

The history of energetic efficiency research: Where have we been and where are we going?

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ABSTRACT: The development of energetic efficiency concepts followed a recognized pattern of knowledge evolution that began with novel insights leading to creative new concepts. The second phase integrated concepts from other fields to create new applicable principles. The third phase was the adoptive or dissemination phase, yielding solutions to industry or societal problems. It is our contention that animal energetics has been in the adoptive phase for approximately 100 yr. Concepts developed during the early phase of nutritional energetics included the concept that life is a combustion process, the laws of thermodynamics, and the Law of Hess. Subsequent efforts established relationships between gas exchange and heat production and established the concept that food not only functions as fuel, but also as a body-building material. Much of the research effort for the last 100 yr has been to 1) devise bases for evaluation of foods that could be related to energy requirements and energy expenditures and 2) establish causes of energy expenditures. Much of the effort has focused on general and broadly applicable

processes (e.g., mice to elephants) of biology or broad-based populations within species. Little effort has been focused on the amount or causes of individual variation in efficiency of energy utilization by cattle, even though differences among individuals have long been recognized. Observed maintenance requirements and energetic efficiencies, for example, have not been substantially altered during the last 100 yr of intensive beef production. Reasons for the lack of change in energetic efficiencies include a lack of a consistent selection goal, loose and inconsistent definitions of efficiency, concentration on output characteristics, and emphasis on population similarities rather than individual variation. It is time to assess new or different tools and concepts to enhance efficiency of dietary energy use by beef cattle. Application of older (e.g., residual feed intake) and newer (e.g., QTL, gene expression microarray) technologies offers the potential to realize improved maintenance and system energetic efficiency through identification of individual animal phenotypic and genomic uniqueness.

Key Words: Beef Cattle, Energy Metabolism, Genome Analysis, Maintenance, Ruminants

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Introduction

The knowledge of efficiency of energy utilization by ruminants developed via a recognized pattern of evolution (Malone, 1994). In this evolutionary pattern, the process is initiated through novel, fundamental insights leading to creative concepts, e.g., the Laws of Thermodynamics, “life as a combustion process.” The second step is the integration of complementary concepts from other fields of inquiry to create principles applicable to the field of inquiry; e.g., the chemical reaction of formation of high-energy phosphate bonds is

applied to explain biological processes, or physiological principles are applied to life processes. The last phase of this maturing evolutionary process is the adoptive or dissemination phase, yielding solutions to industry or societal problems, e.g., the chemical analysis of feedstuffs, and the development of net energy feeding systems. It is our contention that animal science energetics has been largely in the adoptive/dissemination phase for the past approximately 100 yr. It is time to look for new integrative tools with which to enhance beef cattle dietary energy use efficiency.

Historical Energetics

The historical development of nutritional energetics was reviewed by Brody (1945), Kleiber (1961), and Blaxter (1962). We have relied on these treatises for much of this synopsis. Utilization of dietary energy has been

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a subject of research since the eras of Leonardo da Vinci (1452–1519), Joseph Priestly (1733–1804), and Antoine-Laurent Lavoisier (1743–1794). From these and other philosophers and researchers, the generalization that life is primarily a combustion process developed. This concept relating metabolism to combustion permitted the formulation of the following equation.



After those pioneering works, new objectives of research in nutritional energetics became 1) to establish relationships between gas exchange and heat production, 2) to devise bases for evaluation of foods that could be related to energy requirements and energy expenditures, and 3) to establish causes of energy expenditures. The Laws of Thermodynamics and the Law of Hess were developed. The adiabatic bomb calorimeter was developed by Berthelot (1827–1907), which enabled reproducible and accurate determination of the gross energy contents of organic compounds, feed, feces, and urine. Another essential advance was the development of the concept that foods should be partitioned into carbohydrates, fats, and proteins because their metabolism differed. Primary contributors to this concept were Baron Justus Von Liebig (1803–1873) and his students. Liebig maintained that a considerable part of animal food, especially minerals and proteins, do not function as fuel, but as material for bodybuilding. In 1881, Lunin concluded that animals need some unknown substances, other than protein, fat, carbohydrates, and minerals. Those substances were later termed *vitamins* by Casimir Funk (1912).

Considerable effort, over a period of 100 yr or so, was devoted to establishing relationships between gas exchange and heat production. One of Liebig's students, Carl Von Voit, utilized the open-circuit respiration apparatus of Max Von Pettenkofer (1818–1901), the prototype of modern instruments, to do extensive energy balance experiments. Instrumentation of this type was utilized extensively by the groups of Henry Armsby, Wilbur Atwater, Oskar Kellner, and Max Rubner (all students of Von Voit), among others. Recently, although more mechanically and/or electronically sophisticated, instruments based on similar principles have been in use at Beltsville (Flatt et al., 1965), Colorado State University (Johnson, 1986), and Clay Center (Nienaber and Maddy, 1985), among others. Some of the early instrumentation, such as that of Regnault (1810–1878), were of the closed-circuit type. Closed-circuit systems were used extensively for man and smaller animals and some for larger animals (e.g., Hannah Institute, Wainman and Blaxter, 1958) but were never as widely used as the open-circuit type. Work in this area—to a large degree—culminated in 1965 with the publication of the Brouwer equation (Brouwer, 1965). The equation developed to calculate heat production (H, kcal) from oxygen consumption (O_2 , L), carbon dioxide production

(CO_2 , L), methane production (CH_4 , L), and urinary nitrogen (N, g),

$$\begin{aligned} \text{H} = & 3.866 \times \text{O}_2 + 1.200 \times \text{CO}_2 - 0.518 \\ & \times \text{CH}_4 - 1.431 \times \text{N} \end{aligned}$$

has been used almost exclusively for the calculation of heat production from indirect calorimetry measurements since its publication.

Direct calorimetry, the direct measurement of heat produced by the animal, is also founded in the work of Lavoisier, Atwater, Armsby, and Blaxter, and others, used instruments based on the principles developed by Lavoisier. Although instrumentation has changed immensely, calorimeters in use at the University of Nebraska (Nielsen et al., 1997a) are founded in those concepts.

In conjunction with establishing relationships between gas exchange and heat production and establishing causes of animal energy expenditures, several groups devoted tremendous effort toward devising bases for evaluation of foods that could be related to energy requirements and energy expenditures. The Starch Equivalent System, developed by Oskar Kellner and his group (Kellner and Köhler, 1900) was a net energy-based system in which the energy values of feedstuffs were expressed relative to that of starch to meet the energy needs of the animal for fattening. The Kellner system has likely had the greatest influence in the practical feeding of livestock. It was used as the primary system throughout Europe and Russia for many years and serves as the basis on which many others have been built. Atwater and associates (Atwater and Bryant, 1900) developed the Physiological Fuel Values system. Atwater's system was based on metabolizable energy values of carbohydrates, fat, and protein, with the energy values of protein adjusted for the energy value of excreted urea. The Physiological Fuel Values system remains the basis for expressing the energy (caloric) content of foods for humans and laboratory animals. Armsby (1903; 1917), also using respiration calorimetry of the Atwater-Rosa type, defined metabolizable energy (physiological fuel value) as the net energy plus heat increment of feeding. He and associates developed many of the principles on which current net energy systems are based. Current energy systems used in the United Kingdom (ARC, 1965; 1980; AFRC, 1990), France (INRA, 1978; 1989), and Australia (ACC, 1990) are grounded in principles derived from those earlier efforts.

The general equation $\text{ME} = \text{RE} + \text{HE}$ has been recognized since the days of Von Liebig, but, for many years, the primary effort of energetics researchers was to describe and quantify the ME of food and heat produced (HE), with retained energy (RE) seemingly a secondary consideration. Lawes and Gilbert (1861) first employed the comparative slaughter method in experiments. Those experiments were of considerable interest because they demonstrated for the first time that carbohy-

Table 1. Disposition of dietary energy by Kellner's fat steer and contemporary U.S. steer or overall beef production system (U.S. data extrapolated from NRC, 1996)

Item	Kellner "well fed ox," Mcal/d	% of GE intake	Today 600 kg feedlot steer, Mcal/d	% of GE intake	Beef system, cow through feedlot, %
Gross energy input	52.9	100	43.0	100	100
Fecal energy	15.9	30	6.5	15	39.6
Urine energy	1.7	3	1.7	4	4.9
"Marsh gas"	3.4	6	1.1	3	5.4
Heat of tissue syn.	6.3	12	8.9	21	8.0
Idling heat	17.3	33	17.2	40	36.3
Retained in empty body	8.3	16	7.6	18	5.8

drates were the major source of energy leading to the synthesis of fat. Blaxter (1962) stated that "during the last 100 yr, the complete bodies of about 250 cattle and 60 sheep have been analyzed" by the scheme that partitioned the animal into weight of gut contents, body water, body fat, body protein, and body minerals. Garrett et al. (1959) popularized the comparative slaughter technique in their classical manuscript, the Comparative Energy Requirement of Cattle for Maintenance and Gain. This concept was further developed and published in an article titled a System for Expressing Net Energy Requirements and Feed Values for Growing and Finishing Beef Cattle (Lofgreen and Garrett, 1968), which stands as the basis of the system incorporated into current NRC (1984; 1996) recommendations. It should be noted that this system, like other systems currently in use, is rooted in the concepts developed by Armsby, Atwater, Kellner, Brody, Kleiber, Blaxter, and others, but, unlike many of the systems, requirements and value of feedstuffs to meet those requirements were based on the measurement or estimation of energy retained, rather than energy losses.

Much of the essence of the last 50 yr of animal energetics research can be found in 15 publications from the prior symposia on energy metabolism of farm animals held every 3 yr beginning in 1958. Researchers A. J. H. Van Es (1994) and W. P. Flatt (2000) have recently summarized interesting portions of the history of the people and their work. Also of note is a report (NRC, 1935) of a conference sponsored by the Committee on Animal Nutrition of the National Academy of Science held at Pennsylvania State College in 1935 that features papers by Forbes, Mitchell, Brody, Kleiber, and Ritzman.

Energy Use Efficiency

An overview of energy efficiency can be gained by an example of typical diet energy disposition (Table 1). A comparison of Kellner's (1909) respiration calorimetry-monitored "well-fed ox" with a contemporary feedlot steer (extrapolated from NRC, 1996 slaughter balance derivation) portrays moderate differences, except for the markedly lower fecal loss associated with currently used high-grain diets. The fattening steers retain from

16 to 18% of consumed energy. The largest loss is to the maintenance function, "heat of idling," followed by fecal losses and heat of tissue synthesis. On a whole-herd basis, the fecal and maintenance components become predominant, providing, perhaps, a view of the largest efficiency improvement targets. Beyond digestive losses, e.g., as a fraction of the herd's needs for metabolizable energy, the maintenance component predominates, comprising approximately 73% of ME requirements.

The term *efficiency* demands a numerator and a denominator along with terms and units of each. All have taken many forms when used to define "beef cattle energetic efficiencies" particularly when gross, partial, or net efficiencies are defined. The numerator is the caloric content of the product (megacalories of product) or its proxy, whereas the denominator is defined in units of diet (diet input). The units of diet can be weight, or megacalories or joules of GE, DE, TDN, ME, or NE. Additionally, the diet input can be divided into that provided for animal maintenance and that provided for product above maintenance; e.g., product/(total ME minus ME required for maintenance). Thus, enumerable ratios have, and are, being used to describe "energy efficiency of beef production." These efficiency ratios always embody three components:

1. Diet energy cost of maintaining the animal per unit of time.
2. Diet energy cost per unit of product.
3. Rate of product per unit of time (product/fixed maintenance cost).

However defined, the determination of partial efficiencies, e.g., body tissue energy gain/ME above maintenance, would appear to be a straightforward, simple process. But in practice, it becomes a complex problem with multiple levels of confounding, making it difficult, if not impossible, to precisely define *the* partial efficiency or maintenance energy requirement of the producing animal. A prime example of this complication is the frequently observed shifting maintenance requirements as animals adapt to changing levels of alimentation. For example, Marston (1948) reported a shifting of fasting heat production (**FHP**) of sheep in

direct proportion to their prior plane of nutrition. Additional frequent confounders include changing diet digestibility, pattern of fermentation, microbial growth, and protein supply concomitant with changing levels of production or alimentation. Add to these the changing nutrient flux, metabolism, hormonal control, and product composition likely with changing level of alimentation and the simplicity of measuring or calculating “partial efficiency” becomes even murkier. Perhaps this is where a modeling approach, e.g., Oltjen and Sainz (2000), may prove most helpful.

Variations in Maintenance Requirement. Kellner (1909) found that small dogs produced 2.8× more heat/BW at fasting than large dogs, but approximately equal FHP per unit of surface area. Classical mouse to elephant research with mature animals found FHP to be proportional to $BW^{0.734}$ (Brody, 1945) or to $BW^{0.756}$ (Kleiber, 1947), leading to the widely accepted concept of metabolic body size = $BW^{0.75}$. The accuracy of the 0.75 exponent, and the veracity and applicability to define maintenance requirements, has been widely challenged. Some early examples include the following: level of alimentation prior to fasting (Marston, 1948), age (Graham et al., 1974), breed (Frisch and Vercoe, 1977), race (Geissler, 1985), sex (Webster et al., 1982), leanness (Graham et al., 1967; Webster, 1982), unique species (i.e., ovine; Blaxter, 1989), cold adaptation (Young, 1975), and choice of regression model (Calder, 1987). All are examples of factors that have been shown to challenge the universality of $FHP = 77 BW^{0.75}$. The ARC (1980) energy requirement system adopted the exponent of 0.67 for cattle to better fit the young vs. the older, heavier animal’s needs. Webster et al. (1974) in a paper entitled the Irrelevance of Fasting Metabolism suggested that the requirement of varying ages or weights of cattle are better predicted from regression rather than measurement of heat from a fasted animal. From a review of literature from several species, Blaxter (1972) indicated that if fasting is measured on mature animals of varying BW within a species, the appropriate exponent ranges from 0.83 to 0.93. Other reviews have, however, concluded that no significant advantage is gained by using exponents other than 0.75 (Garrett and Johnson, 1983; AAC, 1990).

An additional factor contributing to variation in maintenance is that some breeds/animals likely have differing abilities to adapt to changing environments or levels of alimentation. Examples include Africander vs. *Bos indicus* or *Bos taurus*, in which the decline in FHP as pasture quality declined was greater for Africander cattle (Frisch and Vercoe, 1977). A report by Reynolds and Tyrrell (2000) found maintenance energy of lactating Angus cows to be equal to expected Holstein requirements in contrast to the widely observed lower requirements of Angus or Hereford cattle when not lactating. The implication is that Angus or beef cattle in general may adapt to lower maintenance when fed at lower levels of alimentation.

Physical Activity. Except for recommendations of increasing maintenance requirements of grazing animals (NRC, 2001), the use and variation of energy in physical activity by cattle has been largely ignored. Thermogenesis of individual human subjects associated with activities that are not purposeful exercise has been shown to be highly variable, heritable, and predictive of weight gain (Snitker et al., 2001) and low in obese individuals (Schoeller, 2001). Snitker also found that the measurement in respiration chambers of these “activities of daily living” correlates ($r = 0.53$) to individuals’ free-living activity. These types of movements, sometimes called *fidgiting*, can elevate sitting or standing thermogenesis by 50 to 80% (Levine et al., 2000) and can be monitored in free-living individuals with inclinometers and accelerometers (Levine et al., 2001a). General usefulness of these monitors is apparently limited by the need to calibrate them to individual subjects (Levine et al., 2001b).

Anatomical Variations. Many attempts have been made to explain the anatomical, physiological, and biochemical causes of varying FHP/BW. Variations in fat-to-lean tissue mass have been widely ascribed to explain group or individual heat production differences, however, not always as demonstrated by McNiven (1984). She imposed nutritional regimens on ewes to change body fat percentage dramatically and showed little difference in FHP or maintenance heat production per unit of BW in these groups. Visceral organ tissue, particularly hepatic, consumes O_2 at a much higher rate/mass than the whole animal and is positively correlated with animals or circumstances varying from mean basal metabolic rates. The basal metabolic rates of divergent human subjects have been successfully regenerated from the mass of individual organs and tissues, separately determined, multiplying by the O_2 consumptions/kg of each tissue and summing these to equal that of the whole subject. Changes in the ratios of visceral organ to whole-body mass also parallel changes in fasting or maintenance heat production in response to changes in level of alimentation, stage of fetal growth, young to old, small to large BW species, or *Bos indicus* vs. *Bos taurus* cattle (Ferrell et al., 1986; Huntington et al., 1988; Johnson et al., 1990).

Physiological Factors. Many “maintenance control factors” have been proposed. In addition to the above, these include T3, Na^+/K^+ ATPase, proton leak, uncoupling proteins, leptin, acetyl-CoA carboxylase 2, malonyl CoA, sympathetic tone, α_2 -agonists, and calcium/calmodulin-dependent muscle protein kinase. Knowledge of these factors has not resulted in the ability to select animals to change their maintenance cost of production. However, this research has helped to define the general requirements of groups of animals, and many very interesting concepts have evolved. Uncoupling proteins (UCP) are widely distributed in tissues beyond the UCP1 found in brown adipose of most newborn animals. These proteins facilitate a proton leak across the inner mitochondrial membrane, estimated to be responsible

for 20 to 30% of basal metabolism oxygen consumption (Brand 2000). Those observations led to the hope that the major controller of animal metabolic rate had been found. The excitement was quenched by the report (Enerback et al., 1997) that UCP2 knockout mice produced no effect on lipid stores or energy balance and that UCP may function as regulators of reactive oxygen species (Echtay et al., 2002) rather than as uncouplers of oxidative phosphorylation. Some enthusiasm was revived with the reports that mice with overexpressed UCP3 were hyperphagic, lost adipose mass, and had higher metabolic rates (Clapham et al., 2000) and that UCP3 is a molecular determinant of T3 effects on resting metabolic rate (deLange et al., 2001). When hypothyroid rats were given T3, UCP3 mRNA and protein were up-regulated, resting metabolic rate was increased 45%, and muscle mitochondrial nonphosphorylating respiration increased 40%. Additionally, work of Lebon et al. (2001) found that T3 increased muscle tricarboxylic acid cycle flux by 70% with no increase in ATP synthesis, indicating accelerated proton leak.

The role of UCP in the control of proton leak or conductance has again been challenged. The mitochondria of UCP3 knockout mice showed unchanged respiration or proton leak rates (Cadenas et al., 2002). The mice overexpressing UCP3 did show greater proton conductance, but they did not respond to known enhancers, or inhibitors. Analogous responses were found by introducing human UCP3 into yeast mitochondria (Harper et al., 2002). Uncoupling was increased, but not in proportion to increased protein; it was responsive to neither activators nor inhibitors.

Proton leak variation between cold-blooded and homeothermic animals, as well as large and small species, has also been linked to membrane lipid unsaturation, particularly to the relative content of docosahexanoic acid (Hulbert and Else, 2000). For example, rat liver mitochondria have a greater 22:6 fatty acid content than a similarly sized lizard along with approximately five times greater proton leak rates. They cite previous research showing that the heart rate of mammals ranging from mice to whales was correlated to the 22:6 content of cardiac lipids (Gudbjarnason et al., 1978). Attention is also given to a general relationship in other membranes of lipid composition to $\text{Na}^+\text{K}^+\text{ATPase}$ activity.

The injection of leptin into rabbits resulted in marked increases in stored body lipid cycling (Reidy and Weber, 2002). Lipolysis and triacylglycerol/fatty acid cycling was increased 50%, primary cycling 85%, metabolic rate 14%, and fuel use was shifted away from carbohydrate toward lipid. The authors postulate that the general role of leptin secretion by adipocytes is to maintain normal body mass, adjust lipid stores via changes in metabolic rate, fuel selection, T3 secretion, UCP levels, and diet intake. They conclude that leptin levels function to adjust the "idling rate" of animals via substrate cycling and UCP-induced proton leak.

Potential Genotype Interactions. Beginning in the 1960s and continuing through the present, the genetic growth rate potential of the beef cattle population in the United States was increased through the introduction of breeds of cattle from the continent of Europe. Attributes of these imported breeds evolved within unique production environments with differing emphasis regarding desired productivity, creating a diversity of genetic potential for production. The assimilation of these breeds into the U.S. beef industry since their introduction was stimulated by cow/calf producers' desire for heavier weights at weaning and a postweaning industry desire for more efficient gain during the finishing period coupled with consumer demand for leaner products during the 1970s and 1980s. These goals could be met by systematically using breeds (Gregory and Cundiff, 1980) differing in mature size and growth relative to the British breeds. Feeding and slaughtering cattle at physiologically younger ages contributed to the latter goals but created problems with meeting industry standards for quality of meat produced (National Beef Quality Audit, 1995), creating the need to again alter production practices. The changes resulted in a need to address the energy requirements for production of beef cattle.

The industry assumed constant energy requirements for maintenance per unit of metabolic body size and efficiency of production among these diverse producing animals (Garrett et al., 1959). This assumption ignored earlier research, demonstrating that animals differing in production "potential" varied in gross (Armsby and Fries, 1911) or maintenance efficiency. Taylor et al. (1962) utilized twins, both monozygotic and dizygotic, to investigate the effect of genetic factors on feed efficiency. These researchers concluded that a proportion of the variation in feed efficiency was under genetic control, but efficiency during any given period can also be affected by previous nutrition. Ferrell et al. (1986) and Koong et al. (1982) conducted studies with lambs and rats to test the effect of previous nutrition on an index of maintenance, fasting heat production. Level of nutrition preceding the measurement of fasting heat production significantly affected the DM requirement for maintenance per unit of metabolic weight in both species. Additionally, the requirements were not static but reflected the most recent feeding level, which is analogous to the shifting FHP noted previously.

Sutherland et al. (1974) suggested that growth rate and efficiency of feed use were variables critical to evaluation of the economical production of meat animals. In the review, the authors considered the physiological parameters possibly affecting gross feed efficiency drawing from research involving many species. Evidence was provided in several species; enhancing growth rate during the postweaning interval was an effective means to improve efficiency and this could be accomplished by increasing body size (Sutherland et al., 1970). Timon and Eisen (1970) pointed out that genetic studies investigating feed efficiency failed to

adequately address the issues of correlated responses in appetite, body composition, or the effect of test protocol, that is, fixed time interval, weight interval, and so on. Evidence from these studies suggested that observed differences in gross efficiencies realized through selection for growth could not be attributed to genetic changes in partial efficiencies for fat and protein deposition. A correlated increase in ad libitum intake (appetite) was observed in the selected mouse lines (Sutherland et al., 1970). Work by Leymaster and Jenkins (1985) reported a positive relationship for ADG between 32 and 73 kg in sheep and the rates of accretion for carcass and offal lipid, protein, and ash. The accretion rates of offal protein had the greatest direct and indirect effects on ADG. Results are critical because work reported by Koong et al. (1985) documented the effect of nutritional environment on metabolically active body tissue and the positive relationship to fasting heat production. Increased emphasis on output performance could create a correlated response in mass of metabolically active organs increasing energy requirement for maintenance. Jenkins et al. (1986) determined significant additive breed effects among Brown Swiss, Hereford, and Angus. Scaled for weight at slaughter, Brown Swiss tended to have the greatest amount of internal tissues, with Hereford the least and Angus intermediate. A similar ranking was observed for yield of milk at time of peak lactation. Taylor et al. (1986) reported that as genetic potential for milk production increased, maintenance efficiency decreased.

With additional breeds available to the industry, cattle began to be classified by output production characteristics, such as growth, carcass attributes, mature size, and milk production potential based on research evaluating performance from birth through slaughter (Mason, 1971; Cundiff et al., 1986). Responding to inquiries by the cow/calf segment of the beef industry, Ferrell and Jenkins (1982) found approximately 73% of the feed ME consumed by a mature cow is expended to maintain body mass. However, the ability to adjust energy expenditure for maintenance is influenced by genetic potential for performance, with animals of greater genetic potential for productivity exhibiting reduced ability to lower maintenance requirements (Frisch and Vercoe, 1977; Taylor et al., 1986). Ferrell and Jenkins (1985) reported that during the postweaning phase, Simmental were less efficient than Hereford at restricted levels, but at ad libitum intakes, more efficient. Jenkins et al. (1991) provided evidence that a breed with greater potential for mature size and lactation yield had greater daily heat production at restricted feeding rates than a breed with lower production potential; however, as rate of DM intake per unit weight increased, the ranking reversed between the two breeds. Solis et al. (1988) reported breed differences in energy requirements for maintenance among Jersey, Holstein, Brahman, Hereford, and Angus. Mating systems designed to utilize between- and within-breed dif-

ferences in energy expenditure for maintenance offer an opportunity for improving energy efficiency.

Introduction of these breeds to the U.S. beef cattle inventory provided an opportunity to assess potential variation among the breeds for efficiency of energy use to improve efficiency. Thiessen and Taylor (1986) evaluated the variation in weight change relative to feed intake among 25 breeds of cattle fed ad libitum from 12 wk of age. Results documented: 1) efficiency (gram weight gain per unit of feed intake) decreases as the animals aged, 2) additive genetic variation among the 25 breeds evaluated increased as the animals grew older, and 3) relative to additive genetic variation, a greater proportion of the variation existed within breeds. This work was a continuation of investigations initiated to study weight changes and efficiency (Taylor et al., 1962; Taylor and Young, 1966). Using monozygotic and dizygotic twins, these researchers suggest that variation existed in the efficiency with which an animal used feed to maintain BW and variation existed among the rates of decline in efficiency among twin pairs. Using monozygotic twins, Hotovy et al. (1991) observed significant genetic variation for FHP and ME required for maintenance, suggesting selection to reduce energy expenditure for maintenance would be successful.

Based on an evaluation involving 25 breeds, Thiessen et al. (1985) reported a genetic coefficient of variation for ad libitum feed intake of approximately 12 to 15% for cattle ranging from 12 to 72 wk. Assuming that feed intake is proportional to mature weight to 0.73 power, then variation among breeds can be evaluated for animals fed ad libitum that are in weight equilibrium (Taylor et al., 1981). The constant is an index of the relative food capacity of mature animals (Kleiber, 1961) and should characterize the genetic potential for appetite. Using feed intake and weight data from the ad libitum animals at weight stasis, this proportionality held among mature cows of the nine breeds; daily DM intake = $0.195BW^{0.73}$. Jenkins and Ferrell (unpublished data) observed variation among breeds in maintenance efficiency at weight stasis for these nine breeds of cattle varying in genetic potential for mature size, milk production, postweaning growth rate, and ad libitum feed intake. Breed estimates of the regression constant ranged from a high of 0.224 for Angus to a low of 0.167 for Limousin, suggesting substantial genetic variation in appetite (Jenkins and Ferrell, unpublished data). Relative to BW at weight stasis, genetic potentials for DM intake/BW of Angus, Hereford, Red Poll, and Charolais were greater than the pooled mean appetite and Limousin, Pinzgauer, and Simmental exhibited lower genetic potential for appetite. Braunvieh and Gelbvieh approximated the sample mean.

In spite of the above-noted selection pressures, the maintenance requirements of cattle appear to have been largely unchanged for the last 100 yr (Table 2). Kellner's (1909) estimates, translated from starch equivalents, surface area base, suggested an ME re-

Table 2. History of maintenance requirement estimates, kcal of ME per BW^{0.75}, of cattle fed corn, hay, or straw

System	Base requirement	Corn ^a	Hay ^a	Straw ^a
Kellner, 1909	5.2 kg of SE/454 kg of BW ^b	116	158	313
NRC, 1963	135 kcal of DE/BW ^{0.75}	111	111	111
NRC, 1976	77 kcal of NEm/BW ^{0.75}	110	125	129
NRC, 1984	77 kcal of NEm/BW ^{0.75}	112	131	178
NRC, 1996	77 kcal of NEm/BW ^{0.75}	112	131	178

^aRequirements for cattle fed corn, hay or straw diets expressed as ME/ BW^{0.75}.

^bStarch equivalent.

quirement of cattle fed grains and oil meals of 116 kcal/BW^{0.75}, not unlike NRC (1963; 1976; 1996), which range from 110 to 112 kcal/BW^{0.75}. The very high estimates of the maintenance requirement for ME from forages determined by the “fat-forming ability” Kellner system were shown to be inaccurate. Such very low efficiencies are only applicable when describing the partial efficiency of ME use for growth. The early NRC systems ignored these low efficiencies but then developed a more modest “forage inefficiency” adjustment.

Evans et al. (2002), as shown in Figure 1, has provided some indirect evidence of slight increases in cattle maintenance energy requirements. The average EPD for maintenance requirements were predicted from mature BW and milk production records. Requirements for cows increased 100 Mcal/yr over a 20-yr period prior to 1990, after which they leveled out. The 100-Mcal rise, however, represents only a 2.5% increase in yearly needs.

Individual Animal Variation. Animal-to-animal variation within class, breed, sex, etc., in maintenance requirement has been noted in several experiments (Table 3). The reported CV for maintenance energy requirements in beef cattle range from 10 to 12%, suggesting that substantial animal-to-animal variation exists for this trait. These variations, coupled with the heritability estimates of Hotovy et al. (1991), as well as indications of the heritability of residual feed intake measures (Herd and Bishop 2000; Herd et al., 2003), suggest ample room for improvements through selection.

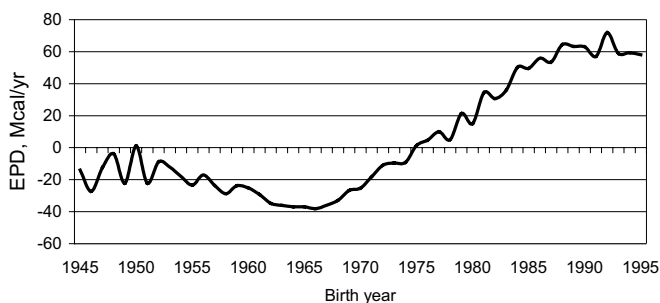


Figure 1. Average EPD (Mcal/yr) for mature cow maintenance energy requirements by birth year in Red Angus cattle (Evans et al., 2002).

Ferrell (1986) reported weight changes for mature cows representing breeds differing in mature size and milk production potential and fed at 120 kcal per unit metabolic body size or ad libitum. Relative to metabolic body size within assigned feeding level, the ADG of individual cows varied, indicating variation among animals in efficiency of metabolizable energy use at approximately weight stasis and positive weight change (production). Nielsen et al. (1997a,b) successfully practiced divergent selection for high and low heat production (**HP**) in mice for 15 generations. Correlated responses were observed for feed intake (increased intakes in the high FHP line and decreased intakes in the low FHP line; respectively), composition (reduced fat in the high line relative to low FHP line), litter size (larger litter size in the high line vs low line) and activity. These results suggest that even though additive genetic variation exists in measures of energy use, implementing selection criteria to change the basal metabolism to improve energetic efficiency will affect other traits in the producing animal.

Residual Feed Intake (RFI) as an Efficiency Measure. In an attempt to develop a selection method without the negative consequences of selection for growth rate, several researchers have investigated individual animal deviation from regression of feed intake as predicted from mean BW and gain during growth trials of 70 d or more. The heritability of RFI ranged from 0.16 (Herd and Bishop, 2000) to 0.39 (Arthur et al., 2001). Steer progeny from parents selected for low RFI also had lower RFI (−0.15 vs. +0.16), consumed less feed (8.03 vs. 8.45 kg of DM/d) as yearlings, but weighed the same (423 and 428 kg BW) at the end of the trial as steer progeny from parents selected for high RFI (Richardson et al., 2001). Body fat of the low RFI steers was not significantly lower, averaging 21.9 vs. 23.1%, although carcass fat/final weight was lower and protein gain during the 70 d test was higher. The authors conclude that selection for RFI is unlikely to have negative consequences regarding mature weight and potentially positive effects on cow maintenance requirements. Changes in meat quality noted by McDonagh et al. (2001) have some negative potential but are expected to have minor practical importance.

Efficiency of Product Formation. The partial efficiency of energy use for product synthesis has been actively

Table 3. Estimates of the variation in maintenance energy requirement between individual animals within group or species

Reference	Species	Measure	% ME _m variation
Van Es (1972)	Cattle	CV	5 to 10
Webster, et al. (1982)	Cattle	CV	14 to 35
Kirchgessner and Muller (1991)	Sows	CV	11.8
	Humans	CV	12.4
Hotovy et al. (1991)	Cows	Range	15

investigated for many years. Kellner (1909) found a 57% partial efficiency of body energy storage from the ME of grains added to a maintenance diet of steers. Brody (1935) reported a partial efficiency of ME use for milk production of 0.61, not unlike recent NRC values. It does appear likely that these partial efficiencies have been little altered.

Partial efficiency variations by product or by feedstuff source, however, are considerable. Although not totally conclusive, most investigations indicate the ranking (most to least) for partial energetic efficiency of product is as follows: lipid > milk > protein > fetal tissue. The apparently low efficiencies of protein (30 to 50%) and fetal tissue synthesis (~10%) may be a matter of book-keeping. Are higher costs of concomitant protein turnover or increased maintenance best included in the cost of the product? Biochemical estimates of ATP/mole of amino acid incorporated into a protein chain, even at 5 mol/mol, show relatively high efficiencies of ~75%.

The major discrepancy between theoretical as compared to observed product formation efficiencies occurs when low quality, fibrous feed ME is utilized for growth. The very low partial efficiencies of 30% or lower have been “explained” as resulting from a high heat increment of acetic acid use (Blaxter, 1989). However, there is substantial experimental evidence that acetic acid can be used efficiently for growth (Johnson, 1972; Orskov et al., 1979). The mechanism responsible for the high heat increment of fibrous diet use for growth, thus, remains a mystery, to intrigue contemporary energeticians.

Baldwin (1995) has summarized the energy flux through the multitude of physiological/biochemical tissue and organ tasks of growing, lactating, or idling animals, e.g., Na/K pumping, futile cycles, protein, urea, lipid, and lactose synthesis. These elegant models have illustrated the dynamic and interactive nature of supplying these energy needs from varying substrate mixtures to meet varying physiological tasks, for example, varying lipid/VFA/protein mixture ratios can result in very different efficiency responses when these nutrients are used for maintenance as compared to their use for growth. These relationships are not easily applied to diet nutrient use, however, due to difficulty of quantifying substrate uptakes from the gastrointestinal tract. Substrate inputs from nutrients default to static estimates of moles per unit of chemical component digested in the gut (Bannink et al., 2000; Mills et al., 2001).

Law of Diminishing Returns. Many energetics scientists noted the applicability of this law to animal efficiency. Brody (1945) cites the philosophy that “the man blessed with plenty of this world’s goods requires a correspondingly larger increase in his good fortune than does the poor man in order to derive the same amount of pleasure.” Brody’s chapter 5, “Principle of Diminishing Increments,” provides extensive evidence of its fit to data for growing steers, rabbits, hens, and lactating cows. J. T. Reid of Cornell expounded frequently on the “A-TDN” concept of lower digestibility and efficiency at increased intakes (e.g., Reid, 1962; Moe et al., 1965). Sir Kenneth Blaxter in Scotland used the Mitscherlich equations to describe diet GE use by ruminants (Blaxter and Boyne, 1978). The research by Ferrell and Jenkins (1998) provides additional impetus to the need to consider this phenomenon in beef cattle energy requirement and efficiency evaluations. Use of NRC (1996), Level 2, allows prediction of level of intake depression; however, it may need refinement because the partial efficiencies of feedstuff energy use were established from estimates of absorbed energy using “maintenance level” digestibility. Actual DE or ME intakes of the animals used to determine NE_g were likely to have been lower than assumed. NRC dairy (2001) has also incorporated procedures to estimating digestibility depression at increasing levels of diet intake.

Future Directions

The history of describing the energetic efficiency of beef cattle has been focused on groups or genotypes and the factors that determine their diet energy requirements. The publication from the Committee on Animal Nutrition of the National Academy of Sciences, Nutrient Requirement of Beef Cattle, has expanded exponentially with each succeeding issue over the last 40 yr. More and more factors have been defined, such as breed/genotype, environment, and BW at maturity, that impact energy, and other nutrient requirements. Part of the expansion results from the deliberate attempt to document the scientific basis for these concepts.

Although these definitions represent important improvements in projecting needs or responses of cattle, we are recommending a change of research emphasis for the future. The focus should be on methods to assess individual animal differences in energetic efficiency, particularly on variations in energy requirements for

maintenance of mature beef cows. This, of course, is not a new dream of energeticists, but one that may be currently reachable. To accomplish the goal, a practical means of identifying individuals of merit must be developed to replace the too costly and cumbersome respiration or slaughter balance methods.

Greater activity within the integrative component of knowledge generation is needed to create new tools required for conducting the studies at the appropriate scale. Research protocols applied today are predicated on integrative research from the late nineteenth century. During the adoptive phase of the last 50 yr, the precision of many measurements may have been increased as have the ability to store and analyze the data, but it is for traits that were identified in the nineteenth and early twentieth centuries.

Recently, Oddy and Herd (2001) suggested that there are five mechanisms contributing to variation in efficiency under genetic control that could be studied, which are as follows: 1) feed intake, 2) digestion of feed, 3) metabolism, 4) activity, and 5) thermoregulation. To this list we would add those that have received most of the attention: 6) rate or gain, 7) BW, and 8) prolificacy. Also, metabolism must be separated into at least two components: 3a) maintenance and 3b) growth metabolism. None of these traits can be ignored, if only to ensure minimum or no negative consequences.

If we assume the processes identified above are correct, what phenotypes can be identified within each of these processes? What measurements need to be recorded? When should it be recorded? For example, informative data to improve energetic efficiency on a mature, grazing ruminant may not be the same as that needed for postweaning animals with access to high-quality diets. Is it possible to accurately determine the energy efficiency of the beef cattle system by making measurements only on young growing animals consuming high concentrate diets? As Webster questioned (see above), is fasting heat production a robust indicator of maintenance efficiency?

Possible Techniques, RFI. The several reports of relative feed intake measurements on individual animals, discussed briefly above, are encouraging. Genetic antagonisms appear inconsequential in most traits examined and the tool may indeed prove useful to define system energetic efficiency. Use of RFI for individual evaluation of large numbers of animals is, however, still cumbersome and several confounding factors are undoubtedly part of this compound trait. Other possibilities may also arise. Variations on this theme may be observed/expected ratios expressed either as observed to expected gain ratio or apparent maintenance requirement. In any case, component process energy loss measurements will need to be made on the growing animals and, particularly, mature cows to calibrate the method at least during development phases.

Heart Rate (HR) Option. This technique extrapolates to daily HP from short-term measurements of O_2/HR and long-term recordings of HR. The technique proba-

bly can be useful, but only under special circumstances and limited conditions. The need to “calibrate” each animal and then to show they are not “stressed” by the measurement process present serious limitations. Dr. A. Brosh (Agric. Res., Israel) estimated that in mature, untrained cows, some 50 or more percentage would not “calibrate.” That is, they would have heart rates during O_2/HR calibration, as normally conducted in a handling chute, that are 10 or 20% or more above their HR average for the balance of the day. Perhaps for development of indexes, one could train young animals and thus calibrate O_2/HR for the majority of a group, as we can generally train them to be apparently calm in chambers. Calibrated O_2/HR monitoring combined with the inclinometer/accelerometers technique may provide a way to investigate activity energy loss variations in production circumstances.

Chips, ChIPs, SniPs, QTLs and Regulons. The most likely infusion of new tools with the most potential to realize improved maintenance and system energetic efficiency will come through identification of individual animal genomic message uniqueness. As stated by a recent technology perspective (Shannon and Arao, 2002), “developments in microarray technology will soon allow the entire human genome to be displayed on one or a small number of chips, providing a powerful tool for discovering and mapping of global regulation networks.” Their transcription perspective described the use of microarray expression profiling using a combination of cDNA chips and chromatin immunoprecipitation to investigate expression groupings termed *regulons*. Although bovine genome mapping, sequencing, and regulon functions lag behind prokaryote and human descriptions, there are multiple candidates such as the maintenance and/or energy loss control factors discussed above to allow the development of targeted energetics microarrays. Such energy flux message profiling and/or QTL will likely need to be calibrated with simultaneous individual animal evaluations using classical methods, e.g., nutrient flux, O_2 consumption, etc. Once developed, these assays can be used to screen thousands of individuals identifying energetic uniqueness of value to the beef cattle industry.

Implications

The discovery that feedstuff nutrient use for the maintenance of animal life and support of animal product formation is a combustion process provided the basis for understanding dietary energy use by animals. Thousands of experiments exploring feedstuff and diet digestion, coupled with measures of either heat loss or product energy retention, have been used to create elaborate, useful net energy schemes to predict animal performance and/or requirements. Despite these advances, neither the requirement of energy for maintenance nor the partial efficiencies above maintenance have changed materially in the last 100 yr, and major mysteries remain unsolved (e.g., the cause of the high

heat increment of forages). New insights into factors controlling the need for and use of energy will likely be required to move forward. It is expected that techniques now becoming available will provide such insight, which in turn, will allow progress toward increased energetic efficiencies in the future.

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