available concentrates to fowl than to milking cows. Among the farm animals, fowl, especially chickens, are relatively efficient protein producers, but they compete either directly with humans for foods or for the land on which to grow food.
produce only 4.1 g protein/Mcal DE ingested, even under an intensive production system in which (1) the dam is grown rapidly and bred at 8 months of age, (2) the meat-producing offspring produce 1 kg of gain per 5 kg of feed consumed and are slaughtered at 1 year of age, weighing 500 kg, and (3) there is no loss resulting from mortality or infertility. The relative inefficiency of beef production is attributable to the high energy cost of rearing and maintaining the breeding herd, of reproduction (long gestation period, primarily single births and a small number of meat producers generated by a given dam) and of the long feeding period required. However, although this meat production by cattle is relatively unaffected, these animals and other ruminants need not necessarily compete with humans for food. Also, under extensive management conditions, ruminants require a low fossil energy subsidy. For these reasons and because of the abundance of cellulose, the future role of ruminants as food producers seems secure despite the increasing human population pressure.

Present evidence indicates that at the same body weights, rapid-growing, slow-maturing cattle such as Holsteins contain more protein and less fat than slower growing, more rapidly maturing cattle such as Aberdeen Angus (R. Anrique, H. Ayala, S. Simpfendorfer, A. Fortin, A. F. Kerz, J. T. Reid and G. H. Wellington, unpublished data). Also, the efficiency of protein production is correspondingly higher per unit of DE input in rapid-growing, slow-maturing cattle. Within breeds, the females mature more rapidly and contain less protein and more fat at the same body weight than do the uncastrated males (figure 4). These characteristics are intermediate in the male castrate. Protein production efficiency also is highest in uncastrated males, intermediate in male castrates and lowest in females.

Future Research Challenge. Analyses of livestock production systems are needed to determine the relative significance to protein production efficiency of the various inputs and the impact of improving them. For example, in swine production, what would be the integrated impact of improving the feed conversion rate from 4:1 to 2:1, of increasing the number of weaned pigs per litter from six to 12 or of producing 20 pigs per litter (by superovulation, with early weaning and by feeding a milk substitute diet) when all other known components are integrated within the system?

Literature Cited


Burlacu, G., M. Illiescu and J. Stravi. 1976. Efficiency...


of level of intake on digestibility of dietary energy by high-producing cows. J. Dairy Sci. 48:1053.


Slyter, L. L., R. R. Oltjen, D. L. Kern and F. C.


