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IN GROWING YOUNG BULLS AND
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FLORAH NGWERUME

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**ESTIMATION OF RESIDUAL ENERGY INTAKE IN GROWING YOUNG BULLS AND
LACTATING COWS USING ANIMAL MODELS**

BY

FLORAH NGWERUME

A THESIS

**Submitted to
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ABSTRACT

ESTIMATION OF RESIDUAL ENERGY INTAKE IN GROWING YOUNG BULLS AND LACTATING COWS USING ANIMAL MODELS

BY

FLORAH NGWERUME

Residual energy intake (REI) is defined as total net energy intake minus the predicted total energy requirements in a production period. The idea of REI as a measure of energetic efficiency is that the more the amount of energy that can be accounted for, or the smaller the REI, the more efficient is the animal in utilizing feed energy.

Using animal models, REI was estimated for growing young bulls and lactating cows separately. In both instances, average daily NEI in a production period was used as a depended variable to fit an animal model that contained covariates of production, maintenance and weight change. REI was computed as sum of animal and residual effects. Animal and residual variance components were estimated by the EM-REML procedure.

For both growing bulls and lactating cows, REI had a small heritability value. The proportion of phenotypic variation in NEI due to REI was relatively small for the young bulls but high for lactating cows.

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1. INTRODUCTION

Cattle produce high quality protein as milk and meat. They can utilize non-protein nitrogen and many materials not digestible by man or simple stomached animals. However improving efficiency of converting feed to milk or meat cannot be overemphasized. This concept of feed efficiency should be an important goal for the cattle industry.

The efficiency with which a growing beef animal converts feed it eats into meat or the efficiency with which a dairy cow convert feed into milk for consumption by man is determined overwhelmingly by the efficiency with which it uses the major nutrient which is energy. A complete description of energy efficiency requires simultaneous consideration of ingested feedstuffs, conversion of feed into energy in the form of Adenosine Tryphosphate (ATP), partitioning of energy into various forms of production, conversion of energy to products and output of measurable products. Traditional measures of efficiency such as feed conversion ratio are closely related to production. However several workers have discussed many aspects of measuring feed efficiency and concluded that efficiencies of energy utilization for meat or milk production have not been influenced by selection for milk production or growth rate. Since supply of feed energy is a major cost in any cattle production system, alternative measures of feed energy efficiency that account for nutrient absorption, rate of basal metabolism and the energy utilization for the processes of growth or

milk production should be explored.

Among many alternative measures of energetic efficiency is the concept of residual energy efficiency or residual feed intake. This concept is best explained by an understanding of utilization of metabolizable energy. The total intake of metabolizable energy can be partitioned into productive (growth and milk production), and non-productive (maintenance and efficiency of the digestive tract) use of energy. These are collectively known as partial energy requirements. The remaining energy after accounting for all the identifiable partial energy requirements is called residual energy efficiency. A measure of residual energy intake for individual animals would thus reveal the differences between animals in utilizing metabolizable energy for production and maintenance and a lower residual energy intake would imply greater energetic efficiency.

2. OBJECTIVES

2.1 Growing Young Bulls

Using data from growing young bulls the objectives of the study were to 1) estimate the partial net energy requirements for growth in terms of daily gain and for maintenance as a function of metabolic body weight; 2) estimate residual energy intake for each animal and; 3) estimate genetic parameters for residual energy intake.

2.2 Lactating Cows

Using data from lactating cows, the objectives of the study were, to 1) estimate the partial net energy requirements for production of solids corrected milk, maintenance in terms of metabolic body weight, and for weight change in a lactation; 2) estimate residual energy intake for each animal and; 3) estimate the genetic parameters for residual energy intake.

3. REVIEW OF LITERATURE

3.1 Introduction

Supply of feed energy constitutes the largest item of expense in beef and milk production enterprises. It is therefore surprising that so little attention has been paid to feed costs in cattle breeding. Selection in dairy cattle has been mainly confined to milk production traits and genetic increases in these traits have resulted. Similarly in beef cattle when selecting animals for meat production it is important to consider those that grow at the shortest possible time and at least costs (Webster, 1977). Therefore, selection in beef breeds has been confined to high growth rates. As such the question is, is it worthwhile to include nutrient intake and utilization in the breeding goal or more specifically what are the traits, their relative importance and genetic parameters. The lack of information about the genetic aspects of nutrient intake and utilization is caused by the technical impossibility (labor and equipment) of measuring feed intake on individual animal basis under normal conditions.

Brelín and Branning (1986), Buttazzoni and Mao (1988) and Walter and Mao (1989) postulated that one way of reducing feed costs in the long term is to breed for better efficiency. However, for information on whether feed control is an urgent step in the practical work with cattle we need to know about the genetic variation in feed efficiency and its relationship with other economic traits such as, milk production, growth rate, carcass traits and metabolic efficiency.

An overview of efficiency measures, and the biological components of feed efficiency namely feed intake, digestion and absorption and partitioning of energy to useful product will be reviewed.

3.2 Overview of Efficiency Measures

3.2.1 Dairy Cattle

For lactating dairy cows gross feed efficiency is usually defined as the ratio of milk output over feed input or its inverse in biological or economic terms (Bauman et al., 1984). Knowledge of the biological component of efficiency is necessary before considering the economic ones. Feed efficiency in dairy cattle is influenced by diet and other environmental factors, genetic ability and physiological state of the cow to utilize nutrients for milk. This total biological complex as described by Korver (1988) is shown in Figure 1.

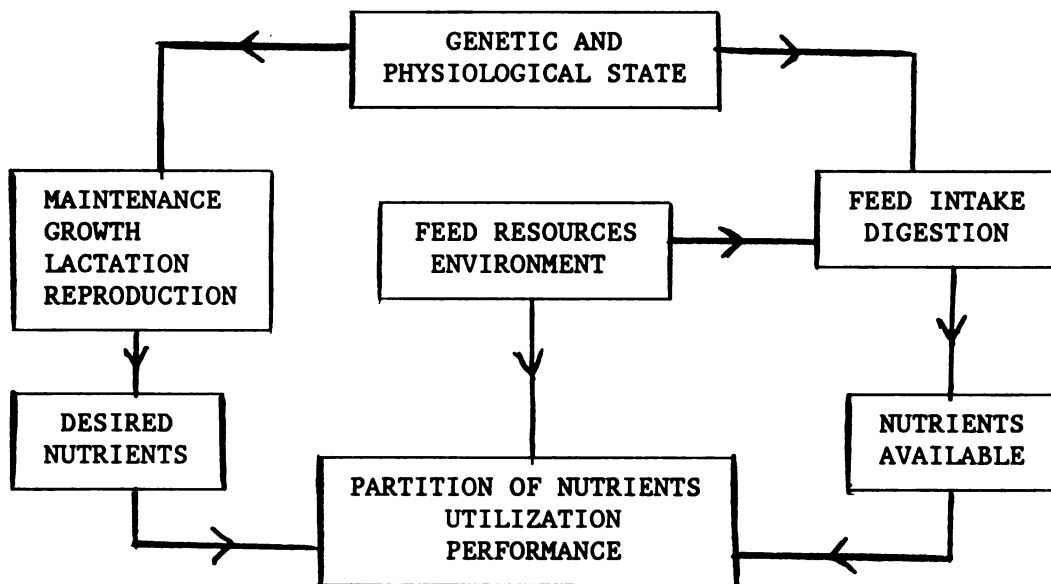


Figure 1. Utilization of nutrients and performance of dairy cattle in relation to genetic state and constraints. (Korver, 1988)

Heritability estimates for gross feed efficiencies are shown in Table 1. The data indicate a heritability between 0.4 and 0.6. The measurements of output and input traits differ between studies but all were an attempt to measure a ratio for energy input to energy output. The literature therefore indicates a clear genetic component for gross efficiency.

TABLE 1. Heritabilities of feed efficiency of milk yield.

Trait	Heritability	SE	Source
GROSS ENERGY EFFICIENCY			
FCM/FU	0.48	0.07	Mason et al. (1957)
Intake (TDN)/FCM	0.63	0.09	Hickman & Bowden (1967)
FCM/DE	0.47	0.23	Hooven et al. (1972)
Milk/DE	0.47	0.23	Lamb et al. (1977)
NET ENERGY EFFICIENCY			
SCM/NE _L	0.32	0.37	Buttazzoni & Mao (1988):STA
SCM/NE _L	0.49	0.36	Buttazzoni & Mao (1988):MTA

FU = Feed Units, FCM = Fat Corrected Milk, ENE = Estimated Net Energy, DE = Digestible Energy, SCM = Solids Corrected Milk, NE_L = Net Energy for Lactation, STA = Single trait analysis, MTA = Multiple trait analysis.

The breeding goal in dairy cows is centered on productive efficiency and the question arises: Is it worthwhile to measure this trait on an individual basis and to incorporate it in a breeding program in addition to milk yield? Freeman (1967) pointed that direct measurements of efficiency under commercial conditions in large numbers of herds does not seem economically feasible. His conclusion was selection for higher milk yield automatically improves gross feed

efficiency and this indirect selection accounts for 70 to 95% of direct selection when selection intensities are equal for the two traits.

Blake and Custodio (1984), extensively reviewed the more recent literature about the correlation between milk yield and feed efficiency and showed a range for the genetic correlation between 0.88 and 0.95. while the phenotypic correlation ranged from 0.60 to 0.95.

Experimental procedures may have inflated the values of these correlations. However, feed efficiency computed as a simple ratio between input and output has been shown to have its limitations.

All of the genotypic and most of the phenotypic correlation were calculated by feeding concentrates or grain according to milk yield, thus forcing a high correlation with efficiency (Blake and Custodio, 1984, Korver, 1988). Also in dairy cattle feed efficiency is normally defined as energy in milk divided by energy intake. However, Blake and Custodio (1984) pointed out that milk production is dependent on two inputs namely feed intake which is a function of appetite and body tissue losses/gains and indirectly related to body size as shown in Figure 2.

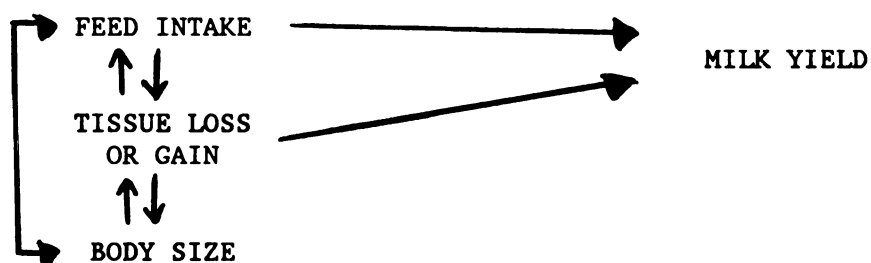


Figure 2. Path diagram of the phenotypic inputs (appetite and body tissue losses to milk yield and the indirect (correlated) relationships between these inputs and with body size. (Blake & Custodio, 1984).

From the above relationship, Blake and Custodio (1984) pointed out that the amount of milk production is the sum of feed consumption times the digestibility coefficient plus the tissue available for catabolism times rate of catabolism. These workers went on to define efficiency as thus the rate of converting dietary nutrients to milk after adjusting for nutrients supplied by catabolism (e.g. negative energy balance or nutrients to replenish tissue reserves). It is apparent from the discussion by Blake and Custodio (1984) that gross feed efficiency is an imprecise measure of production efficiencies since it does not account for the rates of catabolism or anabolism of tissue or protein energy. As such, Blake and Custodio (1984), illustrated diagrammatically (Figure 3) the possible relationship of the components of milk feed efficiency that should be considered when measuring this trait.

3.2.2 *Beef Cattle*

Differences in converting feed into body tissue are important in determining income from beef cattle operations. However, measuring feed consumption is costly because of increased labor requirements (Koch et al., 1963). In beef cattle, gross feed efficiency is defined as a ratio between feed intake and weight gain in a given interval of growth (Brelín and Martinsson, 1986). Feed efficiency calculated this way has been found to have a high genetic correlation with growth ranging from -0.60 to -0.95 and heritability values ranging from 0.3 to 0.6 (Brelín and Brannang, 1982; Brelín and Martinsson, 1986). However, as in dairy cattle, feed efficiency calculated this way is a complex measurement including a number of interacting factors.

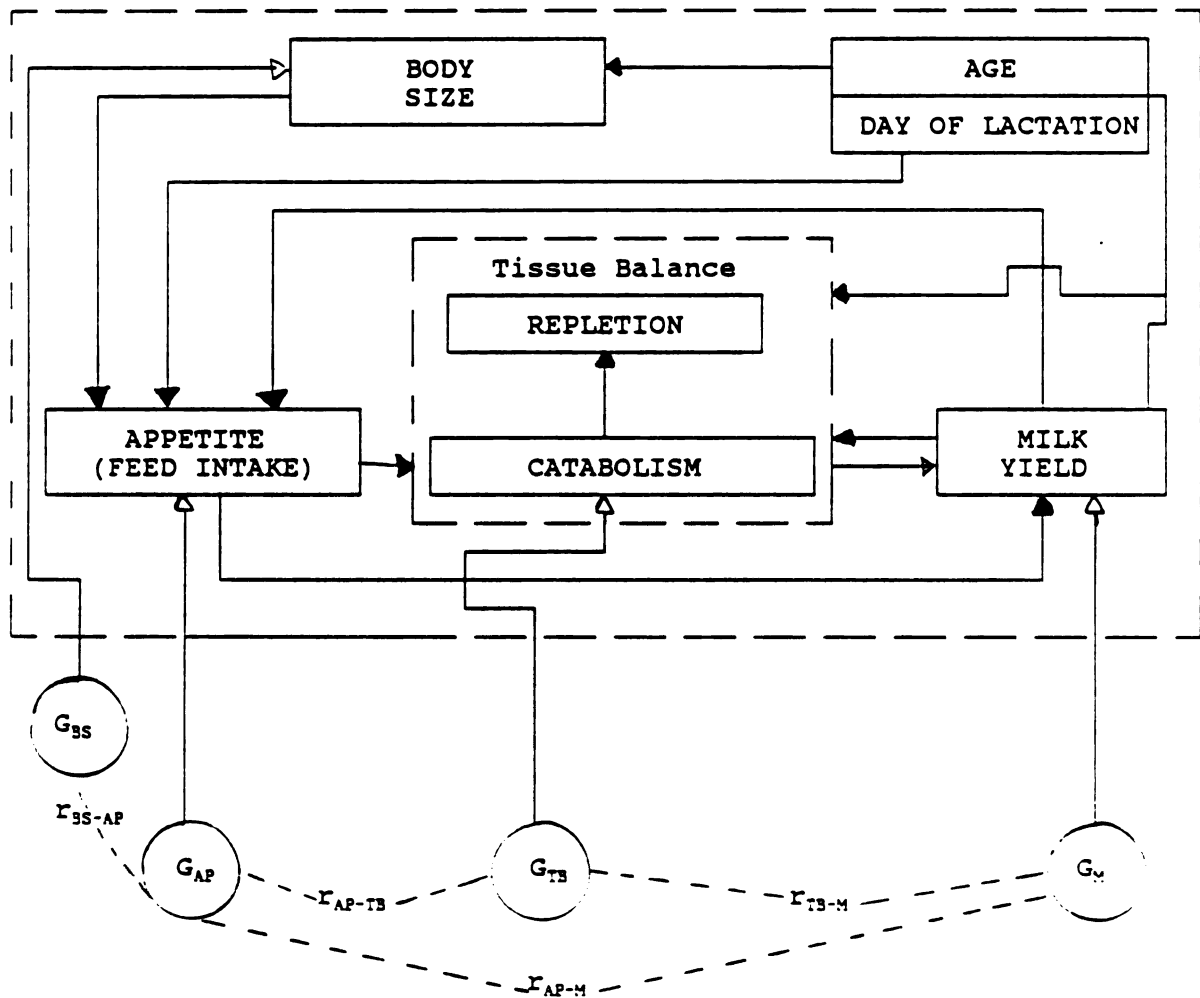


Figure 3. Milk production system of the dairy cow. Elements within the broken line box represent phenotypic and environmental relationships (closed arrows) and associations among phenotypes (G , open arrows) lie outside. BS = body size, AP = appetite, TB = tissue balance, M = milk yield. (Blake and Custodio, 1984).

Meyer and Garret (1967) pointed out that gross feed efficiency assumes that all feed consumed is utilized for body gain and ignores maintenance requirements and other uses of energy. It also assumes that the origin passes through zero when gain is graphically plotted against feed consumption. Weil (1962) stated that to use a ratio for expressing information about two quantities, these three conditions must be met: (1) the two items considered should increase or decrease linearly, (2) the regression for the two variables should intercept at zero and (3) the variance of the variables should increase with increasing magnitude of the variables. Koch et al (1963) discussed the problems of gain to feed ratios for measuring the efficiency of feed use by beef cattle where the primary interest was in animal breeding. They reported that variation in the composition of gains (fat, lean or bone) and in the maintenance requirements prevents gross feed efficiency from being a precise measure of energy conversion rate. Karlsson (1979) also pointed that due to the strong genetic correlation between growth rate and mature size, fast growing animals will on average be less mature and therefore leaner at a given liveweight thus giving rise to better feed efficiency. The composition of growth regarding fat and other tissues also affects feed efficiency, as the feed energy required for a unit weight gain of feed is considerably larger than for other tissues (Orskov and McDonald, 1970; Pullar and Webster, 1977; Geay, 1984 and Brelín and Martinsson, 1986).

It is therefore apparent from the reports of several workers above that gross feed efficiency is an imprecise measure of feed efficiency both in dairy and beef cattle. As such more accurate alternative

measures of efficiency should be defined. Buttazzoni and Mao (1988) suggested use of net energy efficiency for dairy cows. This was defined as the ratio of energy contained in milk over the portion of energy intake used to produce it above maintenance requirements. They pointed that net efficiency is a better biological indicator of a cow's productivity than gross efficiency because it measures the efficiency of energy required for maintenance and for changes in body reserve status. Buttazzoni and Mao (1988) estimated heritability values of 0.32 and 0.49 under single and multiple trait analysis respectively for net energy efficiency for milk yield (NE_L). The genetic correlation between milk yield and NE_L was 0.56. Koch et al (1963) suggested that the most useful criterion for evaluating efficiency of feed use in beef animals may be the amount of edible product produced for a given energy rather than the fraction of energy in the feed which was converted to animal tissue.

Residual energy intake (REI) has also been suggested as an appropriate measure of feed efficiency (Koch et al 1963, Brelvi and Brannang, 1982; Luiting, 1987; Korver, 1988 and Jensen, 1989). REI is defined as actual energy intake minus predicted energy requirements in a production period and is thus independent of production. As such a lower REI would indicate a better efficiency since most of the energy would be partitioned into desired uses of energy. Korver (1988) pointed that REI reflects differences in animals in utilizing net energy for maintenance and production. REI has been reported moderately heritable. Koch et al (1963) found a heritability value of .28 in young bulls and Korver (1987) estimated a value of .25 in heifers from

AI bulls. In poultry values ranged from .25 to .40 (Luiting, 1987).

In order to improve productive efficiency genetically, it is therefore of paramount importance to clearly specify the concept of feed efficiency, partly to obtain a biologically more uniform measure and partly because growth rate and milk production are already taken into consideration in other ways in the breeding process. The biological components of efficiency include feed intake, digestion and absorption, utilization of metabolizable energy for production and maintenance.

3.3 Feed Intake

In the first part of lactation nutrient intake especially of energy and protein, does not meet requirements of a high-yielding cow. Negative energy balance can be reduced by increasing density of the diet through a higher proportion of concentrates (Korver, 1988).

Gravert (1985) (Table 2) showed results of 32 sets of monozygous twins with 96 lactations. Cows were fed a mixed ration of roughage and concentrates ad libitum. Heritability of energy intake during the initial 20 weeks of lactation was 0.16 and its genetic correlation with milk production was only 0.12. Results suggested that selection on milk yield would not automatically increase feed intake of dairy cows in the first part of lactation. Hooven et al., (1972) found the correlation for 31-60 days lactation of 0.52 and heritability was 0.24 and found an estimate of 0.86 in the second part of lactation. (Table 2). These results clearly reflect the differences between different parts of lactation.

Performance testing of AI bulls provides the possibility for

selection on feed intake in a breeding program. Korver et al. (1987) reported on the results of 202 young heifers 24 sires fed roughage ad libitum. They found heritability for roughage intake (dry matter per day) of 0.55 and for intake per unit metabolic weight of 0.17. The phenotypic variation was 0.66 kg DM/day, respectively. Corresponding results on 127 lactating heifers fed a roughage ration fed ad libitum supplemented with a fixed amount of concentrate was 0.8 kg DM/day. The genetic relationships between feed intake in young AI bulls and feed intake of female progeny is not yet known.

Table 2. Genetic relationships (including heritabilities, underlined) between feed intake, feed efficiency and milk yield. (Hooven et al., 1972).

	FCM	GFE	FI
31-60 days lactation			
FCM yield (FCM)	<u>0.48</u>	0.89	0.52(0.12) ^a
Gross Feed Efficiency (GFE)		<u>0.44</u>	0.07
Feed Intake (FI)			<u>0.24</u> (0.16) ^a
121-150 days lactation			
FCM	<u>0.56</u>	0.93	0.86
GFE		<u>0.56</u>	0.61
FI			<u>0.26</u>

^aGravert (1985)

Several studies have focused on between breed variation in feed intake and feed conversion. Oldenbrook (1984) observed in experiments with Holstein Friesian (HF), Dutch Friesian (DF) and Dutch Red and White (DRW) cows, that the largest differences in dry matter intake was

between HF and DRW (on average 8%) in favor of HF. In his further studies when Jerseys were involved, Oldenbrook (1986) showed a significant breed-ration interaction when comparing Friesians and Jerseys on a completely mixed high and low-concentrate diet. Jerseys were favorable on a low concentrate ration and Friesians on the high concentrate ration. Richardson et al. (1971) also reported that efficiency on a lactation basis showed a significant genotype-ration interaction which might be the result of the level of concentrates since the experimental Jersey heifers were fed concentrates according to milk production. Korver (1982) and Korver (1988) showed results of a comparison of Friesians under feeding strategies with a fixed concentrate level or concentrate fed according to milk yield with roughage ad libitum in both cases. The coefficient of variation was 9 and 15%, respectively. These results indicate more fully expression of genetic differences when diets are altered according to expected requirements. Feeding levels therefore account for the main part of the differences in production between herds. These studies also make apparent the importance of genotype by feeding level and that feeding by strategy interaction represent scale effects.

3.4 Digestion and Absorption

Very few attempts have been made to determine the heritability of digestibility within different types of cattle. Van Es (1961) cited by Korver (1988) showed that little variation exists among cows in their ability to digest a given diet. Grieve et al. (1976) and Custodio et al. (1983) examined the relationship between estimated transmitting ability for milk production and digestibility of dietary components in

Holstein cows. Both studies concluded that transmitting ability and digestibility were not correlated when dairy cows were fed a mixed diet ad libitum. Davey al., (1983) found similar results when he compared two genetically different groups of Holstein cows.

In a literature review Warwick and Cobb (1976) reported differences in dry matter digestibility between *Bos taurus* cattle and *Bos indicus* cattle, but the differences were too small and inconsistent and of doubtful practical significance.

Walter (1986) examined the effect of varying the rate of energy absorption as well as the amount of residual milk on milk energy utilization. Using various half lives of energy absorption (0 to 1.5 days) very little effect was found on energy input and energy utilization.

3.5 Partitioning of Energy to Useful Product

For growing young animals selected for meat production, there are essentially two main uses of metabolizable energy namely growth and maintenance. For lactating, cows there are typically four major uses of energy which have been categorized: maintenance, lactation, pregnancy and weight change. Energy utilization for each of these forms of output will be reviewed.

3.5.1 *Energy Requirements for Maintenance*

Maintenance energy requirements consist of energy necessary for basal metabolism, conduct of voluntary body activity and generation of heat necessary to maintain body temperature (Milligan and Summers, 1986; Korver 1988). For the producing female maintenance requirements constitute a major proportion of the energy requirements for cattle

production (Ferrel and Jenkins, 1985). Considerable variation exists among animals in the maintenance requirement per unit metabolic body size when comparisons are made across a range of species and ages.

Several investigations have been made to estimate energy requirements for maintenance with either lactating or dry cows. Hashizume et al. (1965) found an estimate of 116 kcal ME/kg^{3/4} for lactating cows. Van Es and Nijkamp (1969) concluded that 96 to 111 kcal of ME/kg^{3/4} were required for the maintenance of a 500 kg lactating cow. Moe et al. (1970) estimated maintenance requirements from 350 energy balance trials with lactating cows to be 122.1 and 111.3 kcal/kg of metabolic body weight. Data reported by Ferrel et al (1976) indicated the maintenance of pregnant and non pregnant heifers to be similar. However data reported by Moe et al (1970) indicated that the maintenance requirements of lactating Holstein cows were considerably greater than the maintenance requirements for dry cows.

Walter and Mao (1989) estimated the proportion of ME intake utilized for maintenance by lactating Holstein cows. They reported negligible differences in energy used for maintenance during negative or positive energy balance (20.81 and 19.95% respectively). During the whole lactation period, 20.11% of ME intake was used to meet energy requirements for maintenance. Saama et al. (1990) did a similar study using data from energy chamber experiments. On average, 25% was of ME intake was used for maintenance of lactating Holstein cows.

Energy requirements for maintenance by lactating beef cows have also been evaluated by several workers. Garret (1974) cited by Ferrel

and Jenkins (1985) obtained an estimate of 112 kcal ME/kg^{3/4} per day for nonpregnant nonlactating cows. Similar estimates were obtained by Klosterman et al. (1968) for dry nonpregnant Hereford or Charolais cows.

Neither Klosterman et al. (1968) nor Russel and Wright (1983) observed differences in maintenance requirements between cow types but reported that maintenance decreased with increased body condition of beef cows. Ferrel and Jenkins (1985) reported data on a series of their experiments with different breeds and breed crosses to evaluate the influence of cow type on maintenance requirements during different physiological states (Table 3). From these data Ferrel and Jenkins concluded that the genetic potential for milk production was positively related to maintenance energy requirements and physiological state of the cow.

Numerous investigations have evaluated the influence of cattle breed or breed cross on energy requirements for maintenance for selected beef and dual purpose steers or bulls. Blaxter and Wainman (1965) found lower basal metabolism for steers of beef breeds than for dairy breeds.

Garret (1969) observed lower maintenance requirement for Hereford steers than for Holstein steers. Frisch and Vercoe (1977) reported that cattle of *Bos indicus* had a lower basal metabolism than cattle of *Bos taurus*. Table 4 shows some of the results of estimates of maintenance requirements for beef steers or bulls of different breeds. These data indicate a substantial amount of difference in energy requirements for maintenance among cattle germ plasm.

Table 3. Estimates of ME Required for Maintenance of Various Breeds or Breed Crosses (Ferrel and Jenkins, 1985).

Breed or Breed Cross	Physiological State	Maintenance Kcal/Kg ^{3/4}
Angus-Hereford	nonpregnant nonlactating	130
Charolais X	"	129
Jersey X	"	145
Simmental X	"	160
Angus	nonpregnant lactating	149
Hereford	"	141
Simmental	"	166
Charolais	"	165
Angus	nonpregnant nonlactating	115
Hereford	"	120
Simmental	"	134
Angus	pregnant lactating	151
Red Poll	"	157
Brown Swiss	"	156

3.5.1.1 Sources of Variation

Most of the estimates indicate that ME requirements for maintenance vary among cow types and also suggest that variation in maintenance exists beyond that associated with size or milk production potential.

Energy requirements for maintenance may differ among animals differing in genetic potential for production. Andersen (1980) and Webster (1980) showed differences due to sex. Close (1982) reported differences due to temperature in his studies with pigs. Blaxter and Boyne (1982 cited by Ferrel and Jenkins 1975) also showed differences

due to season. Van Es (1980) and Geay (1984) reported variation in maintenance energy requirements with liveweight of the animals. Geay

Table 4. Estimated Maintenance Requirements of Various Types of Cattle.

	Breed	Maintenance
Vercoe (1970)	Brahman x British steers, 327 kg	102 ^a
	Shorthorn x Hereford steers, 290 kg	112 ^a
Garrett (1971)	Hereford steers, 240-410 kg	106 ^a
	Holstein steers (DP), 230-390 kg	115 ^a
Chestnutt (1975)	Angus steers, 220-500 kg	142 ^a
	Hereford x Friesian steers (DP), 210-500 kg	130 ^a
	Friesian steers (DP), 180-500 kg	161 ^a
Frisch & Vercoe (1976)	Brahman x British steers, 230 kg	73.5 ^b
	Africander x British Steers, 230 kg	85.7 ^b
	Hereford x shorthorn steers, 232 kg	84.3 ^a
Vermorel et al (1976)	Charolais bulls, 16mo.	100 ^a
	Friesian bulls (DP), 16mo	113 ^a
Andersen (1980)	Simmental x bulls, 300-500 kg	114 ^c
	Charolais X bulls, 300-550 kg	109 ^c
	Hereford X bulls, 300-550 kg	102 ^c
	Black & white X danish bulls, 320-560 kg	94 ^c
	Angus x Danish bulls, 320-560 kg	95 ^c
	Charolais x Danish bulls, 320-560 kg	99 ^c
	Brown Swiss x Danish bulls (DP), 320-560 kg	92 ^c
	Red Danish x Danish Bulls, 320-560 kg	93 ^c
Byers & Rompala (1980)	Charolais Steers, 260-544 kg	161 ^c
	Simmental x Angus steers, 190-402 kg	122 ^a
Van Es (1980)	Hereford x Friesian steers (DP), 250 kg	124 ^a
	" " " " 450 kg	117 ^a
	Hereford x Friesian bulls " 250 kg	145 ^a
	" " " " 450 kg	137 ^a
Byers (1982)	Red Angus steers, 219-453 kg	115 ^a
	Simmental Steers,	115 ^a
Truscott et al (1983)	Hereford steers, 141-487 kg	145 ^a
	Friesian steers (DP), 166-568 kg	153 ^a

^akcal/kg^{.75}^bg/kg^{.75}^ckcal/kg^{.73}

DP - Dual Purpose

(1980) observed that ME requirements for maintenance declined by 3.0 Kcal/kg^{3/4} for each increase in 100kg body weight with Charolais bulls, by 10.5 Kcal/kg^{3/4} with Friesian bulls.

Body composition differences among breeds, sexes or ages of cattle have led many investigators to suggest variation in body composition to be the primary source of variation in fasting or maintenance energy expenditure. Graham et al., (1967), Graham et al. (1974) and Ferrel et al., (1979) showed maintenance expenditure to be highly correlated with body lean or protein mass and lowly correlated with body fat. Pullar and Webster (1974) found that lean rats had a higher fasting heat production than genetically obese rats. However, other data indicate that body composition may not be the predominant factor in determining maintenance requirements. Garret (1980) indicated no differences in maintenance of steers and heifers although steers contained greater amounts of lean tissue than heifers at similar weights. Different body composition and fasting heat production values for genetically lean, obese and contemporary Hampshire x Large white pigs were observed among the lines of pigs (Tess et al., 1984). However adjustment of the fasting heat production data to equal body size and composition did not remove differences among the lines.

3.5.2 *Energy Utilization for Growth*

The energy requirements for growth are generally thought to be depended on the composition of growth (Webster, 1980 Garret, 1980 Andersen et al., 1980 and Geay, 1984). In his study Garret (1980) determined fasting heat production in trials involving 708 steers and 341 heifers. The energy value of gain in mJ/kg of the British breed

steers (23.4) was 11% higher than for the heifers (28.1) and 35% lower than a small sample of Charolais steers (14.7). Although he did not study the composition of gain he pointed out that the Charolais steers had gained more protein than fat since protein is produced with less efficiency than fat in growing ruminants.

Byers and Rompala (1980) measured composition of empty body growth at intervals during growth of eight Charolais and eight Angus x Simmental steers (AxS). For the AxS steers efficiency of energy use for growth was 62.0% and was 44.8% for the Charolais steers. The increased proportion of protein in the gain of Charolais steers was probably a factor in the lower efficiency of energy use for gain of Charolais when compared with AxS steers. They also observed that within each group of animals the efficiency of use of energy for growth was positively related to the fraction of body gain as fat. Byers and Rompala further on reported that increasing rate of gain from 1.0 to 1.5 kg/day with either Charolais or AxS steers resulted in very little additional protein gain but rates of fat deposition increased rapidly with increasing increasing rate of gain from 1.0 to 1.5 kg/day. These findings seem to suggest that efficiency of energy utilization for protein deposition is lower than that of fat. This hypothesis has been supported by many workers (Orskov and McDonald, 1970; Pullar and Webster, 1977; Webster, 1977 and Geay, 1984).

In their study with lean and congenitally obese rats, Pullar and Webster (1977) observed values of 0.45 and 0.75 for energy efficiencies of protein and fat deposition respectively. Orskov and McDonald (1970), in their study with lambs, found ME requirements for protein and fat

deposition to be 16.25 kcal/g and 11.44 kcal/g respectively. Geay (1984), based on data from 52 experiments in his review of literature gave preferred values of 0.20 and 0.75 for protein and fat accretion respectively on energy basis.

Energetic efficiency of growth has been found to vary with diet. Geay and Robelin (1980) examined the influence of energy content of the diet on energy utilization for growth in bulls and heifers. Diets used in this study were long grass hay or dehydrated lucerne with two different proportions of concentrates. It was observed through slaughter techniques that for the same ME intake, the daily gain of liveweight protein and energy was lowest for diets with least metabolizability but the decrease was less in bulls than heifers. These observations were attributed to the efficiency of ME utilization for fat deposition that drops when crude fiber content of the diet increases or when its metabolizability decreases.

Orskov and McDonald (1970) used barley and soybean meal diets with varied crude protein concentrations of approximately 10, 12.5, 15.0, 17.5 and 20.0%. Three feeding levels 100, 85 and 70% of estimated maximum voluntary feed intake were used. The total deposition of protein was not significantly affected by feeding level but rose significantly with increasing protein level in the feed. Total deposition of fat decreased with increasing protein concentrations in the feed. They also observed that total fat deposition decreased with feeding level. Menke (1980) proposed a curvilinear function for the description of the relationship between metabolizable energy intake and retention of energy as protein which permits the calculation of the

maximum potential energy retention in protein deposition at different feeding levels. Menke (1980) also pointed that a function for prediction of protein must include the effects of diet composition (protein:energy ratio and amino acid pattern) and feed intake as well as effects of endogenous factors of age, sex and breed of the animal. Tyrell and Moe (1980) performed 59 energy balance measures on eight Hereford heifers during the fattening period. They found that partial efficiency of use of metabolizable energy for tissue gain was not affected by diet.

Garret (1970) found that sex had a significant effect on the energy required for growth . A high quantity of energy was required per unit weight of gain in the heifers as compared to the steers. Their results at different ages of the animals are shown on the Table below.

Table 5. Composition of gain of ad lib fed steers and heifers (Garret, 1970)

Period(days) Sex	0-98		98-196		196-294	
	Steers	Heifers	Steers	Heifers	Steers	Heifers
Fat%	35.30	47.10	48.50	55.60	60.00	69.70
Protein%	14.50	12.20	11.90	10.50	9.60	7.70
NE mJ/kg	4.12	5.12	5.24	5.83	6.21	7.02

Some estimates of energy requirements for growth have been reported. Tyrrel et al (1974) found that six Hereford heifers required an average of 1.95 Mcal to deposit one Mcal of tissue for gain. For each additional one Mcal in daily rate of growth they observed 95% of

it was retained as fat while only 5% as protein. Jensen (1989) using data from Holstein-Friesian and Brown Swiss growing young bulls found estimates of 9.26 mJ/kg of gain for bulls from 14 days to 200 kg and 23.0 mJ/kg of bulls between 200 kg and slaughter weight.

From these observation it is true that fat deposition increases with age and the reverse is true for protein. Also as fat increases the net energy required for a kg of gain increases.

In summary growth is a confusing process to evaluate because everything is changing at once. However, from the above studies it is apparent that relative growth rate declines throughout from birth to maturity. The proportion of fat relative to protein deposited in the growing animal increases progressively as the animal proceeds to maturity. The amount of food energy required to maintain energy balance increases throughout growth. All these factors combine to reduce throughout growth the net efficiency with which food is converted to body tissue and reduce even more the efficiency with which it is converted to protein or lean tissue.

3.5.3 *Energy Utilization for Weight Change in Support of Lactation*

The catabolism and metabolism of tissue in support of lactation is different from growth for it involves primarily fat tissue with little or no protein in many circumstances (Walter, 1986). The basis of liveweight change in lactating animals has been documented by Moe et al (1971). Intense selection of dairy cattle for high milk has resulted in a situation in which the genetic ability to produce milk during early lactation exceeds the ability of the animal to ingest sufficient feed to meet requirements for energy (Moe et al., 1971). Because production

of milk during early lactation has a high priority in the dairy cow, production of milk may continue high despite insufficient energy intake. When this situation exists the cow must draw upon body tissue reserves to provide the energy which is lacking in the diet. This situation will end as soon as body energy reserves have been exhausted thus resulting in body weight loss. However to re-establish the animal to the same condition as at parturition, the animal must be allowed sufficient feed intake for body energy deposition either during late lactation or during the dry period.

Flatt et al. (1970) described a cow Lorna which was given a diet supplying over one half of the maintenance energy needs. The cow lost 10 to 20 Mcal body tissue daily while producing 27 to 35 Mcal (85 to 110 lbs) milk daily. In late lactation, the cow deposited large amounts of body tissue (15.2 to 18.8 Mcal) daily while still lactating 15.0 to 22 lbs of milk daily. The same trend of body tissue mobilization in early lactation was for replacement later in lactation was also observed in cows between 6 and 10 weeks post-partum. On average Flatt et al. (1970) observed that cows in their study had an average body tissue loss of 6.9 Mcal/day in mid lactation (24 weeks). The effects of stage of lactation were highly significant.

Composition of energy value of the body tissue gain or loss by cattle are variable. Energy equivalence value derived from various studies with cows range from 6.3 to 7.9 Mcal for body tissue loss (Reid and Robb, 1971). It appears that body tissue gain or loss could range from as much as 100% water to 90% fat (Reid and Robb, 1971). Mobilization of body tissue thus occurs in most cows during peak

periods of lactation.

Bauman and Curie (1980) reported that cows took approximately 16 weeks post-partum to consume enough energy each day to meet daily requirements for milk production. They calculated that over the entire first month of lactation one third of the energy in milk is from mobilization of body reserves. Broster et al (1975) conducted a study on feed utilization by lactating dairy cows for a period of the first 24 weeks of lactation. They observed that the animals lost weight in early lactation and started regaining the weight after peak period. They also did regression of daily milk yield (Table 6). The regression coefficient was large during early lactation and smaller in mid-lactation. Thus the first six weeks of lactation appear to be most important for tissue mobilization toward milk production.

Table 6. Regression of liveweight change on milk yield (kg/day) measured at various stages of lactation (Broster et al., 1975).

Weeks of lactation	Regression coefficient	SE
1-6	-0.122	0.0189
7-12	-0.042	0.0109
11-16	-0.062	0.0160
15-20	-0.052	0.0148
19-24	-0.040	0.0132

Several workers have estimate partial energy requirements for weight change in lactating cows. Moe et al (1971) using 350 energy balance trials with lactating dairy cow estimated a value of 1.339 Mcal

of ME for kg of body tissue gain. They calculated an overall efficiency value of 75% for utilization of ME for weight change in lactation. They also estimated a value of 0.54 as the efficiency of conversion of body tissue to milk. Van Es (1976) estimated overall efficiency of tissue deposition in late lactation as 50%. Walter and Mao (1989) estimated values of 4.461, 0.581 and 1.920 Mcal of net energy (NE) required for a kg of weight change over periods of negative energy balance, positive energy balance and over entire lactation respectively.

3.5.4 Energy Utilization for Pregnancy

The efficiencies of supporting pregnancy in the animal have not been widely researched. In general more emphasis has been placed on the study of efficiencies for growth and lactation. However, the importance of pregnancy cannot be overlooked. As pointed by Bauman and Curie (1980) pregnancy imposes a substantial cost to the animal because total requirements for nutrients at the end of pregnancy are 75% greater than in non pregnant animal of the same weight.

As early as 1957 Jacobsen et al. derived a function of the energy content of fetal tissue as

$$V = 7.24 * e^{0.0174t}$$

where v is the rate of energy deposition (in kcal/day) on day t. These workers reported that the support of pregnancy increased heat production in the dam between 2 and 2.5 times. Although they did not compute the efficiency of maintaining pregnancy their results seem to suggest that maintenance energy requirements during pregnancy increase. This is confirmed by Bauman and Curie (1980) who reported that out of

88 kcal/kg per day required for pregnancy, 63% was heat.

The apparent efficiency of utilization of metabolizable energy for pregnancy is exceedingly low (10 to 25%) in sheep (Rattray et al., 1974; Graham, 1964) and cattle (Moe et al., 1970, 1971, 1972). Moe et al. (1970) estimated the ME required for gestation from the results of 97 balance trials carried out with pregnant non lactating cows. The estimate required to maintain pregnancy ranged from 60 to 65 e^{.0174t} kcal on day t. These values corresponded to efficiencies of 11 to 12%. Moe and Tyrell (1972) reasserted that the efficiency of use of ME for pregnancy was low (<25%). Walter and Mao (1989) estimated the ME requirements to support pregnancy using data from lactating cows. Their results indicated that less than 1% of ME intake was need for pregnancy. In sheep Rattray et al. (1974) estimated that the efficiency was between 12 and 14%. This apparent low efficiency, they reported stems from ignoring the sizable cost of maintenance of products of conception.

3.5.5 *Energy Utilization for Lactation*

It is well established that ME is utilized with varying partial efficiencies according to use for maintenance, lactation, growth and fattening. Lactation along with growth and weight gain, has been the form of production most investigated. Although the broad subject of energy efficiency during lactation encompasses the efficiencies of digestion and milk production as well as endocrine effects, this review will focus on the production efficiency of milk.

Many factors have been reported to affect energy utilization for lactation. The type of diet affects ME utilization as reported by

Garret and Johnson (1983). A major portion of this effect probably relates to the particular pathway of metabolism taken by each specific nutrient. The pattern of nutrients comprising ME and therefore the number of transformations would vary with diet.

Kronfeld et al (1980) observed that when protected fat is fed to dairy cows, increases are observed in milk fat and in the calculated efficiency of ME utilization for milk energy. Bauman et al. (1984) pointed that the apparent increase in efficiency reflects a very low energy cost associated with the transfer of absorbed fatty acids to milk fat as compared with the energy costs of de novo synthesis of milk fatty acids.

Van Es and Nijkamp (1969) found that percentage of crude protein in the diet had no effect on lactation efficiency nor did crude fiber percentage. Broster et al (1980) in their study using heifers in either first or second lactation and fed at either high or low levels of energy, observed that the group fed a low level in early lactation had the highest efficiency of conversion of energy intake into milk. Contrary to these findings Grieve et al. (1977) determined that energy efficiency for lactation increased with feed intake. Hashizume et al (1965) reported greater energetic efficiency for lactation in cows fed high levels of concentrates than those fed low levels.

The extent to which individual cows vary in the efficiency with which they utilize ME for milk synthesis is more difficult to quantify because few if any experiments have directly addressed this question. In summarizing 332 energy balance trials Moe et al (1972) observed that 97% of the variation in energy balance was associated with the

variation in ME intake, diet and metabolic size. This seem to suggest that little variation exists among cows in the partial efficiency with which ME is utilized for lactation. Trigg and Parr (1981) were unable to detect any association between predicted genetic merit and the partial efficiency with which cows utilized ME for the synthesis of milk or body tissue.

Nutrient partitioning has been the major source of variation among animals in the energetic efficiency of lactation (Bauman and Curie, 1980). Moe (1981) in reviewing the extensive energy balance trials at the USDA energy laboratory concluded that the major differences among diets as well as among individual cows was in the amount consumed and energy partition that is milk production or fattening rather than the efficiency with which ME is used. This point was illustrated by Bauman et al (1984) when they compared two cows Azalea and Bugle (Table 7). Despite consuming equal amounts of the same diet, they exhibited marked differences in nutrient partitioning during first 67 days of lactation. Whereas Azalea averaged 12.3 kg/day of 3.5 % fat corrected milk (FCM) and gained 39.1 kg of body weight, Bugle produced 26.3 kg of FCM/day and lost 51.8 kg of body weight.

Similar differences in nutrient partitioning are seen in genetically diverse lines. Animals of high genetic merit produce more milk, have greater voluntary intakes and use more of their body reserves in early lactation than those of low merit (Bryant and Trigg, 1981; Davey et al., 1983). The increase in productive efficiency that occur in genetically superior cows are primarily due to dilution of maintenance requirements.

Table 7. Example of animal differences in nutrient partitioning (Bauman et al, 1984).

Variable	Azalea	Bugle
Initial body weight kg	517	519
Intake of diet	-----Equal-----	
Liveweight change	+39.1	-51.8
Mean daily milk kg 3.5% FCM	12.3	26.3

Estimates of energy required for milk production during positive or negative energy balance have been computed (Moe et al., 1970; Walter and Mao, 1989). These estimates differed between studies and slightly with stage of lactation within studies (Table 8).

Table 8. Partial energy requirements for milk production (Moe et al 1970, Walter and Mao, 1989)

Physiological State	Moe et al(1970) Mcal ME/kg SCM	Walter & Mao(1989) Mcal ME/kg SCM
Negative energy balance	1.512	0.706
Positive energy balance	1.576	0.741
Overall Lactation	1.552	0.706

Efficiencies of energy conversion to support lactation were also quantified by several workers. Hashizume et al. (1965) found the efficiency of ME of diets containing 45 and 71% of concentrate consumed in excess of maintenance was used with efficiencies of 74.0 and 68%

respectively for milk. Coppock et al. (1964) used six mature lactating nonpregnant cows to study the utilization of ME for milk production. Using diets calculated to provide 50, 75 and 100% of estimated net energy from alfalfa, efficiencies of ME in excess of maintenance were 65, 61, and 54% respectively for lactation. Van Es and Nijkamp (1969) reported results of 41 balance trials with lactating cows. These workers concluded that ME was used for milk production with an efficiency of 54 to 58%.

**4. Estimation of Residual Energy Intake in Growing Young Bulls
Using an Animal Model**

4.1 ABSTRACT

Residual energy intake is defined as total net energy intake minus the predicted energy requirements for maintenance and production in a production period. The less energy intake left unused or the less REI, the greater efficiency in using net energy intake. It is therefore a good measure of energetic efficiency. REI was estimated for each of 650 growing young bulls from 31 Holstein-Friesian or Brown Swiss sires. Animals were fed ad libitum diets consisting of 100%, 75%, 50% or 25% expected energy from concentrates from 200 kg liveweight to slaughter. The feeding experiment was conducted for a period of five years. Average daily net energy intake (NEI), metabolic body weight and daily gain (DG) in a production period on each of the bulls were analyzed. An animal model for NEI containing fixed effects of year-treatment, initial age of the animals at beginning of experiment and breed, covariates of average DG and $BW^{3/4}$, random animal effects of sires and bulls, and residual was used. Animal and residual effects were parts of residual energy intake of a bull. Animal and residual variance components were estimated by an Expectation Maximization algorithm of Restricted Maximum Likelihood procedure. Partial net energy requirements for growth and maintenance were 26.23 mJ/kg and 0.74 mJ/kg^{3/4}, respectively, for the 650 bulls. The heritability estimate for REI was a very low value of .14. The proportion of phenotypic variation in NEI due to REI was 28%.

4.2 INTRODUCTION

Feed energy constitutes the largest item of expense in any cattle

production enterprise. One way of reducing these costs in the long term is to breed for better feed efficiency (Brelín and Branning, 1982; Brelín and Martinsson, 1986; Korver, 1987; Buttazzoni and Mao, 1988). Before considering efficiency in a cattle breeding system, more information about an appropriate measure of efficiency, the genetic variation in efficiency and its relationships with other economically important traits such as growth rate and carcass traits must be known.

Feed efficiency has been traditionally calculated as a ratio of feed intake and weight gain in a given interval of growth (Koch et al., 1963). Feed efficiency calculated this way has been found to have a very high genetic correlation with growth rate, usually ranging from .70 to .95 (Brelín and Branning, 1982). Therefore selection for feed efficiency per se is considered needless as it is automatically improved along with the selection for growth rate. However, feed efficiency calculated this way is a very complex measurement including a number of interacting factors (Koch et al., 1963; Korver, 1988). Variation in the composition of gains (fat, lean or bone) and in maintenance requirements prevents this measure from being a precise estimate of energy conversion rate (Koch et al., 1963). The composition of gain regarding fat and other tissues affects feed efficiency as the energy required for a unit weight of fat is considered larger than for other tissues (Webster, 1980; Geay, 1984). A high growth rate always causes the proportion of feed energy necessary for maintenance to decrease which automatically results in better feed efficiency (Brelín and Martinsson, 1986). However, on the other hand the proportion of feed energy often used for maintenance usually increases when an animal

gets larger which affects feed efficiency in the other direction (Geay, 1984). Due to strong genetic correlation between growth rate and mature size (Karlsson, 1979), fast growing animals on average would be less mature, therefore leaner, at a given liveweight, thus giving rise to better feed efficiency.

In order to genetically improve utilization of feed energy the concept of feed efficiency must be clearly specified because a biologically more uniform measure is desirable and because growth rate is already taken into consideration in the selection process. Koch et al. (1963), suggested that the most useful criterion for evaluating efficiency of feed conversion in beef animals maybe the amount of desired or marketable product produced for a given energy rather than the fraction of energy in the feed which was converted to animal tissue. Brelin and Branning (1982) measured feed efficiency as the amount of feed energy which was required with ad libitum feeding of a standardized diet to produce a carcass of the same weight in a given period of time. This trait described as the average metabolic efficiency of feed conversion for growing cattle from birth to slaughter was termed true feed efficiency. True feed efficiency was intended to express the ability of the animal to resorb feed energy and to utilize it for maintenance and growth.

Residual energy intake (REI) defined as actual energy intake minus predicted energy requirements in a production period has been suggested as a good measure of energetic efficiency (Koch et al., 1963; Brelin and Martinsson 1986 and Korver 1988). REI would reflect the differences between individuals in utilizing metabolizable energy for maintenance

and production (Luiting, 1987 and Korver, 1988). If more energy an animal takes is used for production and maintenance a lower REI would thus indicate better efficiency. This approach of energetic efficiency involves computation of partial energy requirements for production (daily gain) holding maintenance constant or vice versa. However, difficulties might appear since maintenance which is defined as a function of metabolic body weight ($BW^{3/4}$) will be highly confounded with daily gain. The genetic nature of REI is, however, not well understood and therefore needs to be investigated.

Using data from growing young bulls, the objectives of this study were to (1) estimate partial net energy requirements for growth and maintenance, (2) estimate residual energy intake for each animal and (3) estimate the genetic parameters of REI.

4.3 MATERIALS AND METHODS

4.3.1 Experiment

A feeding experiment was carried out in Denmark using 650 bull calves from a total of 31 sires of either Holstein-Friesian or Brown Swiss. The experiment was conducted for a period of five years from 1978 to 1982. Bulls were introduced to the experimental diets at the age of 28 days. From 28 days to 200 kg live weight, the feeding level was restricted to 75% of expected ad libitum intake. From 200 kg liveweight to slaughter weight the animals were randomly allocated to four dietary treatments of 0%, 25%, 50%, 75% of expected energy from roughages. The 0% diet was all concentrate and the other treatments were fixed amounts of concentrates and roughages fed 3-4 times per day.

This feeding regime was to ensure feed availability at all times of the day. In 1978 and 1979 concentrates were fed in fixed amounts based on weight and roughages were fed ad libitum. In the last three years from 1980 to 1982 roughages and concentrates were fed as total mixed rations. Energy composition of all the diets is shown in Appendix I.

The animals were randomly assigned to three slaughter weight groups. Target slaughter weights were 340, 470 and 600 kg liveweight.

Calves were weighed biweekly. Age of the animals was also recorded when they were weighed. Feed intake was recorded daily (sum of 4 intakes) and summed over a 2-week interval between weighings.

Weighbacks were taken twice a week. Thus feed intake was recorded as the sum of all feed given in a two week period minus the weighbacks. The energy content of roughages used was determined both in vitro via chemical composition and using in vivo experiments with sheep reared close to the maintenance level in order to obtain digestibility of the diet. Net energy intake was computed according to the Danish Feed evaluation system based on the Scandinavian feed units (SFU).

4.3.2 Data

A total of 9,798 2-week records of 650 young bulls were available for analysis. There was a total of 20 year-treatment subclasses and 37 age classes. Each individual bull had 2-week repeated records and these ranged from 4 to 25 records per animal. The number of records in the year treatment subclasses ranged from 218 to 854. Tabulation of the data is shown in Appendix I.

4.3.3 Model

To estimate the partial energy requirements for growth and

maintenance, and residual energy intake the following animal model was used:

$$y_{ijk} = \mu + T_i + A_j + H_k + b_1(DG_{ijk}) + b_2(BW_{ijk}^{3/4}) + a_{ijk} + e_{ijk}$$

where:

y_{ijk} was the average daily net energy intake in production period for a bull in the k th breed, in j th age group, and i th year-treatment;

μ was the overall mean;

T_i was the fixed effect of the i th year treatment with $i = 1, 2, \dots, 20$;

A_j was the fixed effect of the j th age group with $j = 1, 2, \dots, 12$;

H_k was the fixed effect of the k th breed with $k = 1, 2$;

DG_{ijk} was the average daily gain of the m th bull in the corresponding production period of y_{ijkmn} ;

b_1 was the partial energy requirement for growth;

$BW_{ijk}^{3/4}$ was the average metabolic body weight of the m th bull in the corresponding production period of y_{ijkmn} ;

b_2 was the partial energy requirement for maintenance;

a_{ijk} was the random animal effects of sires and bulls with $N(0, I\sigma_a^2)$

e_{ijk} was the random residual with $N(0, I\sigma_e^2)$.

After energy intake took account of the fixed classification effects and the partial energy requirements for growth and maintenance, the terms that were left namely $a_{ijk} + e_{ijk}$ were collectively

estimates of residual energy intake (REI). Variance components estimates for sire, bulls and residual error were estimated by the restricted maximum likelihood (REML) approach utilizing the expectation maximization (EM) algorithm as described by Jensen and Mao (1988). The convergence criterion was set at 10^{-5} for the residual variance. Appropriate relaxation factors were used to accelerate convergence.

To analyse data on repeated records a sire mode was used. This model and the results from the model are show in Appendix II.

4.4 RESULTS AND DISCUSSION

Mean, SE, SD and CV for NEI, DG and $BW^{3/4}$ are shown in Table 9. The CV for all the variables was high. Daily gain had the highest CV among the animals and amongst all variables. There was a substantial variation in average daily gain ranging from -1.71 kg to 3.79 kg. Total NEI in a two week period also showed a high variation ranging from 296.85 Mcal to 1422.14 Mcal for different bulls.

Table 9. Mean, SE, SD, and CV for net energy intake (NEI), daily gain (DG) and metabolic body weight($BW^{3/4}$).

	Mean	SE	SD	CV%
NEI (mJ)	51.63	.38	9.72	18.82
ADG (kg)	1.24	.01	.19	15.36
$BW^{3/4}$ (kg)	78.29	.38	9.81	21.34

4.4.1 Partial energy requirements for growth

The estimated partial net energy requirement for growth was 29.62 mJ/kg/day overall 650 bulls (Table 10). Jensen (1989) estimated partial energy requirements for each of the same 650 bulls using a within bull covariate model. The average of such requirement estimate was 23.0 mJ/kg/day which approximated closely our overall result, despite the fact that his average daily estimate was for the entire period of 200 kg to slaughter.

Energy utilization for growth has been shown to depend on the composition of body gain (Kielanowski, 1976; Pullar and Webster, 1977; Thorbek, 1977 and Webster, 1980). In older animals, a larger proportion of weight gain consists of fat (Andersen, 1984 and Geay, 1980). The partial efficiencies of utilization of energy for protein and fat have been reported to be different (Orskov and McDonald, 1970; Pullar and Webster, 1977 and Geay, 1984). In their experiment with lean and genetically obese rats, Pullar and Webster (1977) observed values of .45 and .75 for efficiencies of protein and fat deposition, respectively. Based on data from 52 experiments Geay (1984) in his extensive literature review gave preferred values of .20 and .75 for protein and fat accretion respectively on energy basis. The low efficiency of metabolizable energy used for protein deposition correspond to the expensive high rate of turnover. Since there is a large difference in the partial energy efficiencies of protein and fat deposition, the energy requirements for growth should therefore be viewed in terms of body composition. Unfortunately for this study information on composition of gain for each animal in each of the

weighing interval was not available.

4.4.2 Maintenance energy requirements

The partial net energy requirement for maintenance was 0.79 MJ/kg of metabolic body weight per day (Table 10). Again, Jensen (1989) estimated partial net energy requirements for maintenance for each of the same 650 using a within bull covariate model. The average estimate obtained was 0.68 MJ/kg of metabolic body weight per day, a value that closely approximated our result despite the whole production period from 200 kg to slaughter he used in his study.

Maintenance requirements consists of the energy necessary to maintain basal metabolism, conduct voluntary body activity and generate heat necessary to maintain body temperature. Based on data from an experiment with young bulls Andersen (1980) showed within breed variation in maintenance requirements for beef bulls. He obtained estimates of 0.541, 0.468, 0.355 MJ/kg^{3/4} for ad libitum feeding, 85% and 70% of ad libitum intake respectively. Maintenance energy requirements have been reported to depend on weight of the animals (Van Es, 1980 and Geay, 1984). Van Es (1980) estimated requirements for Hereford x Friesian bulls and found estimates of 124 Kcal/kg^{3/4} at 250 kg liveweight and 117 kcal/BW^{3/4} at 450 kg liveweight. Geay (1984) also observed an apparent decrease in maintenance requirements as liveweight increased. The metabolizable energy required for maintenance declined by 10.5 Kcal/W^{3/4} for each increase in 100 kg body weight.

Table 10. Partial net energy requirements for growth and maintenance.

DG (mJ/Kg/day)	26.23
BW ^{3/4} (mJ/Kg ^{3/4})	0.74

4.4.3 Residual Energy Intake

For residual energy intake, the estimated phenotypic SD was 2.72 mJ, additive genetic SD was 1.03 and heritability value was .14 (Table 11). This value is much lower than the reported literature values (Andersen, 1980; Brelvi and Brannang, 1982; Jensen, 1989). Andersen (1980) using a small data set obtained a value of .31 and Brelvi and Brannang estimated a value of 0.28. Jensen (1989) used the same data set we used and estimated a heritability value of 0.275. The model used by Jensen (1989) contained some fixed factors that were different from those in the model used in this study. The difference in the heritability values may also be due to the fact that in his study Jensen used a two stage model. REI for each bull obtained from a within bull covariate model was used as a dependent variable in a sire model. In this study REI was estimated simultaneously with the partial energy requirements for production and maintenance.

The proportion of the phenotypic SD in total net energy intake due to REI was 28%. This in conjunction with a low heritability seem to suggest that most of the variation due to REI is due to environment.

Table 11. Estimates of additive genetic and phenotypic SD and heritability values for REI.

Additive SD	1.03
Phenotypic SD	2.72
SD(REI)/SD(NEI)	.28
Heritability	.14

4.5 CONCLUSIONS

For growing young bulls in performance test, a much greater proportion of net energy intake was used to meet the requirements for growth as compared to that for maintenance. The energy requirement for growth relate closely to composition of gain as documented in the literature, however this study was unable to substantiate such relationship due to the lack of data. The estimates for both growth and maintenance partial net energy requirements from the animal model using average daily NEI in growth period were consistent with those from an intrabull covariate model used by Jensen (1989).

The phenotypic variation in total net energy intake due to REI was a relatively small value of 28%, but heritability estimate for REI was only 0.14. This seems to suggest that variation in REI in growing young bulls was largest due to causes other than additive genetic variation.

**5. Estimation of Residual Energy Intake for Lactating Cows
Using an Animal Model**

5.1 ABSTRACT

Residual energy intake (REI) is defined as the remaining energy from total net energy intake (NEI) after all the energy uses for production and maintenance have been accounted for. The idea of REI as a measure of feed efficiency is that the greater the proportion of energy intake that can be accounted for or the smaller the REI the more efficient is the animal. REI was estimated for each of 247 Holstein cows from 127 sires and 226 dams distributed in five herds across the US. Cows were in four parity groups. Data consisted of daily milk yield, net energy intake and dry matter intake, biweekly measures of milk components and body weight measures taken at unequal intervals throughout lactation. Average daily NEI in a lactation was used as a dependent variable in a model that contained fixed effects of parity and herd-season subclass; covariates of average daily solids corrected milk and metabolic BW and weight change in a lactation; random animal effects of cows, dams and sires; and random residual. From this model REI was a sum of cow, dam, sire and error effects. Partial energy requirements for SCM, maintenance, and weight change estimated for all cows were 0.54, 0.15 and 1.52 Mcal/kg, respectively. Heritability value for REI was .016 with phenotypic SD being 2.455. The proportion of the phenotypic SD in NEI due to REI was a high 68%.

5.2 INTRODUCTION

In dairy production, feed is the major part of production costs. Improving a cow's efficiency of converting energy intake to produce

milk should be unimportant goal for the dairy industry. However, genetic selection in dairy cattle has not considered feed intake or feed efficiency. Such negligence is partly due to lack of information about the genetic aspects of nutrient intake and utilization.

Gross feed efficiency in dairy cattle is defined as the ratio of milk output over feed intake or its inverse. It has been found to be influenced by diet, and other environmental factors, genetic ability and physiological state of the cow to utilize nutrients for milk (Bauman et al., 1984, Blake and Custodio, 1984). Heritability of gross feed efficiency (GFE) has been reported to range from 0.4 to 0.6 (Hickman and Bowden, 1971). Blake and Custodio (1984) cited the genetic correlation between milk yield and GFE being from 0.88 to 0.95, while the phenotypic correlation ranged from 0.60 to 0.95. Because of the high genetic correlation between GFE and milk yield, selection for GFE has been considered as needless because it would be automatically improved via selection for milk yield.

However, data used to compute all the genetic parameters for GFE came from dairy cattle fed concentrates according to milk production thus forcing a high correlation. The high phenotypic correlation could be due to the decrease in maintenance energy as milk production increases. GFE assumes that all feed consumed is utilized for milk production and does not adjust for maintenance and other net energy uses (Meyer and Garrett, 1967, Buttazzoni and Mao, 1988, Walter and Mao, 1989). Blake and Custodio (1984) pointed that milk production is not only depended on feed intake but also on body tissue losses or gains, a factor that is not considered in the computation of gross feed

efficiency, thus making gross efficiency an inaccurate measure of productive efficiency.

Blake and Custodio (1984) suggested that feed efficiency for lactating cows should be defined as dietary nutrients to milk after adjusting for nutrient supplied by tissue catabolism. Mao, Walter and Buttazzoni (1988, 1989) suggested net energy efficiency as a better biological indicator of a cow's productive efficiency. They defined net efficiency as the ratio of energy contained in milk over the portion of energy used to produce it above net energy requirements for maintenance and for changes in body tissue reserves. Net efficiency is thus a better biological indicator of productivity than GFE.

Residual energy intake (REI) or residual efficiency is defined as the remaining energy from total net energy intake (NEI) after all the energy uses for production and maintenance have been accounted for (Brelvi and Brannan, 1982, Koch et al., 1963, Korver, 1988, Luiting, 1987). The idea of REI as a measure of efficiency is that the greater the proportion of energy intake that can be accounted for or the smaller the REI the more efficient is the animal. REI thus reflects the differences among animals in utilizing net energy for production and maintenance. In laying hens heritability for REI ranged from .25 to .40 (Luiting, 1987) and in growing bulls the estimate was .28 (Koch et al., 1963, Jensen, 1989).

The objectives of this study were using data from lactating cows to 1) estimate the partial energy requirements for SCM, maintenance, and weight change during lactation for all cows; 2) estimate REI for each animal and; 3) estimate the genetic parameters for REI.

5.3 MATERIALS AND METHODS

5.3.1 Data

An experiment involving five herds distributed across the US provided records on 247 cows distributed in four parity groups. Cows were identified by 127 sires and 226 dams. In each of the five herds, cows were assigned to three groups based on their projected production, which was determined by the average milk production during the first three weeks. Cows that produced less than 28 kg/day over the first 3 weeks were classified low producers, between 28 and 34 kg/day were medium and those over 34 kg were high. All heifers were in one group regardless of production. Total mixed rations were fed to all heifers and cows with varying forage to concentrate ratio according to production group and lactation. Ingredients for diets varied among location. In each case, however, energy provided was 10% more than the estimated cow's energy requirements according to NRC (1978).

Production data were recorded at regular intervals and included daily milk yield, biweekly measures of milkfat, protein, lactose and solids not fat. Feed intake was measured daily and included dry matter intake (DMI) in kilograms and intake of net energy (NEI). Additionally BW for each individual cow were taken throughout lactation according to the following protocol: four measurements the first month, one measurement every 2 months for the next 8 months and on each of days 300 and 301 of lactation. BW change for each cow during lactation was computed as the difference between the mean of the last 2 and last 4 BW measures. Based on the calving dates three seasons were identified as

October and November, December through February and March through October. There were 14 herd-season subclasses. The lactation length of each cow was at least 180 days. Tabulation of data is shown in Appendix II.

From each lactation average daily NEI, solids corrected milk (SCM) and $BW^{3/4}$, and weight change were used for analysis.

5.3.2 Model

The following model was used to partition net energy intake into energy requirements for production, maintenance, and BW during a lactation for all cows, to estimate REI for individual cows and to estimate genetic parameters for REI.

$$y_{ijk} = \mu + P_i + HS_j + b_1(SCM_{ijk}) + b_2(WC_{ijk}) + b_3(BW_{ijk}^{3/4}) + a_{ijk} + e_{ijk}$$

where:

- y_{ijk} was the average daily NEI of a cow in a lactation;
- μ was the overall mean;
- P_i was the fixed effect of parity with $i = 1, 2, 3, 4$;
- HS_j was the fixed effect of herd by season with $j = 1, 2, \dots, 14$;
- SCM_{ijk} was the average daily SCM production as a covariate;
- b_1 was the partial energy requirement for milk production;
- WC_{ijk} was weight change in a lactation as a covariate;
- b_2 was the partial energy requirement for weight change;
- $BW_{ijk}^{3/4}$ was the average metabolic body weight as a covariate;
- b_3 was the partial energy requirement for maintenance;
- a_{ijk} was the random animal effects with $N(0, I\sigma_a^2)$;
- e_{ijk} was the random residual with $N(0, I\sigma_e^2)$.

REI was the sum of animal and residual effects. Variance components estimates for animal and residual effects were estimated by the Restricted Maximum Likelihood (REML) utilizing the Expectation Maximization algorithm as described by Jensen and Mao (12). Convergence criterion was set at 10^{-5} for the residual variance. Appropriate relaxation factors were used to accelerate convergence.

5.4 RESULTS AND DISCUSSION

The mean, SE and CV for NEI, SCM, $BW^{3/4}$ and weight change are shown in Table 12. Weight change had the highest CV among cows and amongst all variables. Weight change varied substantially among cows. Some cows lost as much as 60 kg while other cows gained as much as 360 kg. Based on CV values, SCM, NEI and $BW^{3/4}$ each had a fair amount of variation among lactating cows.

Table 12. Simple statistics of variables used in analysis.

	Mean	SE	SD	CV%
NEI(Mcal)	29.06	0.23	3.64	12.52
SCM(kg)	23.04	0.24	3.74	16.22
$BW^{3/4}$ (kg)	123.73	0.61	9.57	7.74
Weight change(kg)	91.53	3.41	91.53	58.57

5.4.1 Partial energy requirements for SCM.

Partial regression coefficient for NEI on production (SCM) was 0.54 (Table 13). This value represent the partial energy requirements

for SCM. Using the same data Walter and Mao (1989) estimated partial energy requirement for each of the 357 cows using within cow regression models. The average requirement for SCM of all cows from a two stage regression model was 0.34 Mcal/kg an estimate that is slightly lower than ours. Differences in models used in the two studies would contribute to the discrepancy. However, both estimates were below the values published by Moe et al. (1971). They estimated values of 1.54, 1.64 and 1.85 Mcal/kg of SCM with diets containing 50%, 75% and 100% of estimated net energy from roughages respectively.

Efficiency of net energy utilization for production depends on a number of factors. Moe et al (1971) asserted that the amount of energy required by a lactating cow depends upon the genetic potential of the cow and the level of production desired. Davey et al. (1983) pointed out that animals of high genetic merit for production partition energy differently than those of low genetic merit. Likewise, Custodio et al. (1983) found that increased production of FCM corresponds with increased efficiency for FCM with a high significant residual correlation of .75 for the two traits. Hashizume et al. (1965) substantiated the effect of quality and quantity of ration in influencing efficiency of utilization of energy for milk production. Greater energetic efficiency was observed in lactating cows fed high levels of concentrate than those fed low. Quantity of ration also affects energy efficiency of milk production.

5.4.2 Maintenance Energy Requirements.

Partial net energy requirements for maintenance was estimated to be 0.15 Mcal/kg. Again Walter and Mao (1989) estimated the same value

from a within cow two-stage regression model. Both estimates were below the estimates of the NRC (1989) guidelines of 0.073 Mca/kg and some of the estimates published earlier (Moe et al., 1970, 1971, Moe, 1981, Walter and Mao, 1989). The differences in maintenance requirement between lactating cows can be due to a number of causes. Garret and Johnson (1983), demonstrated the importance of diet and physiological state on maintenance requirements. Because of the close relationship between diet, physiological state and energy balance one might expect the latter to affect maintenance requirements as well. Pregnancy may increase maintenance requirements of lactating cows as reported by Flatt et al (1969a).

5.4.3 Energy requirements for weight change

Partial energy requirements for weight change was 1.51 Mcal/kg (Table 13). Our value was lower than 1.92 Mcal/kg an estimate obtained by Walter and Mao (1989). The differences between the two was small but again could be due to the different models. Moe et al (1970) obtained a value of 1.24 Mcal/kg for weight change gain.

The basis of weight change during lactation is due to the metabolism and catabolism of tissue in support of lactation. Mobilization of body tissue occurs in most cows during peak periods of lactation. Some cows are capable of utilizing remarkable quantities of body tissue for lactation during such periods of negative energy balance. To re-establish itself to the same condition as at parturition, the animal must eat more for body energy deposition either during late lactation or during the dry period.

Table 13. Partial net energy requirements for weight change (WC), maintenance ($BW^{3/4}$) and SCM

WC(Mcal/kg)	1.51
$BW^{3/4}$ (Mcal/kg)	0.15
SCM(Mcal/kg)	0.54

5.4.4 Residual Energy Intake

For residual energy intake (REI), the estimated phenotypic SD was 2.455, additive genetic SD was .315 and heritability was a low value of .016 (Table 14). Literature has reported no results on REI on lactating cows. However, in laying hens, Luiting (1987) reported a heritability estimate of .25 and in growing young bulls heritability was reported to be 0.28 (Koch et al., 1963, Jensen, 1989).

The proportion of the phenotypic SD due to REI was a high 68%. This in conjunction with a low heritability value reflects that the variation in REI of lactating cows may be largely due to environment.

Table 14. Estimates of additive genetic and phenotypic standard deviation and heritability values for REI

Additive SD	0.315
Phenotypic SD	2.455
Heritability	0.016
REI(SD)/NEI(SD)	0.675

5.3 CONCLUSIONS

For the lactating cows, weight change had the highest net energy requirement as compared to milk production (SCM) and maintenance on a per unit basis. The high energy requirements for weight change in lactating cows are mainly due to the high energy demands in late lactation to cater for the tissue energy drain that occurs during negative energy balance. However, on total production basis more energy would still be needed for milk production. The partial net energy requirement for SCM was lower as compared to literature values. The estimate for maintenance was equal to that from a within cow regression model used by Walter and Mao (1989).

The heritability value of REI was only .016. Selection for REI in lactating cows would therefore not be fruitful. The proportion of the phenotypic standard deviation due to REI was a high 68 %. This together with a low heritability for REI indicates that variation in REI in lactating cows is due to causes other than additive genetic effects.

6. SUMMARY

The total intake of metabolizable energy can be partitioned into productive and nonproductive (maintenance) use of energy. These are collectively known as the partial energy requirements. The remaining energy after accounting for all the identifiable partial energy requirements is called residual energy intake (REI). Therefore, a small residual energy intake or a greater proportion of energy that can be accounted for, would imply greater efficiency.

6.1 Growing Young Bulls

Partial energy requirements for growth and maintenance, and residual energy intake were estimated for 650 bull calves from 31 Holstein-Friesian or Brown Swiss sires. Computation of partial energy requirements and residual energy intake using an animal model was based on average daily records in a production period for each young bull on body weights and net energy intake.

Partitioning of energy intake showed that a greater proportion of net energy intake was used to meet the requirements for growth as compared to maintenance. However, energy requirements for growth are more related to composition of gain.

REI was computed as sum of animal effects of sires and bulls and error effects. The heritability value of REI low. The proportion of the phenotypic SD due to total net energy intake was relatively small. These results indicate the lack of additive genetic effects on the variation of REI among bulls.

6.2 Lactating Cows

Data from Lilly Research Laboratories was used to estimate partial energy requirements for production of solids corrected milk, maintenance and weight change for lactating Holstein cows. The data consisted of measurements on milk production, component percentages, body weights and intake through complete lactations of 247 cows in 4 parity groups and from 127 sires and 226 dams distributed across five herds. Cows were fed one of four rations determined by production level. An animal model allowed partitioning of net energy intake into partial energy requirements for production, maintenance, and weight change and computation of REI for each animal as sum of cow, sire, dam and error effects when average daily NEI was used as dependent variable.

Results indicated that more energy calculated as Mcal/kg was required for weight change in a lactation as compared to requirements for SCM production or maintenance. Partitioning of net energy by lactating cows is however dependent on a number of factors such as amount and quality of ration and the physiological status of the animal.

REI had a very low heritability value, but the proportion of the phenotypic SD of NEI due to REI was high. As such variation in REI among lactating cows is largely due to environmental effects such as season or management. Incorporation of REI as a measure of productive efficiency for lactating cows may therefore not be fruitful.

In conclusion, this study examined REI which is a measure of net energy efficiency. However, the relationship between gross energy

efficiency and net energy efficiency is unknown. If these two traits are strongly and positively correlated then use of gross energy efficiency would be recommended.

7. APPENDICES

Appendix I.

Energy content of diets and tabulation
of data for Growing young bulls.Table I.1. Energy composition (mJ/kg) of the four diets used during
the entire experiment

Year	Treatment ^a	Energy content(mJ/KG)
1978	1	6.07
	2	2.70
	3	1.74
	4	1.29
1979	1	6.08
	2	3.60
	3	2.60
	4	2.03
1980	1	6.14
	2	5.70
	3	5.19
	4	4.76
1981	1	6.24
	2	5.64
	3	4.76
	4	4.76
1982	1	6.32
	2	5.05
	3	4.99
	4	4.20

^aTreatments 1,2 3, 4 = 100%, 75%, 50%, 25% of expected energy from concentrates.

Table I.2. Distribution of the records across the years and treatments.

Year	Treatment ^a				Total
	1	2	3	4	
1978	382	489	519	490	1880
1979	464	414	484	557	1919
1980	426	471	580	510	1987
1981	607	854	218	234	1913
1982	518	541	529	511	2099
Total					9798

^aTreatments 1,2,3,4 = 100%, 75%, 50%, 25% expected energy from concentrates, respectively.

Table I.3. Basic Statistics of net energy intake (NEI), daily gain (DG), body weight (BW), and metabolic weight ($BW^{3/4}$) for different year-treatment classes

	Year	Treatment ^a	Mean	SD	CV
NEI	1978	1	700.23	142.90	20.41
DG		1	1245.14	640.54	51.44
BW		1	367.11	108.26	29.50
$BW^{3/4}$		1	83.19	18.45	22.80
NEI		2	679.40	143.15	18.13
DG		2	1240.43	523.23	42.18
BW		2	363.75	100.84	27.72
$BW^{3/4}$		2	82.70	17.21	20.81
NEI		3	619.55	107.43	17.34
DG		3	1228.05	442.38	36.02
BW		3	369.98	103.45	27.96
$BW^{3/4}$		3	83.75	17.59	21.01
NEI	1979	4	542.86	100.15	18.45
DG		4	1135.05	455.11	40.09
BW		4	361.84	99.49	27.49
$BW^{3/4}$		4	82.39	16.95	20.57
NEI		1	705.46	168.43	23.88
DG		1	1320.04	612.92	46.43
BW		1	369.81	110.08	29.76
$BW^{3/4}$		1	83.64	18.72	22.39
NEI		2	700.76	153.28	33.95
DG		2	1256.73	469.51	37.86
BW		2	359.21	99.23	20.62
$BW^{3/4}$		2	81.93	16.16	20.69
NEI	1979	3	642.38	147.64	22.98
DG		3	1246.46	423.11	33.95
BW		3	366.44	105.99	28.92
$BW^{3/4}$		3	83.11	18.06	21.73
NEI		4	574.45	128.73	22.41
DG		4	1143.24	407.87	35.68
BW		4	363.69	104.39	28.70
$BW^{3/4}$		4	82.65	17.78	21.51

Table I.3 (Cont'd.)

	Year	Treatment ^a	Mean	SD	CV
NEI	1980	1	713.32	161.85	22.69
DG		1	1293.43	557.57	43.11
BW		1	371.05	107.50	28.92
BW ^{3/4}		1	83.88	18.31	21.83
NEI		2	963.37	206.87	21.47
DG		2	1269.34	505.93	39.86
BW		2	370.18	103.81	28.04
BW ^{3/4}		2	83.78	17.68	21.10
NEI		3	929.42	205.91	22.16
DG		3	1134.36	481.92	42.50
BW		3	372.45	102.90	27.63
BW ^{3/4}		3	84.18	17.52	20.81
NEI		4	850.32	187.99	22.11
DG		4	1026.05	512.27	49.93
BW		4	372.04	102.52	27.56
BW ^{3/4}		4	84.11	17.46	20.76
NEI	1981	1	900.06	158.39	17.60
DG		1	1314.43	536.99	40.84
BW		1	365.49	104.76	28.66
BW ^{3/4}		1	82.96	17.85	21.52
NEI		2	809.77	144.72	17.87
DG		2	1020.74	490.32	48.04
BW		2	370.47	103.77	27.85
BW ^{3/4}		2	83.83	17.57	20.96
NEI		3	947.34	162.09	17.11
DG		3	1313.56	557.34	42.43
BW		3	357.79	103.34	27.50
BW ^{3/4}		3	84.75	17.54	20.69
NEI		4	817.78	136.41	16.68
DG		4	1033.36	45.78	43.81
BW		4	367.28	96.91	26.39
BW ^{3/4}		4	83.36	16.50	19.79
NEI	1982	1	720.36	138.53	19.23
DG		1	1219.80	562.86	46.14
BW		1	372.15	107.25	28.82
BW ^{3/4}		1	84.08	18.22	21.68

Table I.3 (Cont'd.)

	Year	Treatment ^a	Mean	SD	CV
NEI	1982	2	747.40	183.97	23.58
DG		2	1152.49	433.04	37.58
BW		2	364.58	104.18	28.58
BW ^{3/4}		2	82.81	17.77	21.36
NEI		3	780.39	183.97	23.59
DG		3	1199.43	469.02	39.10
BW		3	362.42	107.79	29.74
BW ^{3/4}		3	82.39	18.32	22.24
NEI		4	730.39	172.29	23.59
DG		4	1261.53	438.09	34.73
BW		4	363.92	107.74	29.61
BW ^{3/4}		4	82.65	18.33	22.18

^aTreatments 1,2,3,4 = 100%, 75%, 50%, 25% expected energy from concentrates, respectively.

Table I.4. Estimates of Year by Treatments subclasses

Year	Treatment	Estimate	SE
1978	1	-1.99	1.61
1978	2	-3.36	1.60
1978	3	-7.86	1.60
1978	4	-11.96	1.56
1979	1	-2.00	1.63
1979	2	-1.86	1.61
1979	3	-6.37	1.60
1979	4	-9.86	1.57
1980	1	-2.17	1.60
1980	2	15.70	1.61
1980	3	13.68	1.57
1980	4	9.48	1.55
1981	1	12.53	1.62
1981	2	7.79	1.54
1981	3	14.13	1.67
1981	4	7.75	1.60
1982	1	0.98	1.65
1982	2	3.31	1.63
1982	3	4.81	1.63
1982	4	0.78	1.65

Table I.5. Estimates of Initial age of young bulls at beginning of experiment

Age (days)	Estimate	SE
140	-3.17	1.59
154	-2.67	1.31
168	-3.20	1.25
182	-2.15	1.21
196	-1.49	1.20
210	-1.30	1.19
224	-1.08	1.19
238	-0.97	1.21
252	1.14	1.27
266	-3.51	1.42
280	0.49	1.74
294	0.00	0.00

Appendix II

GROWING YOUNG BULLS: Sire model and results from the model

Model

$$y_{ijklmn} = \mu + T_i + A_j + H_k + b_1(DG_{ijklmn}) + b_2(BW_{ijklmn}^{3/4}) + S_l + B(1)_m + e_{ijklmn}$$

where:

y_{ijklmn} was total net energy intake in a 2-wk period

μ was the overall mean;

T_i was the fixed effect of the i th year treatment with $i = 1, 2, \dots, 20$;

A_j was the fixed effect of the j th age group with $j = 1, 2, \dots, 37$;

H_k was the fixed effect of the k th breed with $k = 1, 2$;

DG_{ijklmn} was the average daily gain of the m th bull in the corresponding 2-wk period of y_{ijklmn} ;

b_1 was the partial energy requirement for growth;

$BW_{ijklmn}^{3/4}$ was the average metabolic body weight of the m th bull in the corresponding 2-wk period of y_{ijklmn} ;

b_2 was the partial energy requirement for maintenance;

S_l was the random animal effects of sires with $l = 1, 2, \dots, 31$ and $N(0, I\sigma_s^2)$

e_{ijklmn} was the random residual with $N(0, I\sigma_e^2)$

Table II.1. Basic Statistics of the variables analyzed by a sire model

	Mean	SE	SD	CV
NEI (mJ)	751.71	1.96	194.90	25.93
DG (kg)	1.20	0.01	0.51	42.13
BW ^{3/4} (kg)	83.29	0.18	17.77	21.34

Table II.2. Partial net energy requirements for growth and maintenance.

DG (mJ/Kg/day)	29.00
BW ^{3/4} (mJ/Kg ^{3/4})	0.79

Table II.3. Estimates of additive genetic and phenotypic SD and heritability values for REI.

Additive SD	4.09
Phenotypic SD	19.32
SD(REI)/SD(NEI)	.42
Heritability	.05

Appendix III.

Tabulation of data for Lactating Cows

Table III.1. Distribution of cows in different parities

	Parity			
	1	2	3	4
No. of cows	66	58	49	74

Table III.2. Number of cows in different herd season subclasses

Herd	Season	No. of cows
1	1	25
1	2	10
2	1	27
2	2	26
2	3	5
3	1	19
3	2	20
3	3	17
4	1	36
4	2	17
4	3	4
5	1	13
5	2	16
5	3	12

Herds: 1 - California
 2 - Michigan State University
 3 - North Carolina State
 4 - Penn. State
 5 - Illinois

Season: 1 - March-Sept.
 2 - Oct.-Nov
 3 - Dec.-Feb.

Table III.3. Simple statistics of variables used in the analysis by parity

	Parity	N	Mean	SE	SD	CV%.
NEI(Mcal)	1	66	28.96	0.49	3.96	13.69
SCM(kg)	1	66	22.54	0.42	3.41	15.15
BW ^{3/4} (kg)	1	66	124.97	1.08	8.80	7.04
Weight change	1	66	48.31	5.95	48.30	46.48
NEI(Mcal)	2	58	29.03	0.52	4.00	13.78
SCM(kg)	2	58	22.73	0.51	3.93	17.30
BW ^{3/4} (kg)	2	58	123.76	1.24	9.49	7.67
Weight change	2	58	88.46	6.72	51.20	57.89
NEI(Mcal)	3	49	28.92	0.47	3.29	11.39
SCM(kg)	3	49	23.01	0.57	4.02	17.49
BW ^{3/4} (kg)	3	49	121.52	1.34	9.41	7.74
Weight change(kg)	3	49	81.78	6.98	48.84	59.71
NEI(Mcal)	4	74	29.25	0.39	3.31	11.33
SCM(kg)	4	74	23.73	0.42	3.63	15.30
BW ^{3/4} (kg)	4	74	124.05	1.20	10.31	8.31
Weight change(kg)	4	74	89.23	7.14	61.46	68.81

NEI - Net energy intake

Table III.4. Estimates of the fixed effect of parity

Parity	Estimate	SE
1	0.70	0.51
2	0.84	0.51
3	0.94	0.54
4	0.00	0.00

Table III.5. Estimates of the herd year-season subclasses

Herd	Season	Estimate	SE
1	1	-0.57	0.89
1	2	0.62	1.06
2	1	-2.32	0.86
2	2	-1.67	0.86
2	3	-1.52	1.34
3	1	-0.25	0.94
3	2	1.72	0.93
3	3	0.72	1.02
4	1	-4.17	0.89
4	2	-2.67	0.97
4	3	-2.21	1.50
5	1	-1.09	1.02
5	2	-1.28	0.98
5	3	0.00	0.00

Herds: 1 - California	Season: 1 - March-Sept.
2 - Michigan State University	2 - Oct.-Nov
3 - North Carolina State	3 - Dec.-Feb.
4 - Penn. State	
5 - Illinois	

LIST OF REFERENCES

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- Andersen, H.R. 1980. Feeding Trials describing Net requirements for maintenance as dependent on weight, feeding level, sex and genotype. *Ann. Zootech.* 29:85.
- Andersen, H.R. and K.L. Ingavarlsen. 1984. Influence of energy level, weight at slaughter and castration on carcass quality in cattle. *Livest. Prod.* 11:571.
- Bauman, D.E., and W.B. Currie. 1980. Partitioning of nutrients during pregnancy and lactation. A review of mechanisms involving homeostasis and homeorhesis. *J. Dairy Sci.* 63:1514.
- Bauman, D.E., S.N. McCutcheon, W.D. Stanhour, P.J. Eppard and S.J. Sechen. 1984. Sources of variation and prospects for improvement of productive efficiency in the dairy cow: A review. *J. Dairy Sci.* 60:583.
- Blake, R.W. and A.A. Custodio 1984. Feed efficiency: A composite trait of Dairy cattle. *J. Dairy Sci.* 67:2075.
- Blaxter, K.L. and F.W. Wainman. 1976. The fasting metabolism of cattle. *Brit. J. Nutr.* 20:103.
- Brelín, B. and E. Brannang. 1982. Phenotypic and genetic variation in efficiency of growing cattle and their relationship with growth rate, carcass traits and metabolic efficiency. *Swedish J. Agric. Res.* 12:29.
- Brelín, B. and K. Martinsson. 1986. Variation in the efficiency of energy metabolism of individually fed young bulls. *Swedish J. Agric. Res.* 16:89.
- Brooster, W.H., J. Valerie, J.; V.J. Brooster, T. Smith and J.W. Siviter. 1975. Experiments on the nutrition of the dairy heifer. 9. Food utilization in lactation. *J. Agric. Sci. Camb.* 84:173.
- Buttazzoni, L. and I.L. Mao. 1988. Genetic parameters of estimated net energy efficiencies for milk production, maintenance and body weight. *J. Dairy Sci.* 72:671.
- Byers, F.M. Patterns and energetic efficiency of tissue growth in beef cattle of four breeds. In: *Energy metab. Farm. Anim. Eur. Assoc. Anim. Prod.* 29:92.

- Byers, F. M. and R.E. Rompala. 1980. Level of energy effects on patterns of energetic efficiency of tissue deposition in small or large mature size beef cattle In: Laurence E. Mount (ED). Energy Met. Farm Anim. Eur. Assoc. Anim. Prod. 26:141
- Chestnutt, D.M.B., R. Marsh, J.G. Wilson, T.A. McCullough and T. McCullough. 1975. Effects of breed of cattle on energy requirements for growth. Anim. Prod. 21:199
- Close, W.H. 1978. The effects of plane of nutrition and environmental temperature on energy metabolism of the growing pig. The effect of energy utilization for maintenance and growth. Brit. J. Nutr. 40:433.
- Coppock, C.E., W.P. Flatt and L.A. Moore. 1964. Effect of hay to grain ratio on utilization of metabolizable energy for milk production by dairy cows. J. Dairy Sci. 47:1330.
- Custodio, A.A., R.W. Blake, P.F. Dahm, T.C. Cartwright, G.T. Schelling and C.E. Coppock. 1983. Relationship between measures of feed efficiency and transmitting ability for milk of Holstein cows. J. Dairy Sci. 66:1937.
- Davey, A.W.F., C. Grainger, D.D.S. Mackenzie, D.S. Flux, G.F. Wilson, I.L. Brookes and C.W. Holmes. 1983. Nutritional and physiological studies of differences between Friesian cows of high or low genetic merit. Proc. New Zealand Soc. Anim. Prod. 43:67.
- Ferrel, C.L., W.N. Garrett, N. Hinman and G. Gritching. 1976. Energy utilization by pregnant and nonpregnant heifers. J. Anim. Sci. 58:234.
- Ferrel, C.L., J.D. Crouse and R.A. Field. 1979. Effect of sex, diet, and stage of growth upon energy utilization by lambs. J. Anim. Sci. 49:790.
- Ferrel, C.L. and T.G. Jenkins. 1985. Cow type and the nutritional environment: Nutritional aspects. J. Anim. Sci. 61:725.
- Flatt, W.P., P.W. Moe and L.A. Moore. 1969a. Influence of pregnancy and ration composition on energy utilization by dairy cattle. In: Energy Met. Farm Anim. EAAP. Pub. 12:123.
- Flatt, W.P., P.W. Moe, A.W. Munson and T. Cooper. 1970. Energy utilization by high producing dairy cows. II. Summary of energy balance experiments with lactating Holstein Cows. Energy. Met. Farm. Anim. Eur. Assoc. Anim. Prod. Pub. 13:89.

- Frisch, J.E. and J.E. Vercoe. 1977. Food intake eating rate, weight gains, metabolic rates and efficiency of feed utilization in *Bos Taurus* and *Bos Indicus* crossbred cattle. *Anim. Prod.* 25:343.
- Garret, W.N. 1969. Energetic efficiency of beef and dairy steers. *J. Anim. Sci.* 32:5.
- Garrett, W.N. 1971. Energetic efficiency of beef and dairy steers. *J. Anim. Sci.* 32:451.
- Garret, W.N. 1980. Energy utilization by growing cattle as determined in 72 comparative slaughter experiments. In: Laurence E. Mount (ED). *Energy Met. Farm Anim. Eur. Assoc. Anim. Prod.* 26:3.
- Garrett, W.N. and D.E. Johnson. 1983. Nutritional energetics of ruminants. *J. Anim. Sci.* 57:478.
- Geay, Y., J. Robelin and M. Vermorel. 1980. Influence of the metabolizable energy content of the diet on energy utilization for growth in bulls. In: Laurence E. Mount (ED). *Energy Met. Farm Anim. Eur. Assoc. Anim. Prod.* 26:9.
- Geay, Y. 1984. Energy and protein utilization in growing cattle. *J. Anim. Sci.* 58:766.
- Graham, N.McC. 1967. The metabolic rate of fasting in sheep in relation to total lean body weight and the estimation of maintenance requirements. *Austr. J. Agric. Res.* 18:127.
- Graham, N.McC., T.W. Searle and D.A. Griffiths. 1974. Basal metabolic rate in lambs and young sheep. *Austr. J. Agric Res.* 25:757.
- Gravert, H.O. 1985. Genetic factors controlling feed efficiency in dairy cows. *Livest. Prod.* 12:87.
- Grieve, D.G.; G.K. Macleod, T.R. Batra; E.B. Burnside and J.B. Stone. 1976. Relationship of feed intake and ration digestibility to estimated transmitting ability, body weight and efficiency in first lactation. *J. Dairy Sci.* 59:1312.
- Hashizume, T.H., H. Morimoto, T. Masubuchi, M. Abe and T. Hamada. 1965. Some aspects of energy utilization by cows during gestation and lactation. In: *Energy metabolism of Farm animals. EAAP. Pub.* 11:1409.
- Hickman, C.G. and D.M. Bowden. 1971. Correlated genetic responses of feed efficiency, growth and body size in cattle selected for milk solids yield. *J. dairy Sci.* 54:1848.

- Hooven, N.W. Jr., R.H. Miller and J.W. Smith. 1972. Relationships among whole and part lactation gross feed efficiency, feed consumption and milk yield. *J. Dairy Sci.* 55:1113.
- Jakobsen, P.E.; P.H. Sorensen and H. Larsen. 1957. Energy investigation as related to fetus formation in cattle. *Acta. Agric. Scand.* 7:103.
- Jensen, J. and I.L. Mao. 1988. Transformation algorithms in analysis of single trait and of multitrait models with equal design matrices and one random factor per trait. A review. *J. Anim. Sci.* 66:2750.
- Jensen, J. 1989. Genetic assessment of biological merit in cattle. Ph.D. Thesis. Michigan State University, East Lansing.
- Karlsson, U. 1979. Correlated responses of selection for growth rate in Swedish Dual Purpose cattle breeds. *Acta. Agric. Scand.* 29:295.
- Kielanowski, J. 1976. Energy cost of protein deposition. In D.J.A Cole, K.N. Boorman, P.J. Buttery, D. Lewis, R.L. Neale and H. Swan (ED). Protein metabolism and nutrition. *Eur. Assoc. Anim. Prod. Pub* 16:207.
- Klosterman, E.W., L.G. Sanford and C.F. Parker. 1976. Effect of size, and condition and ration protein content upon maintenance requirements of mature beef cattle. *J. Anim. Sci.* 27:242.
- Koch, R.M., L.A. Swiger, D. Chambers and K.E. Gregory. 1963. Efficiency of feed use in beef cattle. *J. Anim. Sci.* 22:486.
- Korver, S., H. Vos and J.H.J. van der Werf. 1987. Performance test results of young Bulls in relation to feed intake and efficiency of female progeny. *Eur. Assoc. Anim. Prod. Pub.* 34:93.
- Korver, S. 1988. Genetic aspects of feed intake and feed efficiency in dairy cattle. A review. *Livest. Prod. Sc.* 20:1.
- Kronfeld, D.S.; S. Donoghue; J.M. Naylor; K. Johnson, C.A. Bradley. 1980. Metabolic effects of feeding protected tallow to dairy cows. *J. Dairy Sci.* 63:545.
- Lamb, R.C., J.L. Walter, M.J. Andersen, R.D. Plowman, C.H. Mickelsen and R.H. Miller. 1977. Effect of sire and interaction of sire with ration on efficiency of feed utilization by Holsteins. *J. Dairy Sci.* 60:1755.
- Luiting, P. 1987. Genetic variation of energy metabolism in poultry. In: M.W.A Verstegen and A.M. Henken (ED), *Energy Met. Farm Anim.* 446.

- Mason, I.L., A. Robertson and B.Gjeslstand. 1957. The genetic connection between body size, milk production and efficiency in dairy cattle. *J. Dairy Res.* 24:135.
- Menke, K.H. 1980. system for prediction of retention of protein and fat in growing animals. In: Laurence E. Mount (ED). *Energy Met. Farm Anim. Eur. Assoc. Anim. Prod.* 26:175.
- Meyer, J.H., W.N. Garret. 1967. Efficiency of feed utilization. *J. Anim. Sci.* 26:638.
- Milligan, L.P. and M. Summers. 1986. The biological basis of maintenance and its relevance to assessing responses to nutrients. *Proc. Nutr. Soc.* 45:185
- Moe, P.W., H.F. Tyrell and W.P. Flatt, 1970. Partial Efficiency of energy use for maintenance, lactation, body gain and gestation in the dairy cow. *Proc. 5th. Symp. Energy Met. Farm Anim. EAAP. Pub.* 13:65.
- Moe, P.W., H.F. Tyrell and W.P. Flatt, 1971. Energetics of Body tissue mobilization. *J. Dairy Sci.* 54:548.
- Moe, P.W. 1981. Energy metabolism of dairy cattle. *J. Dairy Sci.* 64:1120.
- National Research Council. 1989. Nutrient requirements for dairy cattle. 6th. rev. ed. Natl. Acad. Press. Washington DC.
- Oldenbroek, J.K. 1984. Holstein Friesian, Dutch Friesians, and Dutch Red and Whites on two complete diets with a different amount of roughage: Performance in first lactation. *Livest. Prod. Sci.* 11:401.
- Oldenbrook, J.K. 1986. The performance of Jersey heifers and heifers of larger dairy breeds on two complete diets with different roughage contents. *Livest. Prod. Sci.* 14:1.
- Orskov, E.R. and I. McDonald. 1970. The utilization of dietary energy for maintenance and for fat and protein deposition in young growing sheep. *Eur. Assoc. Anim. Prod. Pub.* 13:121.
- Pullar, J.D. and A.J.F. Webster. 1977. The energy costs of protein and fat deposition in the rat. *Br. J. Nutr.* 37:355.
- Rattray, P.V., W.N. Garret, N.E. East and N. Hinman. 1974. Efficiency of utilization of metabolizable energy during pregnancy and the energy requirements for pregnancy in sheep. *J. Anim. Sci.* 38:383.
- Reid, J.T. and J. Robb. Relationship of body composition to energy intake and energetic efficiency. *J. Dairy Sci.* 54:553

- Richardson, D.O., O.J.R. R.D. Plowman; and J.T Miles. 1971. Importance of sire by ration interactions in production and feed intake traits of dairy cattle. *J. Dairy Sci.* 54:1518.
- Russel, A.J.F. and J.A. Wright. 1983. Factors affecting maintenance requirements of beef cows. *Anim. Prod.* 37:329.
- Tess, M.W., G.E. Dickerson, J.A. Nienaber and C.L. Ferrel. 1984a. The effects of body composition on fasting heat production in pigs. *J. Anim. Sci.* 58:99.
- Thorbek, G. 1977. The energetics of protein deposition during growth. *Nutr. Metab.* 21:105.
- Trigg, T.E. and C.W. Parr. 1981. Aspects of energy metabolism of Jersey cows differing in breeding index. *Proc. New Zealand Soc. Anim. Prod.* 41:44.
- Trustcott, T.G., J.D. Wood, N.G. Gregory and I.C Hart. 1983. Fat deposition in hereford and Friesian Steers. 3. Growth efficiency and fat mobilization. *J. Agric Sci. (Camb.)* 100:277.
- Tyrell, H.F. and J.T. Reid. 1965. Prediction of the energy value of cow's milk. *J. Dairy Sci.* 58:1215.
- Tyrell, H.F. P.W. Moe and R.R. Oltjen. 1974. Energetics of growth and fattening compared to lactation in cattle. In: *Energy Metab. Farm Anim. Eur. Assoc. Anim. Prod. Pub.* 26:227.
- Tyrell, H. F. and P.W. Moe. 1980. Energetics of growth in cattle. In: *Energy Metab. Farm Anim. Eur. Assoc. Anim. Prod. Pub.* 26:227.
- Van Es, A.J.H. and H.J. Nijkamp. 1969. Energy, carbon and nitrogen balance experiments with lactating cows. *Proc. 4th Symp. Energy Metab. Eur. Assoc. Anim. Prod. PUB.* 12:209.
- Verco, J.E. 1970. Fasting metabolism and heat increment of feeding in Brahman by British and cross cattle. in : *Energy Metab. Farm Anim. Eur. Assoc. Anim. Prod.* 13:85.
- Vermorel, M., J.C. Bouvier and Y. Geay. 1976. The effect of type (normal and double muscled Charolais and Friesian) on energy utilization by growing cattle at 2 and 16 months of age. In: *Energy metab. Farm Anim. Eur. Assoc. Anim. Prod.* 19:217.
- Walter, P.W., I.L. Mao. 1989. Modeling Net energy efficiencies as quantitative characteristics in lactating cows. *J. Dairy Sci.* 72:671.

- Walter, P.W. 1986. Determining parameters of energy in dairy cattle using data from production herds. Ph.D. Thesis. Michigan State University. 122p.
- Warwick, E.J. and E.H. Cobb. 1976. Genetic variation in nutrition of cattle for meat production. World Review Anim. Prod. 12:1.
- Webster, A.J.F. 1980. The energetic efficiency of growth. Livest. Prod. Sci. 7:243.
- Weil, W.B. 1962. Adjustment for size- a possible misuse of ratios. Am. J. Clin. Nutr. 11:249.

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