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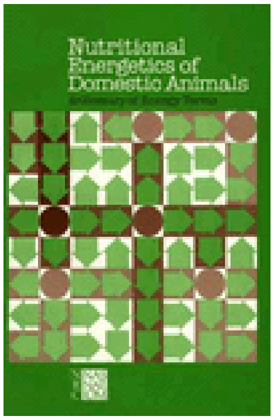

Nutritional Energetics of Domestic Animals and Glossary of Energy Terms

Sybcommittee on Biological Energy, Committee on Animal Nutrition

ISBN: 0-309-59751-X, 54 pages, 6 x 9, (1981)

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THE NATIONAL ACADEMIES
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Nutritional Energetics of Domestic Animals & Glossary of Energy Terms

Second Revised Edition, 1981

Subcommittee on Biological Energy
Committee on Animal Nutrition
Board on Agriculture and Renewable Resources
Commission on Natural Resources
National Research Council

NATIONAL ACADEMY PRESS
Washington, D.C. 1981

NOTICE: The project that is the subject of this report was approved by the Governing Board of the National Research Council, whose members are drawn from the councils of the National Academy of Sciences, the National Academy of Engineering, and the Institute of Medicine. The members of the committee responsible for the report were chosen for their special competences and with regard for appropriate balance.

This report has been reviewed by a group other than the authors according to procedures approved by a Report Review Committee consisting of members of the National Academy of Sciences, the National Academy of Engineering, and the Institute of Medicine.

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This study was supported by the Bureau of Veterinary Medicine, Food and Drug Administration of the U.S. Department of Health and Human Services, by Agricultural Research, Science and Education Administration of the U.S. Department of Agriculture, and by Agriculture Canada.

Library of Congress Cataloging in Publication Data
National Research Council. Committee on Animal Nutrition. Subcommittee on Biological Energy.
Nutritional energetics of domestic animals and glossary of energy terms.
Edition of 1966, prepared by the Committee on Animal Nutrition of the National Research Council, published under title: Biological energy interrelationships and glossary of energy terms.
Bibliography: p.
1. Animal nutrition. 2. Animal nutrition–Terminology. 3. Bioenergetics–Terminology. I. National Research Council. Committee on Animal Nutrition. Biological energy interrelationships and glossary of energy terms. II. Title. [DNLM: 1. Animal nutrition– Nomenclature. 2. Energy metabolism–Nomenclature. SF 95 N2775n]
SF95.N3 1981 636.08•52 80-28912

ISBN 0-309-03127-3

First Printing, January 1981
Second Printing, October 1990

Available from
NATIONAL ACADEMY PRESS
2101 Constitution Avenue, N.W.
Washington, D.C. 20418

Printed in the United States of America

Preface

In 1962 a report was prepared for the Committee on Animal Nutrition (CAN) by Lorin E. Harris entitled *Glossary of Energy Terms*. This report was intended for use as a reference in connection with the *Nutrient Requirements of Domestic Animals Series*.

The report was revised in 1966 as *Biological Energy Interrelationships and Glossary of Energy Terms*, and research workers were urged to re port their data according to the calorie system so that sufficient information could be obtained to construct feed composition and nutrient requirement tables for various species of animals with quantities given in calories. These efforts have been most successful, and tables of feed composition and nutrient requirements prepared by the species-oriented subcommittees of the Committee on Animal Nutrition are routinely included in each report of the *Nutrient Requirements of Domestic Animals Series*.

Several new systems of feed evaluation have come into use since 1966, with varied and sometimes conflicting use of terminology. The Committee on Animal Nutrition therefore requested the appointment of a subcommittee to (1) develop more systematic terminology for the description of energy utilization by animals and (2) reconcile the terminology used in feeding systems with the more idealized scheme for describing energy metabolism of animals.

The CAN Subcommittee on Biological Energy was appointed to address these issues. Two formal meetings were held, the first on September 29-30, 1977, in Washington, D.C., and the second on March 2-3, 1978, in Chicago, Illinois. The activities of the subcommittee were expanded to address the compromises included in the development of practical feeding systems in order to have a system simple enough to be accepted for general use.

The information contained in this report is the result of the efforts of the members and the suggestions by individuals engaged in energy metabolism research. In particular, David R. Ames, Henry S. Bayley, John E. Cantlon, Richard C. Ewan, John E. Halver, and Glen P. Lofgreen assisted by preparing critical reviews, and their suggestions are deeply appreciated. Also reviewing this report were the members of the Committee on Animal Nutrition, the Board on Agriculture and Renewable Resources, and the Commission on Natural Resources. Staff of the Board on Agriculture and Renewable Resources, Philip Ross (executive secretary), Selma P. Baron (staff officer), and Sheridan E. Caldwell (secretary) assisted the subcommittee in the production of this report.

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Nutritional Energetics of Domestic Animals and Glossary of Energy Terms

INTRODUCTION

The quantitative nutrient requirements of domestic animals are complex and change depending upon sex, physiological state, and a variety of environmental factors. The energetic economy of the animal is sustained by the catabolism of fuels. The total intake of food by animals feeding *ad libitum* is related to their energy needs and to the concentration of available fuels in the diet. Many assumptions are required to condense the total energetics of an animal into the relatively simple tabulations used in practice to quantify the dietary energy requirements of domestic animals and man. The primary objective of this publication is to outline the most commonly used systems for the description of energy requirements in terms of an idealized flow of energy through an animal. To this end, some classical measures of energy metabolism are defined in a system of abbreviations. These have been useful to describe the flow of energy and with suitable modification can be used to describe the flow of any element through an animal.

It is beyond the scope of this publication to present in detail methods used to measure metabolic transfers in animal systems. Rather, the objective is to define energy metabolism terminology within a general biological framework applicable to all animal species. A brief account of conventional schemes for the description of energy metabolism is presented along with the historical basis for each. Finally, the energy systems in common use within the United States and Canada for various species of domestic animals are outlined. The appendix contains a complete list of abbreviations and symbols commonly used to describe energy transactions in domestic animals.

UNITS OF MEASUREMENT

Energy is an abstraction that can be measured only in its transformation from one form to another. Thus all of the defined units to measure energy are equally absolute. The joule has been adopted by *Le Système International d'Unites* (SI; International System of Units) and the National Bureau of Standards (U.S.A.) as the preferred unit for expressing electrical, mechanical, and chemical energy. The joule is defined in mechanical terms (i.e., the force needed to accelerate a mass), but can be converted to ergs, watt-seconds, and calories. The converse is also true.

The joule has replaced the calorie as the unit for energy in nutritional work in some countries. One reason for replacing the calorie is the acceptance of the joule as the metric measure of energy by SI (Moore, 1977). Another reason for replacing the calorie was some variation in the fourth figure regarding its exact relationship to the joule, a factor of greater importance to the physicist than to the nutritionist. The conversion of the calorie to the joule has now been arbitrarily standardized as 1 cal (calorie) = 4.184 J (joule). Nutritional investigators generally standardize their bomb calorimeters using a thermochemical standard, usually specially purified benzoic acid whose heat of combustion has been determined in electrical units and computed in terms of joules/ gram mole.

Joule (J). The joule is 10^7 ergs, where 1 erg is the amount of energy expended in accelerating a mass of 1 g (gram) by 1 cm/s (centimeter per second). The international joule is defined as the energy liberated by one international ampere flowing through a resistance of one international ohm in 1 s.

Calorie (cal). The calorie is defined as 4.184 J. This amount of energy raises the temperature of 1 g of water from 16.5° to 17.5°C. In practice, both the joule and the calorie are so small that nutritionists work with multiple units:

Kilojoule (kJ) and *Kilocalorie* (kcal) are 10^3 times greater than the joule and the calorie, respectively, and

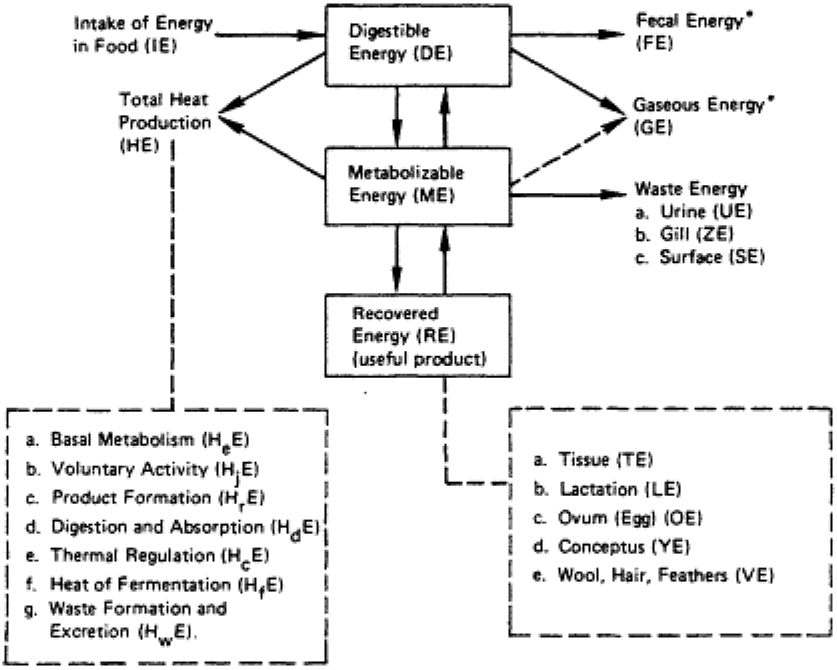
Megajoule (M J) and *Megacalorie* (Mcal) are 10^6 times greater than the joule and the calorie, respectively.

Gross Energy (E) is the energy released as heat when an organic substance is completely oxidized to carbon dioxide and water. It is often referred to as "heat of combustion" and generally measured in an oxygen bomb calorimeter.

Metabolic Body Size ($W^{.75}$) is the body weight in kilograms of an animal raised to the three-fourths power. It is useful in comparing metabolic rates of mature animals of different body sizes. The exponent .75 is generally used, but other exponents have merit and may be more appropriate in some situations.

BIOLOGICAL BASIS OF ENERGY PARTITION

Lavoisier (as cited by Blaxter, 1956) during the eighteenth century first enunciated the principles of combustion both outside and within the body. In 1894, M. Rubner (as cited by Blaxter, 1962) working with dogs first demonstrated that the fundamental laws of thermodynamics apply to an intact live animal system. The flow of energy through an animal as outlined in Figure 1 is an attempt to reconcile traditional methods of describing energy transactions in an animal with present knowledge of intermediate steps in the utilization of dietary nutrients.



*Under some circumstances the energy contained could be considered to be a useful product for fuel.

Figure 1 The idealized flow of energy through an animal.

Figure 1 shows dietary energy (IE) passing through two stages, digestible energy (DE) and metabolizable energy (ME), enroute from food energy (IE) to retention as some useful product (RE). Energy is lost in forms other than useful products, such as fecal energy (FE), gaseous energy (GE), urine (UE), gill excretion (ZE), and surface or skin secretions (SE), and as heat (HE). The first law of thermodynamics, or the law of conservation of energy, requires that IE = FE + GE + UE + ZE + SE + HE + RE. Within this framework, each energy fraction can be partitioned on the basis of origin, metabolic pathway, and other criteria. For example, energy yielding components in feces are, in part, of food origin (F_iE) and, in part, of metabolic origin (F_m E). The sum of these fractions is gross energy contained in the feces or FE = $F_iE + F_mE$.

The methods used for measurement and pitfalls in interpreting energy exchange in an animal are beyond the scope of this publication. However, the assumption inherent in all measurements of energy exchange is steady state equilibrium. In quantitative nutrition an animal seldom, if ever, truly reaches a steady equilibrium state. Thus, if the time scale of the fluctuations of energy balance about the equilibrium is greater than the period of observation, the measurements will be in error. For example, measurement of heat exchange for a period of a few minutes can give a very precise measure of heat emission at that period in time, but is not representative of the average rate over 24 h (hour). Similarly, the feces produced voluntarily by an animal during a given period can be measured very accurately, but feces are a result of food ingested and metabolic processes that occurred at some time prior to their excretion. Therefore the flow of energy through the animal as diagramed in Figure 1 represents a system that can only be measured approximately over any particular time interval. Knowledge and understanding of a biological system are required to determine the time constants and appropriate methods to use in obtaining the best measurements of energy flux for any particular application.

DEFINITION OF TERMS

A number of abbreviations have been used in the past to describe energy fractions in an animal system. The system of abbreviations used in Figure 1 to describe the flow of energy has application to other nutrients as well. The first measurement in a nutritional evaluation of energy exchange is defined as gross energy (E). The nutritional fractions typically measured in an animal system are abbreviated by a series of uppercase letters as shown in Figure 1. Therefore total intake of food energy is IE, where I is the amount of food consumed and E is the gross energy per unit weight of food. Similarly, total energy contained in feces is FE, where F is the amount of feces voided and E is the gross energy per unit weight of the feces.

Intake of Food Energy (IE) is the gross energy in the food consumed. IE is the weight of food consumed times the gross energy of a unit weight of food.

Fecal Energy (FE) is the gross energy in the feces. FE is the weight of feces times the gross energy of a unit weight of feces. FE can be partitioned into energy from undigested food (F_iE) and energy from compounds of metabolic origin (F_mE).

Apparently Digested Energy (DE) is energy in food consumed less energy in feces: $DE = IE - FE$.

True Digested Energy (TDE) is the intake of energy minus fecal energy of food origin ($F_iE = FE - F_eE - F_m E$) minus heat of fermentation and digestive gaseous losses: $TDE = IE - FE + F_e E + F_m E - H_fE - GE$.

Gaseous Products of Digestion (GE) includes combustible gases produced in the digestive tract incident to fermentation of food by microorganisms. Methane makes up the major proportion of combustible gas normally produced in both ruminant and nonruminant species. Hydrogen, carbon monoxide, acetone, ethane, and hydrogen sulfide are produced in trace amounts and can reach significant levels under certain dietary conditions. Present knowledge indicates that energy lost as methane in ruminants and nonruminant herbivores is quantitatively the most significant GE loss.

Urinary Energy (UE) is the total gross energy in urine. It includes energy from nonutilized absorbed compounds from the food (U_iE), end products of metabolic processes ($U_m E$), and end products of endogenous origin (U_eE).

Metabolizable Energy (ME) is the energy in the food less energy lost in feces, urine, and combustible gas: $ME = IE - (FE + UE + GE)$.

N-Corrected Metabolizable Energy (M_n E) is ME adjusted for total nitrogen retained or lost from body tissue: M_n E = ME - (k × TN). For birds or monogastric mammals, gaseous energy is usually not considered. The correction for mammals is generally k = 7.45 kcal per gram of nitrogen retained in body tissue (TN). The factor of 8.22 kcal per gram of TN is used for birds representing the energy equivalent of uric acid per gram of nitrogen. A number of different values for k have been suggested and used (see species sections).

True Metabolizable Energy (TME) is the intake of true digestible energy minus urine energy of food origin: TME = TDE -UE + U_e E.

Total Heat Production (HE) is the energy lost from an animal system in a form other than as a combustible compound. Heat production may be measured by either direct or indirect calorimetry. In direct calorimetry, heat production is measured directly by physical methods, whereas indirect calorimetry involves some indirect measure of heat such as the measurement of oxygen uptake and carbon dioxide production using the thermal equivalent of oxygen based upon respiratory quotient (RQ) and theoretical considerations. The commonly accepted equation for indirect computation of heat production from respiratory exchange is HE (kcal) = 3.866 (liters O_2) + 1.200 (liters CO_2) - 1.431 (g UN) - 0.518 (liters CH_4) (Brouwer, 1965). Heat production may also be measured by difference from the determination of total carbon and nitrogen balance or from a comparative slaughter experiment. These methods arrive at total heat production by different calculations and are subject to systematic errors of measurement.

Basal Metabolism (H_eE) reflects the need to sustain the life processes of an animal in the fasting and resting state. This energy is used to maintain vital cellular activity, respiration, and blood circulation and is referred to as the basal metabolic rate (BMR).

For the measurement of BMR the animal must be in a thermoneutral environment; a postabsorptive state; resting, but conscious; in quiescence; and in sexual repose. It is difficult to determine when ruminants reach the postabsorptive state, but a common criterion is the absence of methane production. The length of the fasting period should be specified. A common benchmark of fasting metabolism is when the respiratory quotient becomes equivalent to the catabolism of fat or near 0.7. This has been achieved experimentally in 48 to 144 h after the last meal.

Heat of Activity (H_jE) is the heat production resulting from muscular activity required in, for example, getting up, standing, moving about to obtain food, grazing, drinking, and lying down.

Heat of Digestion and Absorption (H_dE) is the heat produced as a result of the action of digestive enzymes on the food within the digestive tract and the heat produced by the digestive tract in moving digesta through the tract as well as in moving absorbed nutrients through the wall of the digestive tract.

Heat of Fermentation (H_fE) is the heat produced in the digestive tract as a result of microbial action. In ruminants, H_fE is a major component often included in the heat of digestion (H_d E).

Heat of Product Formation (H_rE) is the heat produced in association with the metabolic processes of product formation from absorbed metabolites. In its simplest form, H_rE is the heat produced by a biosynthetic pathway.

Heat of Thermal Regulation (H_c E) is the additional heat needed to maintain body temperature when environmental temperature drops below the zone of thermal neutrality, or it is the additional heat produced as the result of an animal's efforts to maintain body temperature when environmental temperature goes above the zone of thermal neutrality.

Heat of Waste Formation and Excretion (H_w E) is the additional heat production associated with the synthesis and excretion of waste products. For example, synthesis of urea from ammonia is an energy costly process in mammalian species and results in a measurable increase in total heat production.

Heat Increment (H_iE) is the increase in heat production following consumption of food by an animal in a thermoneutral environment. Included in H_iE are heat of fermentation (H_fE) and energy expenditure in the digestive process (H_dE) as well as heat produced as a result of nutrient metabolism (H_r E + H_w E). Heat increment is usually considered to be a non-useful energy loss, but under conditions of cold stress H_iE helps to maintain body temperature.

Recovered Energy (RE), commonly called *Energy Balance*, is that portion of the feed energy retained as part of the body or voided as a useful product. In animals raised for meat, RE = TE, whereas in a lactating animal, RE is the sum of tissue energy, lactation energy, and energy in products of conception: RE = TE + LE + YE.

CONVENTIONAL SCHEME

The law of conservation of energy, and the law of initial and final states are the fundamental principles that form the basis of bioenergetics. Thus, if an increased amount of energy is found in one place (an animal body), an equal quantity of energy has been removed from another place (the food that has been consumed). Also, the amount of energy transformed in an isolated system (the breakdown and synthesis of chemical substances in the animal, for example) as a result of a change in the system depends only on the initial and final states of the system. That is, the amount of heat produced or absorbed during a chemical transformation is independent of the number and kind of intermediate steps involved or the rate at which the transformation occurs. Inherent in the above principles is the concept that all known forms of energy (chemical, electrical, magnetic, and gravitational) can be converted quantitatively to heat.

The basis of bioenergetics as defined by the two laws and application to whole animal nutritional energetics may be stated by using the terminology defined earlier (Figure 1):

$$IE = FE + GE + UE + ZE + SE + HE + RE.$$

This simple identity partitions the energy consumed by an animal into the major components associated with animal energetics. It can be expanded to include a few or many of the intermediate steps involved, and each individual component can be subdivided into several constituent parts, but the expression will still remain compatible with the two laws. That is, the use or failure to use information obtained in detailed studies of the energetics of intermediate transformations does not prejudice the balance of the equation.

All energy balance techniques and all systems used to describe the relationship between an animal's requirement for energy and the ability of a foodstuff to supply this energy are related to this classical energy balance identity. In general use, each term is a rate with the basis of time an interval of 24 h. Shorter or longer periods can be used.

The terms of the balance equation have been defined earlier. The components IE, FE, UE, GE, ZE, SE, and RE are heats of combustion determined in a bomb calorimeter and represent the total energy released during the oxidation of that component to carbon dioxide and water. Other terms used to describe the heat of combustion are gross energy or, simply, energy value. The gross energy (E) of a substance is the sum of the E value of its constituents and is thus related to chemical composition. For example, the E values of foods can be estimated by using average factors to convert quantities of protein, fat, and carbohydrate to amounts of energy. This estimate will be less precise than values obtained by bomb calorimetry.

Gross energy intake (IE), or the total energy contained in a feedstuff, is of little value in assessing the worth of a particular diet or dietary component as a source of energy for the animal. Gross energy expressed as kilocalories per unit of dry weight can indicate in a relative way the potential of a substance to furnish energy. Many feedstuffs are composed of carbohydrates that have an E of approximately 4.2 kcal/g; a higher E value could indicate the presence of protein and/or lipids, whereas a lower value might be explained by the presence of large amounts of inorganic substances. In either case, the gross energy value does not provide any clue as to how available the energy is to the animal.

Digestible energy (DE) does provide some clue as to availability of energy. Similar terms are apparent absorbed energy or energy of apparently digested food. The word "apparent" is sometimes used in conjunction with digestible energy to recognize the fact that not all the energy in feces (FE) is derived from food residue. As was mentioned previously, FE has two major components, fecal energy of food origin (F_iE) and fecal energy of metabolic origin ($F_m E$). Actually, there is a third component, fecal energy of microbial origin. Because the energy of the microbes originated either with the feed or with the metabolic products, it need not be considered separately. It should be recognized that there are additional losses of energy associated with the digestion of a food or feedstuff that in the conventional determination of DE are not subtracted from IE. Gaseous products of digestion (GE), for example, are actually losses associated with the digestive process.

Metabolizable energy (ME) is an estimate of the dietary energy that becomes available for metabolism by the tissues of the animal. Metabolizable energy is defined by the relationship:

$$ME = IE - (FE + UE + GE)$$

or

$$ME = IE - (FE + UE + GE + ZE) \quad \text{for fish}$$

The equations and the energy balance identity indicate that metabolizable energy can appear in only two forms—either as heat (HE) or in the energy of products formed (RE). Thus ME = RE + HE.

For the overall assessment of energy balance in an animal, metabolizable energy does not need to be corrected for the metabolic (F_m E) and endogenous (U_eF.) sources of energy. However, in some investigations, particularly when feedstuffs are being compared as sources of ME, it may be advantageous to correct for F_m E and U_eE to obtain a true metabolizable energy value (TME). The true metabolizable energy content of a feedstuff will be higher than the ME content.

Metabolizable energy has sometimes been adjusted to the basis of nitrogen equilibrium (M_n E). The goal of this computation for feed evaluation was to remove from the estimate of ME any bias associated with the particular conditions (i.e., physiological state of the animal or feeding management) that happened to prevail during a particular experiment. The justification for this "correction" is controversial. The adjustment is neither necessary nor justified for a particular energy balance trial.

Tissue energy retained or lost from the animal's body plus energy recovered as useful animal products (RE) is commonly known as energy balance. In keeping with the general energy balance identity, RE is the heat of combustion of all animal products (TE, LE, YE, OE, etc.) that may be produced *or lost* with a given energy intake (IE) not accounted for in any other category. RE may be a positive or a negative quantity.

$$RE = IE - (FE + UE + GE + HE)$$

or

$$RE = ME - HE.$$

Total heat production (HE) is the amount of energy that is transferred from the animal to the environment in a form other than combustible energy. The total heat production consists of many components: fasting metabolism in animals or basal metabolism in humans (H_eE), heat associated with voluntary activity (H_jE), heat of product formation (H_rE), heat for thermal regulation (H_c E), heat of digestion (H_d E), heat of waste formation and excretion (H_w E), and heat of fermentation (H_fE). In many applications of these relationships the components $H_rE + H_d E + H_w E + H_fE$ are combined and considered to be the heat increment or H_iE. There are several equations that help to visualize the components of HE.

$$HE = H_eE + H_jE + H_rE + H_cE + H_dE + H_wE + H_fE$$

$$H_iE = H_rE + H_dE + H_wE + H_fE$$

$$HE = H_eE + H_jE + H_cE + H_iE$$

In nonstressful environments where H_cE would be zero or negligible, the components of HE consist of the heat produced under fasting conditions (H_eE), the heat produced as a result of activity (H_jE), and the heat increment of feeding (H_iE):

$$HE = H_eE + H_jE + H_iE.$$

A rearrangement of a previous equation (RE = ME - HE) gives HE = ME - RE. It is evident that RE will be a negative quantity if ME is less than HE. That is, an animal will be using energy from body tissues any time total heat production exceeds metabolizable energy intake.

RELATIONSHIP OF ENVIRONMENTAL TEMPERATURE TO ENERGY METABOLISM

The relationship between the climatic environment and the partition of dietary and body energy into various components is related to body size (surface), amount of insulation (surface covering), level of feeding, ration balance, and type of production. Climatic conditions may influence rate of loss of energy in feces, urine, gases, and heat, thereby playing a significant role in energetic efficiency. Extensive attention has been given to this by Kleiber (1961) and Brody (1945) and in an NRC publication on the subject of environmental effects on animal production (in preparation).

The relationship between animals and their thermal environment begins with the thermoneutral zone (TNZ), which is sometimes referred to as the thermal comfort zone or the zone of thermal indifference. The thermoneutral zone is defined as the effective ambient temperature (EAT) where heat production at the thermoneutral rate is offset by net heat loss to the environment without aid of special heat-conserving or heat-dissipating mechanisms. Below the TNZ lies the cool zone, where animals invoke mechanisms that conserve metabolic heat. These are mainly postural adjustments and changes in hair or feathers and in peripheral blood vessels that affect cover insulation and tissue insulation, respectively. As EAT decreases within this zone, metabolic rate of the fed animal remains at the thermoneutral level. The various insulative and behavioral responses to cold stress are at maximal effectiveness at the lower limit of the cool zone, a point called the lower critical temperature (LCT). Below this point lies the cold zone, where the only way an animal can maintain homeothermy is to increase its rate of metabolic heat production. As effective ambient temperature rises above the upper limit of the thermoneutral zone, the animal is in the warm zone, where thermoregulatory reactions are mainly limited to passive facilitation of heat loss. Decreasing tissue insulation by vasodilation and increasing effective surface area by changing posture are major mechanisms used to facilitate rate of heat loss. As the environment rises above the warm zone, the homeothermic animals must call into play active heat-dissipating mechanisms employing evaporative heat loss, such as sweating and panting. Then the animal is in the hot zone. The EAT at which the animal passes from the warm zone to heat stress is called the upper critical temperature (UCT).

It is important to recognize that the relationship between cold, critical temperatures, TNZ, and heat remains consistent. Cold temperatures always refer to those temperatures below the TNZ even though the TNZ may change. Factors that alter critical temperatures or cause a shift in the TNZ are insulation, plane of nutrition, activity, solar radiation, or any other factor altering rate of energy exchange between the animal and its environment. For example, lower critical temperature may change from 0°C in a sheep with fleece to 20°C in shorn sheep, other factors remaining constant. In other words, ambient conditions are of little value in predicting the effect on energy needs unless one also knows the thermoneutral zone of the animal involved. Other factors remaining constant, it is magnitude of cold (degrees below LCT) or magnitude of heat (degrees above UCT) that is important in relating animals to their thermal environment.

Some studies (Young, 1976) have indicated lower energy digestibility during cold. Often, increased intake is credited with lower digestibility during cold, but covariate analysis has shown that decreased dry matter digestibility is due to temperature alone. Although all available information relating energy digestibility to heat stress does not agree, most data tend to support the hypothesis that digestibility increases during heat stress. This may be a result, in part, of decreased voluntary intake rather than a direct effect of increased temperature.

Feed consumption increases the rate of heat production. This additional amount of heat is referred to as heat increment (H_iE) and can be identified in Figure 1 as H_rE, H_d E, H_w E, and H_fE. The sum of these sources of heat is important in describing animals' TNZ, since additional heat production lowers the TNZ. For example, thermoneutral temperature is relatively low for animals with high levels of production compared with similar animals on a maintenance diet largely because of relatively high total heat production. It is important to understand the difference in effect of heat increment on animals exposed to cold as compared with animals exposed to heat. During cold, heat increment is useful in offsetting increased rate of heat loss. Conversely, heat increment aggravates the problem at high temperatures by adding more heat to an already heat-stressed system. Consequently, the relationship of heat increment to energetic efficiency is positive during cold but negative during heat.

An animal exposed to temperatures below its critical temperature must compensate for increased energy loss by additional energy expenditure. Two major characteristics of the animal determine the rate of heat loss on exposure to cold: (1) thermal gradient between core temperature and ambient temperature and (2) amount of insulation provided by hair coat or fleece, tissue, and air interface. In general, the thermal gradient and animal insulation can be used to predict the rate of heat loss by the following linear relationship:

$$\text{Insulation} = \frac{\text{rate of sensible heat loss}}{\text{temperature gradient}} = \Delta E.$$

By estimating the amount of total insulation, the increased energy requirement per degree of cold stress may be determined by the following equation:

$$M_m\,E = aW^{.75} + b(\Delta T/\Delta E),$$

where

M_m E = metabolizable energy for maintenance (kcal/day),

ΔT = magnitude of difference between lower critical temperature and effective ambient temperature,

ΔE = total insulation of animal (kcal/T/M^2/day),

a = coefficient of maintenance requirement for animal in TNZ (kcal ME/$W^{.75}$/day),

b = surface area of animal (M^2), and

$W^{.75}$ = metabolic body size (kg).

The relationship between heat production and environmental temperature cannot be extrapolated for temperatures above the thermoneutral zone. Instead, the energy requirement increases nonlinearly during heat stress. This increase is attributed to the need for thermal regulatory mechanisms such as sweating and panting. It has also been reported (Kleiber, 1961) that the Q_{10} effect of increased core temperature (increases that are within the range expected for homeothermy) may contribute significantly to an increased rate of metabolic heat production during exposure to heat stress. While nonlinear increases in metabolic heat production have been reported, more work is needed to better define relationships between magnitude of heat stress and increased rate of heat production.

Above the upper critical temperature, core body temperature and heat production increase, the latter according to Van't Hoff's law (Kleiber, 1961):

$$H_tE = H_0 E\, Q_{10}^{0.1T},$$

where
H_tE= metabolic rate at temperature T°C,
H_0 E = metabolic rate at 0°C, and
Q_{10} = Van't Hoff's quotient (approximately 2).

The above process becomes fatal if the cellular processes remain uncontrolled. An example is taken from Kleiber (1961) for illustrative purposes.

The metabolic rate (kcal/day/M^2) of some human subjects was 890 at 24°C (known to be within the zone of thermal neutrality) and 1515 at 2°C. The latter was assumed to be the thermostatic heat requirement at 2°C. The thermostatic heat requirement is directly proportional to the difference between body temperature (37°C) and environmental temperature (2°C). The formula is

$$\Delta HE/\Delta T = Q(T_i - T_e).$$

where

$\Delta HE/\Delta T$ = rate of heat production needed to supply thermostatic heat requirement (kcal/day/M^2),

Q = effective heat transmissivity (kcal/M^2/day/°C),

T_i = body temperature (°C), and

T_e = effective environmental temperature (°C).

From the above,

$$Q = \frac{\Delta HE/\Delta T}{T_i - T_e} = \frac{1515}{37-2} = \frac{1515}{35} = 43 \text{ kcal/M}^2\text{/day/°C.}$$

The lower critical temperature (T_c) can be defined as the point at which the thermostatic heat requirement (heat to maintain body temperature) is equal to defined metabolic rate. It is the temperature below which the animal can no longer regulate E to keep HE = 0, and metabolic rate must increase in proportion to the need for heat. Thus

$$\Delta HE/\Delta T = 43(37 - T_c) = 890$$

or

$$T_c = 16.3°C.$$

One expects the rate of heat production to be (ideally) independent of environmental temperature in the TNZ. Above the upper critical temperature it increases independently of animal control. Below the lower critical temperature it increases (controlled) to a maximum (summit metabolism) as temperature declines. When the rate of heat loss exceeds metabolic capacity, body temperature falls and death results from hypothermia. However, in poikilothermic animals a reduction in body temperature causes only a reduction in metabolic rate.

Level of feed (energy) intake does not influence the thermostatic heat requirement directly. It does, however, influence the upper and lower critical temperatures. As metabolic rate increases with increased feeding within the zone of thermal neutrality, the lower critical temperature decreases. For example, at a metabolic rate of 1275 at 24°C, T_c = 7.4°C. Although not precisely defined, the upper critical temperature would be expected to drop with increased intake, but in practice the animal reduces metabolic rate by reducing food consumption at high temperatures.

The influence of environmental temperature on animal production is important. At high environmental temperatures, voluntary feed intake is usually reduced, as one means of helping the animal regulate body temperature and heat load. At decreasing temperatures in productive animals, H_iE becomes a useful product used to meet the thermostatic heat requirement. Other physiological mechanisms can come to bear that improve the heat conservation of the animal.

SYSTEMS USED TO EXPRESS FEED ENERGY VALUES AND AN ANIMAL'S REQUIREMENT FOR ENERGY

The historical aspects of feed evaluation systems have been reviewed by Blaxter (1955, 1956) and Reid (1962). As pointed out by Blaxter, the advances in feed evaluation have been in three major overlapping steps. The beginning was the "hay value" of Thaer published in 1809 and revised at intervals through most of the nineteenth century. The second major advance came from the studies of Henneberg and Stohmann during the period 1850 to 1880 that produced the proximate analysis scheme and the conventional digestion trial. The third major step, also started by Henneberg and Stohmann, who recognized the deficiencies of a feeding system based on "digestible nutrients," was the almost simultaneous formulation of the net energy concept by Armsby in the United States and Kellner in Germany during the early part of the twentieth century. The fundamental principles of Armsby and Kellner are equivalent. Kellner's starch equivalent and the net calorie of Armsby are interconvertible, each expressing the value of the feed in terms of the energy retention (RE) that it promotes. The three steps outlined above in a historical context provide the basis for the feeding systems in current use.

Digestible Energy

Since the loss of energy in feces (FE) associated with the consumption of particular foods or diets accounts for or is related to the varying abilities of these foods or diets to fulfill an animal's requirement for energy, it is possible to evaluate feeds and assess animal requirements in terms of DE. For some feeding situations, particularly the formulation of diets where only a few feeds are involved and the animal's requirements in terms of DE have previously been determined by using similar feeds and levels of animal production, satisfactory results can be obtained. The major weakness of DE as a basis for a ruminant feeding system is that it overevaluates high-fiber feedstuffs (hays, straws) in relation to low-fiber products (grains). In rations for nonruminants the DE concentrations of feed ingredients are similar and the shortcomings of DE as a system for evaluating feeds are minimized. Feed ingredients used in diets for ruminants vary widely in DE content and the weakness of DE is greatest.

Metabolizable Energy

Metabolizable energy is superior to DE for use as a measure to express feed values and energy requirements because it considers losses of energy in the urine (UE) and combustible gases (GE). It has been used to express the feed value and energy requirements of poultry for many years and is the general basis for the physiological fuel values used to describe the energy values of foods and the energy requirements of humans. It is an alternate system for stating the energy requirements of several species and is currently used by several subcommittees of the NRC. As is indicated by the relationship relating ME to RE and HE, it has major significance as a reference unit and as the starting point for nearly all systems that are based on the net energy concept. However, ME has many of the same deficiencies as DE. The reason for this is UE and GE are predictable from DE, and therefore the correlation between DE and ME is very high. True metabolizable energy ($ME + F_m E + U_e E$) may be a sufficiently precise measure of the energy value of feedstuffs for those species (like poultry) whose diets are highly digestible and less variable in composition than diets fed to ruminants and nonruminant herbivores. For ruminants in particular, and for nonruminant herbivores, ME is of most value as an integrant in the development of a feeding system based on the net energy principle.

Total Digestible Nutrients (TDN)

The total digestible nutrient system of feed evaluation developed in the United States is a direct result of the German work on "digestible nutrients." The major feature added was the multiplication of digested fat by 2.25 to account for the higher energy concentration of lipids. Thus TDN is the sum of the digestible protein, digestible carbohydrates, and 2.25 times the digestible fat. Maynard (1953) reviewed the TDN concept, pointing out the inconsistency of a "caloric correction" for digestible fat and the lack of a similar correction for protein. The failure to use an "energy correction" factor for protein has the effect of accounting for some urinary energy losses and therefore makes TDN a hybrid measure (not precisely DE or ME). The failure to make a correction for the energy in protein was not particularly detrimental (in fact may have been helpful) in a practical sense, since feed values and feeding standards based on TDN were estimated on the basis of the fat correction only. Nevertheless, TDN does not measure digestible nutrients as the name implies; it does not provide a more useful basis for a feeding system than DE, and, unlike ME, it is not a measure that has direct relevance to net energy or energy metabolism in general.

Physiological Fuel Values (PFV)

The assessment of the energy value of food for humans was reviewed by Widdowson (1955). These energy values (PFV) are expressed in kilocalories and usually are calculated from the amounts of protein, fat, and carbohydrate present as determined by chemical methods. The bases for these calculations were derived from work in Germany by Rubner from 1880 to 1901 and by At-water (once a pupil of Rubner) during the period 1895 to 1906 in the United States. Physiological fuel values are essentially ME values derived by using average heats of combustion and average digestion coefficients for protein, fat, and carbohydrate. Calories from protein are corrected for energy loss in the urine based on the determination that 7.9 kcal of energy were lost for each gram of nitrogen in the urine of human subjects consuming mixed diets. If 1 g of nitrogen in the urine is assumed to represent the breakdown of 6.25 g of digestible protein, there would be 7.9/6.25 = 1.26 kcal/g of digestible protein. The values calculated according to the general findings of Rubner and Atwater have varied somewhat depending upon the factors used to convert nitrogen to protein, the assumed digestion coefficients for protein, carbohydrate, and fat as well as the chemical procedure used to determine carbohydrate. The physiological fuel values commonly quoted (4, 4, and 9 kcal/g of protein, carbohydrate, and fat) may give reasonable estimates of metabolizable energy that can be used as a basis to formulate diets and approximate the requirements of humans for different functions.

Net Energy Concepts

The net energy (NE) value of a food or diet in the classical sense can be illustrated by the simple identity:

$$NE = \Delta RE/\Delta IE.$$

The ability of food energy to promote energy retention is measured by determining RE at two levels of energy intake. In this simplified expression, RE can be a positive or negative quantity. Since it is more convenient to have NE expressed as the concentration of energy (kcal/g, for example) the denominator of this expression is generally the change in quantity of food consumed rather than the heat of combustion of the food.

Net energy values determined by the "difference trial," as indicated by this classical expression, assume that the relationship between food intake and RE is rectilinear. Actually, the relationship between RE and food intake over the complete range of intake from zero to *ad libitum* is curvilinear (Lofgreen and Garrett, 1968). The convention adopted to accommodate this fact is an approximation with two straight lines (Figure 2). The point common to each line is where RE = 0. Thus energy intakes that result in negative RE represent one segment of the curve (zero to maintenance level of feeding), and energy intake that results in positive RE

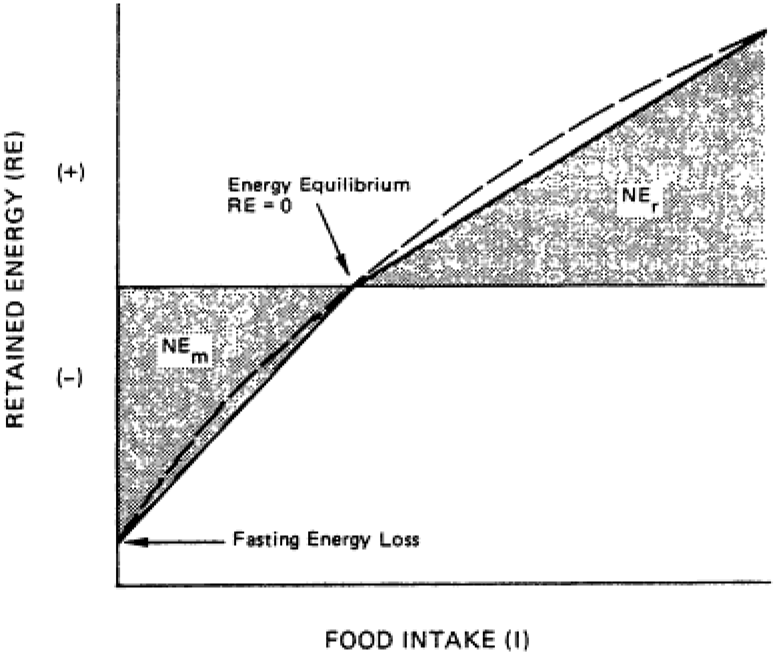


Figure 2 Representation of the relationship between RE and NE. The dashed line shows the curvilinearity between RE and food intake; the solid lines axe linear approximations.

(maintenance to *ad libitum* levels of feeding) represents the other segment of the curve.

To express the relationship between ME, RE, HE, and NE, it is necessary to consider the following expressions:

$$NE_{mr} = NE_m + NE_r,$$

where

$$NE_m = \frac{R_m E - R_e E}{I_m - 0},$$

and

$$NE_r = \frac{RE - R_m E}{I - I_m},$$

but R_m E = 0 by definition and $-R_e$ E = H_e E or fasting heat production. Therefore

$$NE_m = H_e E/I_m,$$

and

$$NE_r = \frac{RE}{I - I_m}.$$

These expressions are the result of the convention that describes the relationship between RE and IE (or RE and food intake, if preferred) as two straight lines intersecting at zero RE (see Figure 2).

Since NE_m is the difference in RE between levels of intake from nil to where RE becomes zero rather than negative, it represents the quantity of energy that the animal would have to use from tissue fat and protein to remain alive. In domestic animals this quantity is equivalent to the fasting metabolism (H_e E). In a similar manner, NE_r is the difference in RE from an intake above maintenance to some higher level (up to the appetite of the animal), and by this definition $R_gE=NE_r$.

The relationship ME = RE + HE can be written in terms of NE_m and NE_r:

$$ME = NE_r + NE_m + H_jE + H_iE.$$

In the application to practical feeding situations, H_jE, the heat associated with activities incident to obtaining food, may be included with H_eE. In this event, $NE_m = H_eE + H_jE$ and the expression is simply

$$ME = NE_r + NE_m + H_iE.$$

The term NE_r (RE in an animal above maintenance) as used in these expressions does not make a distinction between RE as a result of growth (as fat and protein deposition), milk production, fetal development, or egg production.

Thus NE_r could consist of one or several components. In a pregnant lactating dairy heifer, for example, NE_r might have three major components, the energy in the milk, the energy being stored in the products of conception, and the energy stored as a result of growth (protein and fat deposition in the heifer's tissues). In this example,

$$RE = LE + YE + TE,$$

or

$$NE_r = NE_l + NE_y + NE_g.$$

Since the end products of digestion (the constituents that make up the energy of ME) are used at different levels of efficiency for maintenance or conversion to the various productive functions, it is not possible to assign a single NE value to each feedstuff. For the net energy system to have practical application, each feed has to be assigned multiple NE values. Alternate procedures are to adjust the ME value of feeds according to the quantities of energy that are necessary for maintenance and the particular production functions or to scale the animal's energy requirements for the various productive functions to a single NE value. The species sections below will illustrate how some of this information has been adopted for use in practical feeding systems.

Efficiency of Metabolizable Energy Utilization

As was mentioned in the previous section, it is possible to adjust or convert ME values to NE values if the efficiency of ME use (k) for a particular function is known. For example, the k_m or efficiency of ME use for maintenance (NE_m) can be expressed:

$$k_m = H_e E/ME_m$$

thus

$$ME_m = H_e E/k_m .$$

In a similar manner, k_g represents the efficiency with which ME is used to promote weight gain (protein and fat deposition) in an animal. The expression to calculate k_g is

$$k_g = \frac{NE_g}{ME - ME_m} .$$

It is immediately apparent that k_m and k_g have a term in common. Thus

$$NE_g = k_g (ME - H_e E/k_m).$$

Since H_e E is the fasting heat production and is usually expressed as aW^n, the equation becomes

$$NE_g = k_g (ME - aW^n /k_m)$$

or

$$NE_g/W^n = k_g\,(ME/W^n) - ak_g/k_m .$$

This equation has the form of a straight line with slope k_g and an intercept C (which is ak_g/k_m). This is a convenient relationship for estimating k_g and k_m if "a" is known or estimated from fasting heat production (H_e E) provided NE_g, ME, and the size of the animal have been determined. The metabolizable energy for maintenance and k_m can also be estimated from this regression of NE_g/W^n against ME/W^n. If NE_g/W^n is set to zero, then ME becomes ME_m and

$$k_g ME_m = (ak_g/k_m)W^n = CW^n$$

or

$$ME_m = aW^n/k_m = CW^n/k_g.$$

It is important to recognize that the values obtained for k_m and k_g vary depending upon the source of the ME. In general, the efficiency of ME use for growth is greater as the concentration of ME (kcal/g) in the diet increases.

APPLICATION TO GROWING RUMINANTS

From a historical basis the measure of the energy value of feedstuffs for growing ruminants most used in the United States has been TDN. More recently, requirements have been stated in terms of TDN, DE, ME, and NE for sheep (NRC, 1975) and dairy cattle (NRC, 1978a) and TDN, ME, and NE for beef cattle (NRC, 1976). The requirements for growth of cattle expressed as TDN, DE, and ME have been calculated from net energy determinations. In Europe the starch equivalent and the Scandinavian feed unit have been the systems used most extensively. Most of Europe has now adopted a net energy system that uses experimentally derived relationships between ME and NE; i.e., ME is adjusted depending upon the computed efficiency of its utilization for maintenance (k_m) or growth (k_g). This system and the procedures currently in use to adapt it to practical use are found in various publications (Agricultural Research Council, 1965; Harkins *et al*., 1974; Ministry of Agriculture, Fisheries and Food, 1975; Van der Honing *et al*., 1977; Bickel and Landis, 1978; Institut National de la Recherche Agronomique, 1978). In East Germany a net energy system (NE_f) has been adopted. This system evaluates feeds on the basis of their ability to promote fattening and then expresses the requirements for maintenance and growth in terms of this unit (NE_f) (Nehring and Haenlein, 1973). In the U.S.S.R., preparations are being made to replace the oat unit system by a system based on ME (Van Es, 1976). Details regarding this system are not currently available.

It is evident that systems based on the net energy concept are becoming the method of choice for expressing the energy requirements of growing ruminants. The procedures used to apply the concepts to practical conditions have been more variable.

The committees of the NRC have adopted the system of Lofgreen and Garrett (1968) for use with growing ruminants. This system assigns to each feedstuff two net energy values. One value, net energy for maintenance (NE_m), is based on that quantity of feed necessary to prevent tissue loss from the animal's body (RE = 0 and $NE_m = k_m$ [ME] Mcal/kg DM). The second value, net energy for gain (NE_g), is the amount of energy stored in the animal's body as a result of a given amount of a feedstuff being consumed above that necessary for maintenance (RE is positive and $NE_g = k_g$ [ME] Mcal/kg DM). By using this procedure the animal's total energy requirement is factored into a maintenance requirement (requirement for NE_m) and a growth requirement (requirement for NE_g).

The net energy required for growth (equivalent to R_gE) can be factored into the major components of energy required for fat deposition and energy required for protein deposition; i.e., $R_g E = R_fE + R_p E$. Since estimates of the efficiency of ME use for R_gE indicate that k_f and k_p are not identical (Kielanowski, 1976; Pullar and Webster, 1977; Thorbek, 1977) and that $k_f > k_p$, it is apparent that k_g and therefore NE_g are not constant but vary depending upon the composition of the gain. The comparative slaughter procedure used by Lofgreen and Garrett (1968) assigns an average NE_g value to a feedstuff as determined under practical feeding conditions. These NE_g values are used in conjunction with concurrently determined relationships that translate RE into a weight unit (kilogram of gain). The relationship between RE and weight gain is necessarily variable depending upon species, breed, body size, rate of growth, and sex.

The convention using only NE_m and NE_g to state feed values and energy requirements for sheep does not give a separate allowance for wool growth. The energy retained in the fleece (VE) is thus added to the energy retained in the animal's body tissue. In this instance, $R_gE = R_fE + R_p E + R_v E$. The separate efficiency of metabolizable energy use for wool growth (k_v) has not been estimated. Rattray *et al.* (1973) reported that the relationship to convert RE to a weight basis is unchanged by including wool energy in RE provided the weight of the wool is included in the weight gain.

The gross efficiency of ME use for conceptus development (k_y) has been estimated to range between 10 and 16 percent for cattle and sheep (Garrett *et al.*, 1976). The procedure in use to account for the gestation requirement under the NE_m and NE_g convention (NRC, 1976) is to add an equivalent amount of energy to the pregnant animal's maintenance requirement. That is, the NE_m requirement is scaled upward depending upon the estimated energy retention in the conceptus.

The efficiency of conversion of ME to NE_m and NE_g determined by comparative slaughter techniques ranges from about 58 to 70 percent and 25 to 50 percent, respectively, as ME concentration in the dry matter of feeds increases from 2.1 to 3.2 kcal/g. In the system in use in Europe, k_m and kg have been estimated from experiments conducted in respiration calorimeters. In this instance, k_m has varied from 66 to 75 percent and k_g from 33 to 64 percent as ME concentration increases from 2.1 to 3.2 kcal/g.

The difference between the two techniques (comparative slaughter and respiration calorimetry) may be caused by systematic errors, probably in both techniques, that result in a slight overestimation of energy retention by respiration calorimetry and slight under-estimation of energy conversion to animal tissue in comparative slaughter trials. For example, hair and surface cell loss over the several months of a comparative slaughter trial would not be included in energy retained, but might be included in short-term balance studies conducted with a respiration calorimetry technique.

There are other differences between the European and the U.S. systems. Perhaps the most controversial is that the European system uses a level of feeding correction factor to account for a depression in the metabolizability of feeds or diets fed at levels above maintenance. This type of correction has not been applied to the data obtained in comparative slaughter trials. Some correction for level of feed is actually inherent in the comparative slaughter methods used because one level of feeding employed during the trials to estimate NE_g is *ad libitum* consumption.

The use of the net energy concept as the basis for estimating feed values and requirements for growing ruminants is likely to continue. The general relationships now in use will be improved and eventually become more specific with regard to applications under practical conditions. The refinements of any general system to the point where it can be translated to fit with precision into all, or at least most, practical feeding situations adds to its complexity. However, the availability of inexpensive computers and programmable calculators will make it possible to use increasingly sophisticated methods to determine comparative feed values, specific animal requirements, diet formulations, and the prediction of the response of an animal to a particular diet.

It is quite likely that feeds will eventually be evaluated on the basis of how they supply energy and nutrients for some specific animal production response in comparison to other feeds available at the same time. Feeds will be evaluated, diets formulated, and animal response predicted by relatively complex computer programs that will use a detailed chemical and physical description of each feed and a knowledge of the biochemical, physiological, and physical processes involved in animal metabolism. The information necessary for this application has not yet been accumulated.

APPLICATION TO LACTATING RUMINANTS

There has been a steady progression in refinement of the energy evaluation of feeds and in the understanding of energy exchanges for lactating ruminants. Requirements and feed values have been stated in all of the following energy terms: TDN, DE, ME, ENE (Morrison, 1956), NE_m, NE_g, and NE_l. While they have been criticized as measures of useful energy (Moore *et al*., 1953), TDN and DE values are still widely used, in part because a significant bank of data is available for those terms. As ME and NE data become available, they will replace the less precise TDN and DE values. Although ENE values are used and are readily available (Morrison, 1956), the specific origin of these values is unclear. Although it is routine to compute such values in feed analysis measurements, ENE is based on prediction from chemical composition rather than from precise energetic measurements.

The assignment of NE values to feeds depends on the physiological functions in progress. For example, dairy animals can have the functions of maintenance, growth, gestation, and lactation going on simultaneously, and the NE value of the feed may vary considerably. Although not fully understood, the reasons for variation in NE value include the composition of the product formed, the composition of the diet fed, and the energy cost of maintaining tissue in a static mass (Bull *et al*., 1976). If animals are lactating, however, the partial efficiencies of ME use for maintenance and fattening are similar to lactation (Moe and Flatt, 1969), whereas partial efficiencies differ markedly between maintenance and fattening in the nonlactating ruminant (Armstrong *et al*., 1964; Flatt *et al*., 1965; Lofgreen and Garrett, 1968).

A system for applying the NE concept to lactating dairy cattle has been described by Moe *et al*. (1972) and takes advantage of the similarity in partial efficiencies of ME use for maintenance and lactation in lactating animals. A single energy value (NE_l) is used to define all requirements for the lactating cow and to describe the energy value of feeds. In the development of the NE_l system, actual respiration calorimetry energy balance data were used, and various physiological functions were described in milk energy equivalents in order to arrive at a specific relationship between ME input and milk energy (NE_l) output. For example, an adjustment is made to account for cases where tissue energy balance (TE) is not zero (Moe *et al*., 1971). Additional adjustments included are for the energy cost of consuming nitrogen in excess of that required by the animal (Tyrrell *et al*., 1970) and for the energy cost of pregnancy (Moe and Tyrrell, 1972). The results of the adjustments produce a situation in which the total response of the animal to a change in energy intake is recovered as a change in milk energy output. The adjusted data were used to relate milk energy yield to the metabolizable energy intake. Two equations (Moe *et al*., 1972) are

$$\mathrm{LE}\ (\mathrm{kcal/kg}^{.75}) = 0.608\ \mathrm{ME}\ (\mathrm{kcal/kg}^{.75}) - 67.7,$$

and

$$\mathrm{ME}\ (\mathrm{kcal/kg}^{.75}) = 1.547\ \mathrm{LE}\ (\mathrm{kcal/kg}^{.75}) + 122.1.$$

The maintenance requirement for energy expressed as LE was determined from these equations by setting ME = 0. The two estimates of -67.7 and -78.9 average to -73.3, which is a value virtually identical to estimates of fasting metabolic rate. This also means that k_1 is virtually the same as k_m, so that net energy for maintenance and net energy for lactation can be defined as a single value in the lactating ruminant, or $NE_m = NE_l$. In practice, the NE_l required for maintenance is increased by 10 percent to account for environmental conditions different from those of a respiration chamber (NRC, 1978a). Having defined maintenance requirement in units of NE_l, the NE_l value of total mixed rations can be computed.

The following relationships have been developed to relate different measures of feed energy to NE_l (Mcal/kg DM):

$$NE_l = 0.677 \text{ DE (Mcal/kg DM)} - 0.36,$$

$$NE_l = 0.702 \text{ ME (Mcal/kg DM)} - 0.19,$$

$$NE_l = 0.0266 \text{ TDN (\% of DM)} - 0.12.$$

These relationships are all based on energy values actually measured rather than tabulated values. Thus the influence of level of intake on digestive efficiency is removed from these equations, but must be included when DE, ME, or TDN measured at maintenance is to be used to predict NE_l. In practice, a correction for level of intake has been used in the development of the NE_l value of feeds by assuming an average decline in digestibility of 4 percent per multiple of maintenance and an average intake of three times maintenance. The relationship between NE_l (Mcal/kg DM) and TDN thus becomes (NRC, 1978a)

$$NE_l = 0.0245 \text{ TDN (\% of DM)} - 0.12.$$

The use of ME to describe the energy requirement of lactating ruminants is common in some areas of Europe, particularly in the United Kingdom (Ministry of Agriculture, Fisheries and Food, 1975). The system is based on NE for the animal requirements, converted to ME by using the partial efficiency of use of ME for maintenance, lactation, and body weight change as follows:

$$ME_m = NE_m / k_m .$$

Here NE_m is assumed to be 94.6 kcal/$W^{.73}$ and k_m is assumed to be 0.72. Thus

$$ME_m = 131.4 \text{ kcal}/W^{.73} .$$

For lactation the NE requirement is predicted from the energy value of milk:

$$\text{LE (Mcal/kg)} = 0.009464\ \text{BF} + 0.004900\ \text{SNF} - 0.0564,$$

where LE is energy in 1 kg of milk, BF is grams of butterfat in 1 kg of milk, and SNF is grams of solids-not-fat in 1 kg of milk, respectively. Thus ME required for milk is

$$\text{ME}_1 = \text{LE}/\text{k}_1.$$

In Ministry of Agriculture, Fisheries and Food (1975), k_1 is assumed to be 0.62, and

$$\text{ME}_1 = 1.613\ \text{LE}.$$

The coefficient was increased to 1.694 to include a safety margin. Adjustments are made for the energy value of live weight change: 1 kg live weight loss adds 6.69 Mcal to ME available for maintenance and milk production; 1 kg live weight gain requires an additional 8.13 Mcal of ME from the diet.

It must be recognized that certain compromises are involved with each of the estimates needed in these systems. As more precise data become available on the efficiency of various digestive and metabolic functions in dairy cows and other lactating ruminants, adjustments will be made in the systems discussed here.

APPLICATION TO NONRUMINANT HERBIVORES, ESPECIALLY HORSES AND RABBITS

Energy metabolism studies with horses are limited in number, but considerable data on digestibility are available. For this reason the system used to describe energy requirements of the horse is based on DE (NRC, 1978b). Because of a lack of enough data to do otherwise and because of the work component of total energy balance, body weight and its maintenance play a significant role in the evaluation of feeds and energy requirements. When TDN data are available, they are converted to DE by

$$\text{DE (Mcal)} = 4.4\ \text{TDN (kg)}.$$

Maintenance DE, defined as zero weight change plus normal activity in the nonworking horse, is described by the equation:

$$\text{DE}_m\ \text{(kcal/day)} = 155\ W^{.75},$$

where W is the body weight in kilograms.

With regard to growth the DE need above maintenance is estimated from

$$Y = 3.8 + 12.3\ X - 6.6\ X^2,$$

where Y is kilocalories of DE per gram of gain and X is the fraction of adult weight.

When applied to the nursing foal, the utilization of DE is assumed to be 10 percent greater than that in the mature horse. The k_f for mature horses is approximately 0.84 (Kane *et al.*, 1978).

The requirement of DE for pregnancy is considered only during the last 90 days of gestation. Early estimates (NRC, 1973) suggest that the DE need for pregnancy is 6 percent greater than for maintenance. Recent estimates (Ott, 1971; Brewer, 1975) suggest that 12 percent of maintenance is needed. A general formula would be

$$\text{DE}_y = 0.12\ \text{DE}_m.$$

Assumptions involved in the above are as follows:

1. The products of conception contain 1.040 Mcal/kg.
2. The products of conception constitute 10 percent of body weight for animals of 450 kg or more and 12 percent for weight of less than 450 kg.
3. The detectable deposition occurs during the last 90 days of gestation.

4. The efficiency of use of DE for fetal growth and associated tissues is 30 percent.

Requirements of DE for lactation are based on the following:

1. The LE value of mare's milk is 475 kcal/kg.
2. The partial efficiency of use of DE for LE is 0.60.
3. Milk production (percent of body weight) for horses is 3 percent during weeks 1 through 12 and 2 percent during weeks 13 through 24, whereas for ponies it is 4 percent during weeks 1 through 12 and 3 percent during weeks 13 through 24 of lactation.

Thus the DE_1 is

$$\mathrm{DE}_l\ (\mathrm{kcal/day}) = (475/0.60)(W)(F),$$

where W is the body weight in kilograms and F is the production rate (fraction of W).

Although the work output of horses is of major importance, quantitative relationships between level of work and DE requirement for work (DE_j) have not been made. A large number of factors (intensity and duration of work, environmental conditions, and degree of fatigue) influence the energy requirement associated with work. The NRC (1978b) has reported some guidelines for DE_j, added to DE_m, based on body weight and work intensity:

Activity	DE_j/hr/kg
Walking	0.5
Slow trotting, some cantering	5.0
Strenuous, full speed	39.0

Recent data (Willard *et al.*, 1978) suggest that DE_j increases for a given distance traveled, as the speed of travel increases. Thus the influence of work on total daily metabolism is in need of study.

Little information is available on the utilization of energy by the rabbit. The recent NRC publications (NRC, 1966, 1977) have used

TDN and data from other species. Conversion from TDN to DE is assumed to be 4.4 kcal of DE per gram of TDN. When TDN data are not available, the DE value of forage (kcal/kg DM) is estimated from crude fiber content by using the following equations:

$$\text{legumes (DE)} = 4340 - 68\ \text{(percent crude fiber)},$$

$$\text{grasses (DE)} = 4340 - 79\ \text{(percent crude fiber)}.$$

The fasting metabolic rate is computed from the formula of Kleiber (1961): H_eE (kcal/day) = 70 $W.^{75}$, where W is the body weight in kilograms. The results of Hellberg (1949) suggest that a coefficient of 77 may be more appropriate.

The influence of level of intake on digestion has been investigated (Hellberg, 1949), and DE was found to decline with increasing intake at a rate similar to that for ruminants. The net utilization of ME for gain in rabbits is about 70 percent (Hellberg, 1949), and the DE allowance for gain is 9.5 kcal/g (NRC, 1977). The caloric density (DE, kcal/kg) of the diet should be 2100 for adults compared to 2500 to 2900 for young rabbits.

APPLICATION TO SWINE

Total digestible nutrients (TDN), starch equivalents, Scandinavian feed units, oat units, DE, ME, ME_n, and NE are energy units that have been used in swine nutrition. Digestible energy defined as food intake of energy minus the fecal energy (DE = IE-FE) has been used by the Agricultural Research Council (1967) and NRC (1979) to define energy requirements and energy contents of diets for swine. The loss of energy as combustible gas from the digestive tract is usually small (less than 1 percent of IE) and is normally ignored. If diets high in structural carbohydrate and/or protein that escapes digestion in the small intestine are fed to pigs, a fermentation can develop in the digestive tract. Many of the tabular values (NRC, 1971 a) for DE of feed ingredients for pigs have been calculated from tabular TDN values by using 1 kg TDN = 4400 kcal DE.

Metabolizable energy (ME) defined as DE-UE has been used by NRC (1979) to define energy requirements and energy value of diets for swine. In the formulation of diets in the United States, this measure of ME is generally used. Many of the ME values reported by NRC (1971 b) have been calculated by converting TDN to DE as noted above and then calculating ME by using the following relationship:

$$\mathrm{ME} = \mathrm{DE}\left[96 - \left(\frac{0.202 \times \text{percent of crude protein}}{100}\right)\right]$$

Experimentally derived values are primarily from the work of Diggs *et al.* (1965).

Metabolizable energy corrected to nitrogen equilibrium (M_n E) has been reported, but is not commonly used in diet formulation. While the correction to nitrogen equilibrium may be valid for mature animals, nitrogen retention is normal in growing animals, and the correction probably is not necessary. The correction is made by the following formula:

$$M_n E = IE - FE - UE + kRN.$$

The constant k has been estimated from the urinary energy per gram of urinary nitrogen. A value of 7.45 kcal/g of nitrogen (Rubner, 1885) determined with dogs has been used most commonly. A number of other values have been reported from work done with swine: 6.77 kcal/g (Diggs *et al.*, 1959), 9.17 kcal/g (Morgan *et al.*, 1975), 7.83 kcal/g (Wu and Ewan, 1979), and 7.0 kcal/g (NRC, 1979).

Net energy defined as ME - H_iE has been used to describe energy requirements and energy values of feeds. In contrast to cattle and sheep, the pig can utilize ME as efficiently for growth as for maintenance. Therefore the net energy requirements and net energy values of feeds can be expressed as a single value similar to lactating ruminants (Nehring and Haenlein, 1973; Just-Nielsen, 1975; Ewan, 1976). Nehring and Haenlein (1973) reported the evolution of the East German net energy system reported in detail by Schiemann *et al.* (1971). In this system the net energy values of feeds are expressed in terms of the ability to promote fat deposition (NE_f) in mature animals. Both the requirement for maintenance and that for growth are expressed in terms of NE_f.

Studies of the utilization of ME for growth by comparative slaughter techniques have been reported by Just-Nielsen (1975) and Ewan (1976). Just-Nielsen (1975) concluded that a system based on energy gain of growing animals was comparable with the German system based on NE_f.

Nehring and Haenlein (1973) concluded that the net energy system is necessary because performance cannot be predicted from the metabolizable energy value of the feed. The efficiency of utilization of ME for energy gain (NE_g) in growing pigs has been reported to vary from 27 percent for wheat middlings to 75 percent for soybean oil (Ewan, 1976). Kromann *et al.* (1976) by feeding wheat and barley at different ratios also observed different partial efficiencies of utilization of ME for gain for these two cereal grains.

At present, experimentally determined net energy values of feed ingredients and the requirements for maintenance and growth expressed in terms of net energy are limited. Therefore energy requirements of swine are expressed in terms of DE or ME, but the development of a net energy system may provide a more accurate method of ration formulation for swine.

APPLICATION TO POULTRY

For many years the poultry industry relied on productive energy values to define energy requirements and to describe the available energy in feedstuffs. Productive energy is a form of net energy and is determined by measuring the energy stored as fat and protein in growing or fattening birds (Fraps, 1946). This assay is relatively difficult because it involves measuring weight change, feed intake, and change in carcass composition. It also involves several assumptions of questionable validity. Productive energy values are not always additive, and there are data showing them to be unreliable (Davidson *et al.*, 1957; Hill and Anderson, 1958).

Attempts have been made to measure digestible energy values with birds, but these are complicated by the excretion of feces and urine via a common cloaca. Surgical techniques have been used to permit the separation of feces and urine, but there can be no proof that a modified bird behaves in the same manner as a normal bird. Chemical procedures have been used to measure the amount of urine in excreta, but the techniques are not wholly satisfactory.

Metabolizable energy values have been measured with poultry for many years, but it was not until about 1960 that they became widely accepted. In the measurement of metabolizable energy the gaseous products of digestion are ignored, but correction is usually made for nitrogen gained or lost during the assay.

$$M_nE = IE - (FE + UE - kRN)$$

Two constants have been widely used: 8.22 kcal/g of nitrogen, which was derived from the gross energy value of uric acid, and 8.73 kcal/g, which was calculated from the gross energy values of the various nitrogenous compounds in chicken urine (Titus *et al*., 1959).

Recently, it was shown that ME values vary with feed intake because the metabolic fecal (F_m E) and endogenous urinary (U_eE) energy losses are charged against the feed (Sibbald, 1975). This is of importance when feedstuffs of low palatability are being assayed because it is normal to maximize the level of the test material in the assay diet. A bioassay for true metabolizable energy is now available (Sibbald, 1976, 1980):

$$TME = IE - (FE - F_mE) - (UE - U_eE)$$

or

$$TME = IE - (F_iE + U_iE).$$

The assay is faster, less complex, and more accurate than those for M_n E. More important, the data are less affected by variation in feed intake and species of bird used, while the TME values are additive. When the assay uses adult male birds, the deviation from nitrogen balance is small and can be neglected.

APPLICATION TO AQUATIC ANIMALS

Much interest has recently been shown in the nutritional energetics of aquatic animals. Most of the work has been confined to trout, salmon, catfish, carp, and a few other finfish species. Development of large-scale commercial production of fish has emphasized the lack of adequate information regarding the ability of the different species of fish to utilize energy from the diet.

Several unique problems are associated with the study of energy utilization in fish. Usually, the animals are small, less than 500 g each. This requires microtechniques for analysis of fecal and urine samples or the use of groups of animals. The waste products are difficult to separate from the aquatic environment, and leaching and dilution must be considered. Care must be taken to avoid mixing uneaten food with waste products. Most aquatic organisms excrete waste nitrogen from protein catabolism as ammonia through the gills. The gill excretions (ZE) must be collected to account for all energy and nitrogen loss. Body temperature and its relationship to metabolic rate must also be considered (Smith *et al.*, 1978a). Body temperatures of most fish are very near the temperature of the water and can vary over a wide range with no ill effects. Within species, adaptations can be made to compensate for up to 20°C change; between species, adaptation is even greater. Some species live and grow in arctic or antarctic seas at temperatures below the freezing point of fresh water, and others inhabit hot springs at temperatures above 37°C. It must be remembered that there is as much difference between species in fish as in mammals or birds—there are herbivorous, carnivorous, and omnivorous species of fish.

Several methods have been developed to determine DE and ME values of fish foods and dietary ingredients. A metabolism chamber has been developed in which individual fish can be held for total collection of feces, urine, and gill excretions (Smith, 1971). Other have used an indigestible marker and partial fecal collection. Cho *et al.* (1976) use a column from which all settleable material can be removed. Windell *et al.* (1978) use a suction technique to remove the feces from the lower intestine. Others have used various fecal collection methods such as removing fecal matter from the aquarium with a fine mesh net, filtration of aquarium water, and centrifugation. Each of these methods has its advantages and disadvantages. The fish in the metabolism chambers are undoubtedly under some stress because they must be closely confined and tube fed. The metabolism chamber permits collection of urine and gill excretions, which makes possible the calculation of ME. Methods that depend on separation of the feces from the aquarium water presume that fecal loss by leaching is negligible. If ME is calculated, it must be assumed that all insoluble material is fecal waste and that the soluble material is of urinary or gill origin. Smith *et al.* (1980) have shown that considerable loss occurs in the first hour that the fecal matter is in contact with the water. There is handling loss when fecal matter is netted or siphoned from an aquarium. The suction method assumes that digestion and absorption is complete when the material is removed from the lower intestine. Use of an indigestible marker raises the question "was the amount of marker in the analyzed sample representative of the amount excreted?" Methods using an indigestible marker permit studies with groups of small fish that need not be force-fed.

Most ME values reported for fish have not been corrected for nitrogen balance. However, most trials have been done near nitrogen equilibrium. There is no evidence that the constant 7.45 kcal/g of nitrogen, obtained with dogs, is applicable to fish. It is tenuous to apply to fish constants that were obtained with mammals or birds. The heat equivalent of oxygen is different for animals excreting ammonia than for those excreting urea or uric acid. The study of energy metabolism in fish is much the same as with other animals when the unique problems of fish are considered (Smith and Rumsey, 1976). The gaseous products of digestion can be ignored, but the energy loss in the gill excretions (ZE) must be considered. The formula for metabolizable energy then becomes

$$\mathrm{ME} = \mathrm{IE} - (\mathrm{FE} + \mathrm{UE} + \mathrm{ZE}).$$

Care must be taken in estimating energy values from proximate analysis. Carnivorous fish utilize raw starch poorly, and fiber has very little value. Cooking increases the digestibility of starch. Recent work indicates that protein has a higher net energy value for fish than it does for mammals and birds because less energy is expended by fish to excrete the waste nitrogen (Smith *et al*., 1978b).

There are not enough published data to determine if digestibility values alone are sufficient to evaluate feed materials for fish or if the additional work required to determine ME is justified.

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Appendix

UNITS OF MEASUREMENT

J	Joule or work expressed in electrical units of measurement. One joule equals 10^7 ergs.
kJ	Kilojoule, or joule × 10^3.
MJ	Megajoule, or joule × 10^6.
cal	Calorie or work expressed in temperature (heat) units of measurement. One calorie equals 4.184 J in nutritional terms.
kcal	Kilocalorie, or calorie × 10^3.
Mcal	Megacalorie, or calorie × 10^6, also called "Therm."
E	Heat of combustion or gross energy content (J/g) of matter.
I	Amount of food consumed in grams (or appropriate unit of weight).

COMBUSTIBLE ENERGY FRACTIONS

IE	*Intake of Energy*, or total gross energy consumed by an animal.
FE	*Fecal Energy*, or total gross energy contained in feces produced by an animal.

UE	*Urine Energy*, or total gross energy contained in urine produced by an animal.
GE	*Gaseous Energy*, or total gross energy contained in combustible gases produced by an animal, mainly methane produced by ruminants.
ZE	*Gill Excretion Energy*, or the total gross energy contained in combustible waste products excreted via the gill of fish.
SE	*Surface Energy*, or the total gross energy contained in waste products lost from the exterior surface of the animal, such as hair, scurf, oil secretions, and similar non-useful energy losses.
RE	*Recovered Energy*, or total gross energy recovered as some useful product, such as body tissue, milk, egg, or wool.
TE	*Tissue Energy*, or the total gain (or loss) of gross energy contained in body tissue of an animal.
LE	*Lactation Energy*, or the total gross energy contained in the milk produced by a lactating animal.
OE	*Ovum or Egg Energy*, or the total gross energy contained in the egg produced by a laying hen.
YE	*Conceptus Energy*, the energy contained in conceptus, or the total gross energy contained in the embryo and tissues of the placenta.
VE	*Wool Energy*, or the total gross energy contained in the useful product harvested from the "surface" of an animal, such as wool, hair, or feathers.
DE	*Digestible Energy*, or apparently digested energy, is the total gross energy apparently absorbed from the digestive tract. DE = IE - FE.
ME	*Metabolizable Energy*, or apparently metabolized energy, is the total gross energy available for metabolism by an animal. ME = DE - GE - UE.
F_mE	*Metabolic Fecal Energy*, or energy contained in feces of nonfood origin.
U_eE	*Endogenous Urine Energy*, or energy contained in urine of nonfood origin.

TDE	*True Digestible Energy*, or energy truly absorbed from the digestive tract. $TDE = DE + F_m E - GE - H_f E$.
TME	*True Metabolizable Energy*, or energy truly available for metabolism by the animal. $TME = TDE - UE + U_e E$.
$M_n E$	*Nitrogen-Corrected Metabolizable Energy* is metabolizable energy adjusted to zero retained nitrogen.
$TM_n E$	*Nitrogen-Corrected True Metabolizable Energy* is TME adjusted to zero retained nitrogen.

SOURCES OF HEAT PRODUCTION

HE	*Heat Production*, or the total energy loss from an animal in any form other than as combustible matter.
$H_e E$	*Basal Metabolic Rate*, or heat produced by a resting, conscious animal in a postabsorptive state; often called fasting metabolic rate, basal metabolic rate (BMR), or fasting metabolism.
$H_j E$	*Heat of Voluntary Activity*, or heat produced as a result of voluntary movement of an animal such as standing up or lying down, walking, eating, and similar activity.
$H_c E$	*Heat of Thermal Regulation*, or heat produced to maintain body temperature as a result of environmental temperatures outside the zone of thermal neutrality.
$H_r E$	*Heat of Product Formation*, or heat resulting from the biosynthesis of useful products, such as body tissue, milk, egg, or wool.
$H_w E$	*Heat of Waste Formation and Excretion*, or heat resulting from the formation and excretion of metabolic waste.
$H_d E$	*Heat of Digestion*, or heat produced within the digestive tract as a result of digestive processes or associated with absorption of end products of digestion through the wall of the gut. Also included would be heat produced as a result of muscular activity required to move digesta through the digestive tract.

H_fE	*Heat of Fermentation*, or heat produced by the fermentation of food in the forestomach of ruminants; normally would be included as a component of H_d E.
H_jE	*Heat Increment*, or heat produced as a result of the ingestion of food. $H_iE = H_dE + H_fE + H_wE + H_rE$.

FEED EVALUATION TERMINOLOGY

TDN	*Total Digestible Nutrients*, computed as the apparent digestible intake of crude protein and carbohydrate plus 2.25 times digestible fat.
NE	*Net Energy*, defined in its broadest sense as $\Delta RE/\Delta I$, or the net increase in useful product expressed per unit increase in food consumed.
NE_m	*Net Energy for Maintenance*, or $\Delta RE/\Delta I$ measured between I = 0 and I at RE = 0.
NE_g	*Net Energy for Gain*, or $\Delta RE/\Delta I$ measured using a growing animal consuming I in an amount that always results in RE. > 0.
NE_l	*Net Energy for Lactation*, or $\Delta LE/\Delta I$ measured under conditions where TE, YE, and other forms of RE remain constant.
PFV	*Physiological Fuel Values*, estimates of calorie content of food computed from the chemical composition in terms of protein, carbohydrate, and fat.
k_g	*Partial Efficiency of Metabolizable Energy Use for Gain*, or $NE_g/(ME - ME_m)$.
k_m	*Partial Efficiency of Metabolizable Energy Use for Maintenance*, or $H_e E/ME_m$.
ENE	*Estimated Net Energy*, or a "corn equivalent" measure of energy value proposed by Morrison (1956).