128
183
THS

MICHIGAN STATE UNIVERSITY LIBRARIES
3 1293 01070 2318

LIBRARY
Michigan State
University

This is to certify that the

dissertation entitled

DETERMINING PARAMETERS OF
ENERGY UTILIZATION IN
DAIRY CATTLE USING DATA
FROM PRODUCTION HERDS

presented by

John P. Walter

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Animal Science

Major professor

Date April 7, 1986

MSU
LIBRARIES

RETURNING MATERIALS:
Place in book drop to
remove this checkout from
your record. FINES will
be charged if book is
returned after the date
stamped below.

[illegible]

DETERMINING PARAMETERS OF ENERGY UTILIZATION IN DAIRY CATTLE USING DATA FROM PRODUCTION HERDS

by

John P. Walter

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Animal Science

1986

ABSTRACT

DETERMINING PARAMETERS OF ENERGY UTILIZATION IN DAIRY CATTLE USING DATA FROM PRODUCTION HERDS

by

John P. Walter

Data from 354 Holstein cows in 7 herds, on 4 rations based on production level, and in various parities were used to estimate the efficiency of energy conversion for maintenance, lactation, body weight change and pregnancy. In an attempt to reduce the need for expensive balance trials and scarce energy chambers, lactating cows from herds in production were studied, and various indicators of energy efficiency compared to published reports from animals in energy chambers. For each cow, the fractions of energy apportioned to various products were computed over the entire lactation and during periods of positive and negative energy balance. Over 90% of energy required during a lactation was for maintenance or lactation. Proportions of net energy and metabolizable energy intake used for milk production were higher during negative balance than positive, while expenditures for maintenance were comparable. Data were adjusted to account for the delay in energy absorption from feed intake, the amount of residual milk at each milking, and the infrequency of body weights, and eighteen regression models were applied. Among the models fitted were ordinary and two-stage multiple regression models, and models accounting for autocorrelated residuals. Results indicated that efficiencies during positive energy balance were more easily and accurately estimated than efficiencies during negative balance. Multiple regression models were consistently found to overestimate maintenance and underestimate lactation requirements. A two-stage model provided estimates closest to those reported in the literature which were obtained from animals in energy chambers. Models considering autocorrelation of residuals were found to better fit daily variations in energy intake, but overall were not an improvement over the two-stage model. Factors influencing variation among animals of estimates for four models were examined. Herd-season effect was determined to be most significant in affecting coefficients of energy efficiency. Ration, parity, and linear and quadratic covariates of total milk production over the lactation were generally not significant.

ACKNOWLEDGMENTS

I'd like to thank my committee for their guidance and support during my graduate program: Dr. Ivan Mao, Dr. Ted Ferris, Dr. Roy Emery and Dr. Roy Black. Throughout my program Dr. Mao has been a patient and wise advisor, but just as much a friend, confidante and sports teammate. His entire family has been as my own from the moment I arrived, and I'll always remember their kindness.

So many good friends have encouraged me over the past four years... in particular, Dennis Banks, Ted Ferris, John Gill, Clyde Anderson, William Enright and Denis Petitclerc have all made me listen, made me think, and made me smile. My experience has certainly been richer for their friendship.

My family, Mom and Dad, and Mary Pat, Mary Jo, Michelle, Chuck, Tom, Chris, Polli, Carrie and Matt, Lib and Lou, and Paul and Tom have shown more patience than I could have imagined possible. There is much of them in everything I do.

Luca Buttazzoni has made numerous suggestions concerning this research. To him for his thoughtful advice, and to the Eli Lilly company for supplying the data which made this investigation possible, I offer heartfelt thanks.

And finally, thank you Diane, for the warmth of your love and understanding, and for the smile that brought a little sunshine to every day.

A.M.G.D.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

I. INTRODUCTION

For the past several decades, there has been increasing interest in the study of animal energetics. Among many possible reasons for the increase, two are primary:

(1) Rapid advances in the fields of physiology, nutrition, microbiology and systems science, among others, have enabled scientists to focus as never before on cellular and tissue function within the animal; and

(2) Economic pressures have forced the animal industries to consider efficiency of production as an important factor influencing profit and to seek ways to improve that efficiency.

However, despite these developments, the study of energetic efficiency is not without its difficulties. When energy chambers are used to monitor all energy transactions in domestic livestock, the high cost per animal prevents a large number from being studied at once. Also, because the field is still rather young and because there is still an incomplete understanding of the pathways and mechanics of energy metabolism, many plausible models have been advanced through the literature. In the case of dairy cattle, there exist at least three economically important production functions: growth, reproduction and lactation. The latter function is compounded by milk component percentages (especially butterfat and protein) which have economic significance. Many different models to explain the relationship among these systems have been published, making the choice of an appropriate model for study a difficult one. Finally, the interactions of physiology, nutrition, genetics and other areas within many models can require cooperation among researchers with expertise in diverse fields. Such teamwork may be difficult to motivate and maintain.

This study has been a first step in developing methods by which geneticists and other scientists wishing to study efficiency can analyze large bodies of energetics data. As such, it has proceeded in an exploratory manner and early results exerted an influence on later decisions. The main objective during this research was to investigate various statistical models relating energy input to output in lactating dairy cows. These models were applied to data which was not collected from animals in energy chambers, but from cows kept under field conditions at several locations throughout the country.

The purpose of this research was to develop and examine a variety of potential models for estimating efficiencies of energy utilization from data collected on a farm rather than from energy chambers. Guiding the judgement of the relative value of various models we tested were these concerns:

(1) The model should suggest a meaningful biological interpretation. It should consider those characteristics which have been shown to influence energy utilization, rather than utilize complex statistical procedures whose relationship to energy metabolism pathways is unclear.

(2) The model should produce results which agree reasonably well with published results from the same model using data obtained from

energy chamber data.

(3) A model should be equally applicable over an entire lactation. A cow's energy balance, defined as the rate of energy consumed as feed less the rate of energy spent for supporting body functions, will normally vary on both sides of zero throughout her lactation. The ideal model will apply as well to periods of positive energy balance as to those of negative energy balance.

It would be difficult to meet each of these criteria with the same model. Instead they were applied both during model construction and interpretation of results to decide which ones were superior for use with field-collected data.

Potential application of this research can be seen along three broad avenues. For researchers, the ability to monitor the energy balance and partial efficiencies of research animals without requiring expensive energy chambers would stimulate more extensive research into energy utilization. For dairy geneticists, large data sets may now be collected from many commercial operations having extensive breeding records. This could facilitate important work concerning genetic parameters of efficiency for milk production, weight gain, or pregnancy. Eventually, the opportunity to develop sire rankings based on efficiency of production, and ultimately a true economic ranking (considering both outputs <u>and</u> inputs) may be developed. Finally, for the dairyman, research into the sources of environmental variation for efficiency can lead to the farmer maximizing his own net profit by tailoring his herd environment to produce milk, meat and calves most efficiently.

II. REVIEW OF LITERATURE

1. Introduction

With the help of research conducted by animal scientists, dairy farming has evolved over the years into a specialized system for producing as much milk per production unit (the cow) as possible. While in the past this method has been sufficient to ensure adequate return to the farmer, today's economic conditions necessitate consideration of the efficiency, rather than solely the magnitude, of production. It has long been presumed that economics of scale exist in milk production, and therefore that, milk components being equal, a cow producing more milk is economically superior to a cow producing less. While this belief may be justified in some instances, clearly there exists the possibility of increased efficiency of an animal offsetting its lower production, and therefore yielding a higher net return.

The term 'efficiency' has been defined many ways in the literature. Fundamental to any definition are the concepts of inputs and outputs. For economic purposes, these would be weighted by costs and prices, respectively. In the context of energetics, inputs and outputs are measured in units of energy. While it may be conceivable to measure efficiency as the difference between outputs and inputs measured in common units, for this study we will adopt the definition of productive efficiency put forth by Bauman et al (1985b) as the yield obtained of a product in ratio to the nutritional costs associated with that production.

It is clear that, to understand the concept of efficiency, we must understand the various forms of input and ouput of the animal, and the relationships among inputs and outputs. This review will summarize much of the completed research concerning inputs, outputs, and their interaction as it applies to ruminants in general, and dairy cattle in particular.

Because so many physiological functions contribute to the efficiency of bovine metabolism, a complete review of all related published research could fill many volumes. In the following summary, the literature will be presented as it relates to three major areas affecting efficiency research: the efficiency of feed conversion, the partitioning of energy into useful product, and mathematical and statistical models useful for investigating energy efficiency.

2. Efficiency of feed conversion

Consideration of inputs to ruminants can be divided into two sections: the method of evaluation of energy content of feeds or rations, and the value (in energy terms) of particular feeds, either alone or associated with other feeds. In the literature, however, these two sections are closely tied. Therefore this review will consider both the method and the result of evaluation of feedstuffs for their energy content.

The relationship among several measures of energy in a feed, based on its productive value to a cow, is shown in the following equation:

Gross energy

  - energy lost in feces -

  Digestible energy

    - energy lost in urine and methane -

    Metabolizable energy

      - energy lost as heat increment -

      Net energy

It is important to note that each estimates a different utilization of energy, and they have a heirarchical nature.

DeBrabander et al (1982) evaluated six energy evaluation systems for their ability to predict actual energy available to dairy cows. The systems they investigated included four which are or were commonly used in Europe. Also considered were the net energy (NE) system (NRC, 1978), in use in the United States, and metabolizable energy (ME) system described by the Ministry of Agriculture, Food and Fisheries (1975) and used in Great Britain and Ireland. The ME system used in the United States is closely related to the latter system. The accuracy of each system was assessed by regressing the recorded performance of 992 individuals on the energy intake as computed by each method. They found that NE tended to overestimate the energy in roughages compared to concentrates, while also overestimating maintenance requirements. These faults were not found in the ME system. Part of this difference, though, may be due to associative effects between specific feeds in the rations. Sundstøl et al (1980), using sheep to determine the utilization of ME for maintenance, found an associative effect between roughage and concentrate; that is, the actual ME available in a roughage depended on the content of the entire diet and not solely on its own quality.

This agreed with the findings of van Es and Nijkamp (1969). Research by Lingvall et al (1978), reported in Sundstøl et al (1980) showed similar results with lactating dairy cattle: when two groups of cows were fed identical amounts of ME as grass silage or hay, the group fed grass silage produced 5-15% more milk. Van der Honing and Steg (1980), in contrast to findings reported above, reported NE to be readily calculable from ME values, with a coefficient of variation for the estimate of about 2.5%. Using diets of barley and corn to feed steers, Wainman et al (1980) found the ME values of the two feedstuffs to be additive with no evidence of any associative effects.

One difficulty with using ME as a measure of energy intake is the finding that the efficiency of extracting ME from a feedstuff decreases as intake increases (Blaxter and Graham 1955). It has been speculated that this is a result of two separate phenomena:

1. As intake increases, digestibility of a feed decreases significantly. Estimates of this decrease range from 2-4% per unit of intake equivalent to maintenance requirement, (Moe et al 1965, Tyrrell et al 1966, Brown 1966); and
2. As intake increases, urine and heat losses, which are associated with the conversion of DE to ME, are proportionally less (van Es and Nijkamp 1969).

These two effects tend to offset each other, resulting in decreased efficiency at high intake levels.

Vermorel et al (1980) reported that the efficiency of utilizing ME for growth and maintenance was not affected by feeding level, in an experiment with young calves. Theriez et al (1980) duplicated these results with young sheep. These findings may indicate that ME as a measure of energy in feed remains accurate over different levels of feeding. In a discussion paper, van Es (1980) acknowledges the lack of information on high-producing animals with regard to the effect of feeding level on ME utilization, but asserts that for rations which contain less than one-third roughage, the effect of feeding level on ME content is variable.

Other factors exist which can cause variation in the efficiency of conversion of gross energy intake into metabolizable energy or net energy. Nutritionists have not been able to agree on the contribution of associative effects of feedstuffs to a ration's digestibility. Supporting the results of Wainman et al (1980) presented above, Blaxter (1974) and Garrett (1980) found little deviation from additivity for rations having wide ranges of forage/grain ratio and ME content, respectively. However, several studies have found that corn grain fed with corn silage produces a depression in digestibility greater than would be expected by considering either separately (Peterson et al, 1973; Joanning et al, 1981). Feed additives have been investigated to increase metabolizability of a ration, especially by reducing the amount of wasted methane produced as a by-product to microbial fermentation. Chief among these is monensin, which can reduce methane production by 15 to 31% (Garrett and Johnson, 1983), although its effects on diet digestibility are not clear, ranging from slightly negative to slightly positive.

There appears to be little disagreement that among-cow variation in conversion of feed to metabolizable energy is small (Bauman et al, 1985b). The relationship between milk production and efficiency of energy conversion has also been found to be negligible by several researchers (Davey et al, 1983; Trigg and Parr, 1981; Grieve et al, 1976). Thus, it seems as though the main source of variation in synthesis of useful product occurs during the process of partitioning available energy after it has been absorbed into the bloodstream.

3. Partitioning to useful product

In lactating dairy animals, there are typically four major uses of metabolizable energy which researchers have categorized: maintenance including heat increment, lactation, pregnancy and weight change. We will examine the efficiency of producing each of these forms of output.

Flatt et al (1970) detailed their research into partitioning of gross energy intake among various outputs, including feces, urine, methane, heat, milk and body tissue. From their results, ME intake (MEI) and NE intake (NEI) were partitioned into various outputs. These figures for the 12 cows used in their research are shown in Table II.1. In this work, NEI and MEI are computed from the animals' gross energy intakes, taking into account the energy lost through feces, urine and methane, and in the case of MEI, the additional energy lost in heat production. For this reason, the totals of output percentages from both MEI and NEI always sum to 100%.

Table II.1 Proportion of metabolizable energy (ME) and net energy (NE) intake present in various forms of output.

Cow	%NE intake as output in			%ME intake as output in			
	Milk	Tissue	Maint	Milk	Tissue	Maint	Heat
Bethel	38.7	16.4	44.9	22.2	9.4	25.7	42.7
Ruby	54.1	2.1	43.8	31.2	1.2	25.3	42.3
Lorna	66.2	1.8	32.0	39.6	1.1	19.2	40.2
Vertis	68.9	-15.8	46.8	39.3	-9.0	26.7	43.0
Doris	53.3	13.1	33.6	29.8	7.3	18.8	44.0
Diana	59.5	6.2	34.3	36.1	3.8	20.8	39.3
Muzzy	67.3	-0.9	33.5	41.4	-0.5	20.6	38.6
Helene	59.3	7.3	33.4	36.3	4.5	20.5	38.8
Martha	55.8	-7.5	51.7	31.8	-4.3	29.5	43.0
June	68.1	-28.0	59.9	38.1	-15.7	33.5	44.1
Shirley	73.4	-28.0	54.6	38.9	-14.8	29.0	47.0
Bessie	64.0	-8.7	44.7	36.2	-4.9	25.3	43.4

3.1 Energy utilization for maintenance

Maintenance requirements, as we will consider them here, consist of the energy necessary to maintain the basal metabolism, conduct voluntary body activity, and generate the heat necessary to maintain body temperature (Kromann 1973, taken from National Research Council 1966). Maintenance does not take into account excess heat produced by the animal, nor any form of production.

3.1.1. Sources of variation

Many factors have been examined for their effect on maintenance requirements. Some of the earliest studies noted a close relationship to functions of body weight. Rubner (1883) and Meeh (1879) both recognized that using actual body weight to estimate maintenance needs tended to overestimate requirements, and reported that the ratio of surface area to maintenance requirements was fairly constant for many common mammals. Their work was refined by Brody (1945), who determined that the best statistical fit of basal heat production by body weight followed the function

$$\text{Heat production} = a * \text{Body weight}^b,$$

where b is .7 to .75, heat production is measured in Kcal and body weight in kg. In 1965, the European Association of Animal Production agreed to use an exponent of .75 to convert body weight to metabolic body weight. They stressed that their decision was an arbitrary one, and hoped it would facilitate comparisons among many results of energy balance studies. It was also noted that the determination of the proper exponent was an empirical, rather than theoretical, consideration. Along the same line, Thonney et al (1976) and Geers and Michels (1982) reported that there were preferable exponents than .75 on an intraspecial basis, but that across species .75 fit well. Baldwin and Bywater (1984) asserted that this exponent tends to overpredict maintenance requirements for larger animals and underpredict for relatively smaller ones.

Colovos et al (1970) reported that physical activity of cattle influenced maintenance requirements, and presented correction factors to adjust heat production for the amount of time for which the animal was standing. These adjustments were computed from their finding that a double-change in body position, that is, one arising and one reclining, requires 46 kcal of energy for a 600 kg cow. In previous work, Brody (1932) found the same change to use 15 kcal of energy, although his calculations were based solely on oxygen consumption during short intervals of less than 12 minutes. The results of Colovos et al (1970) were from analyzing oxygen, carbon dioxide and methane concentrations over ten hour durations.

The effect of level of production on maintenance was addressed by Brody (1945) who reported that maintenance requirements increased with increased production. However, this finding has been argued among nutritionists. In fact, the question is more one of semantics than one of substance. Brody (1945) attributed increased requirements to the metabolic and physiological needs of the productive process, while others, notably Baldwin and Bywater (1984) preferred to consider maintenance a constant. Their justifications were both for convenience of estimation, and because they believed the requirement differences to be a cost of production and hence attributable to lactation, rather than maintenance.

Taylor et al (1981) have addressed the role of genetics in influencing the efficiency of meeting maintenance requirements. They used 11 pairs of twin Ayrshire cattle in their experiments, in which each trial lasted nearly two years. Little effect of age on maintenance requirements per kg metabolic body weight was found, nor were there any differences in efficiency of meeting maintenence needs due to age. They found significant differences between animals in equilibrium maintenance efficiency, and reported a within-animal repeatability of .7, even when animals were allowed to reestablish equilibrium at higher levels of feeding. They computed a coefficient of variation for efficiency, due to genetics, of 6.4%.

Garrett 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.

However, research by Patle and Mudgal (1977) indicated that the effect of energy balance on energy expenditure for maintenance was small.

Baldwin and Bywater (1984) reviewed differences in maintenance requirements due to differences in relative organ weights among animals. For example, Webster (1981) reported that energy expenditures in gut organs such as the liver and alimentary tract may contribute nearly a third of basal heat production. They speculated that differences in organ weights, especially those involved in mammary and alimentary processes, may account for half of the apparent increase in maintenance requirements in lactating ruminants.

Bauman et al (1985) report that van Es (1961) adjusted maintenance requirements from his own and 237 additional energy balance trials to constant body weight and obtained an estimate of among-cow coefficient of variation of 4-10%. There appears to be little genetic correlation between potential for milk production and maintenance requirements, according to research published by Davey et al (1983).

3.1.2. Estimation of maintenance requirements

Estimation of the requirements of growing or lactating animals for maintenance has been a source of disagreement since the early part of this century. Armsby and Kellner reported different values of feedstuffs for meeting the requirement based on differing ways their estimates were obtained (Garrett and Johnson, 1983): Armsby made his computations from the energy lost by fasting animals, deciding that their true maintenance needs would be supplied by metabolizing body reserves; Kellner preferred to feed livestock just enough to maintain their body weight, with no extra energy for lactation, growth or pregnancy. Figure

II.1, from Blaxter (1962), illustrates their positions. In light of more recent findings which indicate that maintenance requirements would decrease when energy intake is limited (reviewed by Graham, 1980), it is not surprising that the estimates of Armsby and Kellner differed from each other. Webster et al (1974a) questioned the validity of using fasting metabolic level as the basis for estimating maintenance requirements in growing steers, and favored instead the extrapolation of energy intake down to a level of zero gain as a measure of maintenance needs. An analogous process was used by Moe et al (1970) in estimating energy used for maintenance of lactating dairy cows. They estimated energy per unit of metabolic body weight ($kg^{.75}$) for maintenance, along with efficiencies for lactation and growth, by multiple regression.

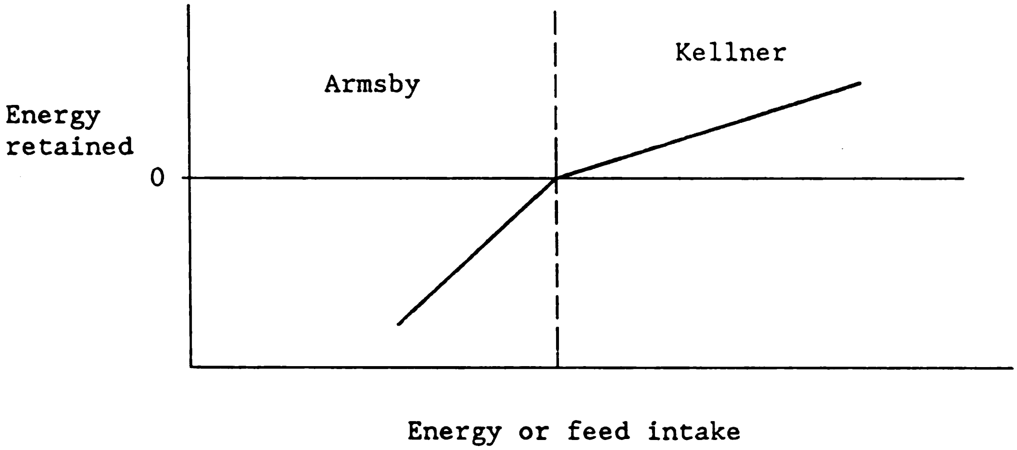

Figure II.1 Representation of the measurement of feed energy value by Kellner and Armsby (Blaxter, 1962). Note that to the left of the vertical dotted line animals are losing body weight. The efficiency of maintenance (k_m) is the slope.

3.1.3. Efficiency of maintenance

The variable k_m is used to denote the efficiency with which nutrients replace body fat and protein as a source of energy for maintenance. For example, if fasting animals lose 10 Mcal/day of body tissue but when fed require intake of 15 Mcal ME/day to maintain body weight, the efficiency of maintenance (k_m) is 0.67. Blaxter and Wainmann (1964) found that k_m was not constant, but tended to increase with feed quality as determined by metabolizability of the ration. Using digestibility of the ration as an indicator of feed quality, van Es and Nijkamp (1969) obtained similar results. They determined that feeding level affected digestibility considerably more than it affected metabolizability. They reported an efficiency of ME for maintenance of 78%. Although the values for k_m reported in the literature vary widely, this estimate is slightly higher than most. In general, k_m has been found to be affected by types of feed as well as metabolizability of feed, as shown in Table II.2 published by the Agricultural Research Council (ARC) in 1980. The figures were obtained from the research of Blaxter and Boyne (1978).

Table II.2. Efficiency of utilization of metabolizable energy for maintenance (k_m): values predicted from the metabolizability of the gross energy of the diet (q_m).

	Values predicted when q_m is:			
Class of feed	.40	.50	.60	.70
Pelleted	0.653	0.673	0.695	0.715
Forages	0.642	0.663	0.683	0.704
Mixed diets	*	0.728	0.749	0.769
All diets	0.643	0.678	0.714	0.750

* - not available

3.2 Energy utilization for pregnancy

The efficiency of supporting a pregnancy in the ruminant has not been widely researched. In general, more emphasis has been placed on the study of efficiencies of growth and lactation for economic reasons, although the importance of pregnancy in commencing the latter two processes cannot be overlooked.

One of the most widely referenced studies of the efficiency of energy utilization during pregnancy was completed by Jakobsen et al (1957). They used 17 calf fetuses, fetal membranes, and dam uteri to obtain a function describing tissue deposition during cattle pregnancy. They determined that the function

$$V = 0.4162 * e^{0.0174t}$$

adequately described this process, where V denoted the energy content in Mcal of the tissue due to pregnancy, and t was the number of days after conception. The derivative of this function yields the instantaneous change in energy content of the fetal tissues, and is expressed as

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

where v is the rate of energy deposition (in kcal/day) on day t. It should be noted that no corrections were presented for birthweight of the fetus, although it seems reasonable to expect that more energy would be deposited in a larger fetus than into a relatively smaller one.

Jakobsen et al (1957) did not estimate the efficiency of maintaining a pregnancy, but they did determine that support of pregnancy increased heat production in the dam between 2 and 2.5 times, or 30 kcal/kg increased weight due to fetal and placental tissues. Bauman and Currie (1980) reported that out of 88 kcal/kg per day required by the pregnancy, 63% was heat, or 55 kcal/kg. Their report summarized the known biochemical and endocrinological pathways for maternal-fetal processes during pregnancy. They also stated that fetal growth and development were energetically comparable in efficiency to other productive processes, and that nutrient requirements at the end of pregnancy were 75% higher than for a non-pregnant animal of the same weight. Langlands and Sutherland (1968), in a study of pregnancy in Merino sheep, found a requirement of 200 kcal/kg fetus per day, or more than double that reported for cattle above. This may be due in part to the small fetal size and in part to the shorter gestation length of sheep compared to cattle.

Moe and Tyrrell (1972) reasserted that the efficiency of use of ME for pregnancy was low (<25%), as they had determined earlier (Moe et al, 1970). In the latter study, they estimated requirements to maintain pregnancy in dairy cattle at 60 to 65 $e^{.0174t}$ kcal on day t of lactation, corresponding to an efficiency of 11%. Rattray et al (1974) estimated that efficiency was between 12 and 14%, depending on the statistical model used. They speculated that the reason for this low efficiency was that maintenance costs to the fetus and supporting maternal tissues were ignored. Sykes and Field (1972) computed the efficiency of ME for pregnancy to be 12-14% in Scottish blackface ewes. Tissier et al (1980) computed body composition from measurements of deuterium uptake rather than indirect calorimetry or successive slaughter to measure body composition. They obtained efficiencies for pregnancy between 13% and 16% in cattle. One reason for their choice of this method was to account for maternal tissue mobilization, which, as Heaney and Lodge (1974) reported, may be a normal feature of late pregnancy that cannot be prevented by ad libitum feeding, even if it were desirable to do so.

The ARC (1980) cautions that efficiency measures ignore the growth of mammary gland, or any increase in maternal energy or protein stores. Other factors have been investigated for their effect on efficiency of pregnancy support. Iwasaki et al (1980) reported that maintenance needs may increase with increasing state of pregnancy, but this may have been due solely to increased maintenance requirements of the fetus. They found that ME intake was not affected by the advancing of late stages of pregnancy, which may lend additional support to the theory of maternal tissue mobilization for pregnancy support. Rattray et al (1980) determined that body condition of the ewe, as determined by feeding level in mid-pregnancy, can influence nutrient partitioning during later stages. Heavy ewes supported fetuses from maternal reserves, while thinner ewes tended to replenish depleted tissues at the expense of the fetus.

3.3 Energy utilization for growth and liveweight change

The physiology of growth in ruminants has been investigated in depth by researchers since the nineteenth century, since all ruminant species, breeds, and sexes undergo some pattern of development which has economic value. In contrast, lactation studies have been primarily focused upon dairy breeds, and both lactation and pregnancy are sex-limited traits expressed only in females.

In this review, the energetics of growth will be discussed in two rather arbitrary divisions: energy requirements for growth and the energy required for weight change in support of lactation. The term growth will be used to denote maturation of the animal (i.e., deposition of protein, fat, and other tissue) as contrasted to catabolism and deposition of tissue, primarily fat, for use by the cow as energy for lactation.

3.3.1 Energy Utilization for Growth

Both National Research Council (NRC,1978) in the United States and ARC (1980) in Great Britain have published energy requirements for growth in beef and dairy cattle. Although published requirements differ between breeds, much of the difference can be attributed to differing body compositions among breeds of cattle. Garrett (1980), using a comparative slaughter technique to study 708 steers and 341 heifers, reported that the energy value of weight gain in British-bred steers was 17% lower than in comparable heifers, but 35% higher than the average value of a small sample of Charolais steers. Although he did not study the composition of the gain, it seems likely that the Charolais breed contained a higher proportion of protein, which is produced with less efficiency than fat in growing ruminants. Similarly, Vercoe and Frisch (1974), using three Australian breeds, found significant differences in efficiency of growth. They cautioned, however, that in their study changes in feedstuff or environmental conditions may have affected computed efficiencies.

In another breed comparison study, Byers and Rompala (1980) evaluated the efficiencies of eight Charolais (C) and eight Angus-Simmental cross (A x S) steers. They computed a 62% efficiency of ME utilization for growth in A x S, with only a 45% efficiency in C steers. They proposed that the higher proportion of fat produced in the A x S animals, compared to C which is higher in protein, accounted for the increased efficiency in the former. Their hypothesis was supported by

Reid et al (1980), who inferred from their work with unpublished data that fat can be gained more efficiently than protein. They agreed that animals measured as more efficient would tend to have a higher ratio of fat to protein than those less efficient, assuming the animals were of similar breed, sex, age, and other characteristics. However, Vermorel et al (1982) contradicted these findings. Studying 24 each of Charolais and Holstein growing bulls, they found no significant differences between the breeds in efficiency of ME use for growth. Neither were there differences due to feeding level or liveweight of the bulls. Despite the Charolais having a higher percentage of energy retained as protein, they reported no significant effect of body composition on efficiency of growth.

There have been numerous other sources of variation in efficiency of growth reported. Geay et al (1980) pointed out that the efficiency with which ME is utilized for fat deposition declines when crude fiber content of the diet increases or when metabolizability of the diet increases. Menke (1980) proposed a curvilinear function to describe the relationship between ME intake and protein retention. He included such factors as body weight, protein:energy ratio and amino acid pattern of the feed as independent variables to predict maximum energy retention as protein and efficiency of protein deposition. Tyrrell and Moe (1980) performed 59 measurements involving energy balance on 8 fattening Hereford heifers over a 55-week period. They reported that partial efficiency of ME use for tissue deposition was unaffected by diet. Meissner (1982) concluded that genotype by diet interaction did not affect efficiency, but did affect total intake and total gain. He used 34 bull calves of three breeds, Afrikaaner, Hereford, and Simmental, on two divergent diets in reaching his conclusion.

When measuring characteristics of growth in ruminants, accurate measurement of maintenance metabolism is essential. Efficiency measures of growth may be strongly affected if fasting metabolism is considered to be maintenance metabolism. Webster et al (1974b) advised that thus using fasting metabolism would bias growth efficiency estimates upward in animals over 200 kg and downward in animals under 200 kg. They recommended that basal metabolic rate be used instead to estimate maintenance. Graham (1982) postulated that short-term calorimetric experiments yield higher values of energetic efficiency than do longer trials with growing animals. He stated that the discrepancy occurs due to an appreciable energy expenditure associated with physiological state, and which responds rather slowly to feed intake. Roux (1982) warned that estimates of efficiency produced simultaneously for both fat and protein deposition must be interpreted with great caution, for nearly colinear independent variables tend to produce estimates which have rather larger standard errors.

Many researchers have determined efficiencies of growth (k_f) in experimental animals. Tyrrell et al (1974) found that 6 Hereford heifers required an average of 1.95 Mcal ME to deposit 1 Mcal of tissue for growth. This corresponds to an efficiency for growth of 51%. They noted that, for each additional 1 Mcal in daily rate of growth, 95% of it was retained as fat, while only 5% was in the form of protein. There is a large variation in the reported values of k_f depending on the quality of ration. For rations containing little fiber, k_f has been estimated at 0.7-0.75, while with high fiber rations the values are closer to 0.4 (ARC, 1980). Baldwin et al (1980), compared real net efficiencies of growth to maximum theoretical efficiencies derived from biochemical paths. Their results are summarized in Table II.3. They noted that, because there are more than one metabolic pathway for fat or milk synthesis, an opportunity exists to selectively use more efficient paths. They posed two questions as motivation for continuing energy efficiency work:

(1) Can we learn to identify animals which are capable of attaining maximum efficiency of production?

(2) If we knew exactly what the less efficient animals were doing, could we manipulate their metabolisms so that their efficiencies would approach those of the more efficient animals?

Table II.3 Comparison of theoretical and realized net efficiencies of growth expressed as percentage of available metabolizable energy

Animal	Theoretical	Realized
rat	75% to 85%	30% to 70%
ruminant	70% to 80%	30% to 60%

(adapted from Baldwin and Smith 1974)

Webster et al (1976) studied the efficiencies of growth in eight British Friesan x Hereford steers. They obtained an average percent efficiency of about 62%. Earlier, Webster et al (1974a) had performed similar experiments with fattening sheep and computed a percent efficiency of fattening in that species of 61%.

3.3.2 Energy utilization for weight change in support of lactation

The metabolism and catabolism of tissue in support of lactation is quite different from growth, for it involves primarily fatty tissue, with little or no protein in many circumstances. This distinction was borne out by work of Reid and Robb (1971), who reported an average overall rate of change of 4.38 Mcal per kg body weight in 53 mature dairy cows of assorted breeds. The value of body tissue gain and loss during lactation, however, was somewhat higher. They found that the energy value of 1 kg of body tissue gained ranged from 4.8 to 9.4 Mcal, while body tissue loss contained 6.3 to 7.9 Mcal/kg. This would indicate a difference in composition between tissues composing empty body weight and tissues gained and lost throughout lactation, with the latter probably being somewhat higher in proportion of fat.

Mobilization of body tissue reserves occurs in most cows during peak periods of lactation. Some cows are capable of utilizing remarkable quantities of tissue for lactation during such periods of negative energy balance, when energy outputs such as milk and maintenance exceed energy intake. Flatt et al (1970) described a cow, Lorna, "who lost 10 to 20 Mcal body tissue daily while producing 27 to 35 Mcal (85 to 110 lbs) milk daily...In late lactation, Lorna deposited an exceptionally large amount of body tissue (15.2 to 18.8 Mcal) daily while still lactating 4.7 to 7.1 Mcal (15 to 22 lbs) milk daily." The same trend, but to a lesser extent, of mobilizing body tissue early in lactation for replacement later in lactation was noted in 21 of 24 cows between 6 and 10 weeks post-calving. Flatt et al (1970) estimated that the net efficiency of milk produced by either mobilization of body reserves or directly from feed intake was approximately the same. Brown et al (1981) proposed that quantitative measures of body fat might increase the accuracy of estimating feed intake, due to increased accuracy of estimating the amount of tissue mobilized for production. However, Neilson et al (1983) found no changes in backfat area, measured ultrasonically, among cows in three production levels during early lactation. Their tests took place during the early part of lactation. One might account for these results by speculating that the source of tissue metabolized during negative energy balance is primarily the body cavity and not over the back. Dairymen would question this possibility, as the improvement in dairy character (general sharpness and angularity) of a cow in early lactation is well known.

Bauman and Currie (1980) reported that cows took approximately 16 weeks post partum to consume enough energy each day to meet daily requirements for milk production, by which time yield had fallen to less than 80% of peak production. They calculated that, over the first month of lactation, typically about one-third of the energy in milk is from metabolization of body reserves. Flatt et al (1970) quantified this process; cows in their study showed an average body tissue loss of 6.9 Mcal/day in early lactation (8 weeks post partum), and average gains of 1.2 Mcal/day in mid-lactation (24 weeks) and 4.9 Mcal/day in late lactation (41 weeks). They found the effect of stage of lactation on amount of body tissue mobilized or stored was highly significant. In fact, when they reduced feed early in lactation they caused a drop in milk production rather than an increase in tissue mobilization, which might indicate that lactating cows preferentially use body tissue to produce milk in early lactation.

Flatt and Moe (1971) observed little fall in liveweight in a cow producing 100 lbs milk/day, while eating only enough feed (about 25 Mcal/day) for about half that yield. The deficit in energy intake was made up by catabolizing about 4.5 lbs fat/day. Moe et al (1971) therefore cautioned that liveweight change alone may not provide an accurate indication of a lactating cow's energy balance. Broster et al (1975) performed a regression of liveweight change on milk yield (kg/day) for heifers on fixed rations at various stages of lactation. Their results are summarized in Table II.4.

Table II.4 Regression of liveweight change on milk yield for heifers at various stages of lactation (Broster et al, 1975)

Weeks of lactation	Regression coefficient and standard error	Residual degrees of freedom
1- 6	-0.122±.019	53
7-12	-0.042±.011	65
11-16	-0.062±.016	51
15-20	-0.052±.015	52
19-24	-0.040±.013	78

Note that the regression coefficient for weeks 1-6 is significantly different from all other regression coefficients. Thus, the first six weeks appear to be most important for tissue utilization toward milk production.

The net efficiency of producing milk from body tissue reserves can be thought of as two distinct processes: storage of feed energy in the form of primarily fatty tissue, and metabolization of body tissue to produce milk. Many researchers have considered both processes.

Patle and Mudgal (1977) worked with 24 Brown Swiss x Sahiwal crossbred cows to obtain an efficiency of 65-68% for utilization of ME as tissue gain during lactation. Moe et al (1970) estimated the efficiency of ME use for body gain at 75% in balance trials with 350 lactating dairy cattle. Milk production from tissue loss was performed with an efficiency of 82% in the same study, which agrees well with results of Moe and Flatt (1969). In trials with 215 lactating, non-pregnant dairy cows in negative energy balance, the calculated the average efficiency of converting body tissue reserves to milk was 85-86%. These efficiencies were estimated by regressing ME intake on milk produced and body tissue change, and a regression of milk produced on body tissue change and ME intake. A value of 83% was used by Forbes (1977) in his simulation work, but his source for this value was not referenced.

Moe et al (1970) computed the overall efficiency of producing milk through the intermediary of body tissue as the product of the efficiencies of going to and from tissue. Their result was 75% x 82%, or a net efficiency of 62%, compared with efficiency of milk production directly from ME intake of 64%. Van Es (1976) estimated that the overall efficiency of tissue deposition in late lactation then withdrawal in the early part of the following lactation was 50%.

3.4 Energy utilization for lactation

Lactation, along with growth and weight gain, has been the form of production most investigated by researchers of production efficiency. Although the broad subject of energy efficiency during lactation encompasses the efficiencies of digestion and milk production as well as endocrine effects, this section of the review will primarily deal with production efficiency of milk. Endocrine pathways and influence will be discussed rather briefly.

Moe et al (1970) 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. This is not, they stated, because cows vary in metabolic efficiency, since the metabolized energy obtained from a sample of feed is approximately the same across cows. Rather, they believed that cows vary widely in their response to additional energy input.

The identification by Moe et al (1970) of genetic potential and production level as the main two sources of variation is a broad simplification, however. Many more sources of variation have been examined.

3.4.1 Environmental and genetic factors affecting energy utilization for milk

3.4.1.1 Quantity of ration. Using four groups of twenty Holstein heifers in either the first or second two months of lactation, and fed at either high or low levels of energy, Broster et al (1969) reported that the group fed at low level early in lactation had the highest efficiency of conversion of energy intake into milk. Although these more efficient heifers produced less milk than their better-fed counterparts, both groups mobilized similar amounts of body tissue, which made the former group appear more efficient. These findings correspond well to the work of Flatt et al (1970), who found that cows in early lactation had a tendency to mobilize a maximum amount of body tissue for lactation. Decreasing feed intake reduced milk output, but did not affect the amount of tissue mobilized for lactation. In contrast, Grieve et al (1977), studying 49 first lactation Holsteins, determined that energy efficiency for lactation increased with feed intake. Trigg et al (1980) experimented with eight sets of monozygous twins to determine the effect of underfeeding early in lactation. As expected, underfed cows produced less milk, but they concluded that this was due to differences in energy partitioning. Underfed cows were found to mobilize less fat for milk than adequately fed animals. The underfed animals recovered to produce at near normal levels when an adequate feeding regimen was resumed.

3.4.1.2 Quality of ration. As Coppock et al (1964) decreased the ratio of hay to grain in the diets of six mature, lactating, non-pregnant cows, the efficiency of milk production decreased from 65% down to 54%. However, Hashizume et al (1965) reported greater energetic efficiency for lactation in cows fed high levels of concentrates than those fed low. They used six cows in a crossover design experiment, i.e., each cow was fed in a Hi-Lo-Hi or Lo-Hi-Lo concentrate scheme, with each level lasting 26 days. Flatt et al (1970) found that of ME% of ration had no effect on the partitioning of nutrients toward lactation or weight change. Because concentrate is higher than roughage in ME content, and because the primary differences in energy efficiency for lactation are due to partitioning differences, their findings tend to indicate an effect of concentrate level on lactation efficiency intermediate to the former two studies. Similarly, Schneider et al (1979) found little effect of ration metabolizability on efficiency for milk production, although in their study all diets had rather high metabolizability. They drew their conclusions from respiration experiments conducted on 40 lactating cows.

Other components of a ration have been examined for their effect on energy efficiency for lactation. Tyrrell et al (1982b) fed different levels of protein to lactating dairy cows and concluded that ration protein had no effect on ME utilization for milk production. Kronfeld et al (1980) observed increases in calculated efficiency of ME utilization for milk when a higher percentage of fat was fed. Highly saturated tallow was used as their source of fat in the diet. They speculated that the energy cost to transport absorbed fatty acids was less than that to synthesize them, and accounted for the increased efficiency. Similarly, 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. They examined 41 cows on balance trial to reach their conclusion.

3.4.1.3 Frequency of feeding. Though they admitted that their results were not conclusive, Sutton et al (1982) found indications that frequent feeding may increase the partitioning of energy to milk. Sixteen Friesian cows were used in that study. These findings were reinforced by work of Kirchgessner et al (1982), who also found that efficiency of ME utilization for milk production increased slightly as frequency of concentrate feeding increased. In their experiment, concentrates were fed in two frequencies, twice and six times per day. The computed gain in efficiency was 3%, from 61% to 64%. In contrast to both of the previous studies, Van der Honing et al (1976) found no differences in efficiency resulting from increasing frequency of feeding concentrates from twice to eight times daily. In summary, the effect of increased number of feedings is likely to be small, if it exists at all.

3.4.1.4 Realized and potential milk production. It has been hypothesized that animals which produce more milk may be more efficient than their less productive counterparts. The relationship between milk production and efficiency has been the subject of several publications. Hooven et al (1968) studied 661 lactations of 318 daughters from 17 sires. They defined efficiency as the ratio of fat-corrected milk to net energy intake. Because milk production requires the majority of net energy intake, the correlation between efficiency and production might be expected to be rather high, though probably less than unity. In fact, they reported a genetic correlation estimate of 0.92. They also computed a heritability of 0.46 for efficiency. Whether their sample of animals was representative of the population of dairy cows is questionable, however. The heritability for fat-corrected milk (FCM) production which they computed was 0.62, about twice that reported by most other sources. Neilson et al (1983) also found gross efficiency strongly affected by milk yield. A factorial design having three levels each of milk yield and average backfat with an average of eight animals per subcell was used. Custodio et al (1983) likewise found that increased fat-corrected milk production corresponds with increased efficiency for FCM, with a highly significant residual correlation of 0.75 between the two traits. Additionally, correlations between daughter efficiency for FCM production and sire Predicted Difference for Milk or dam Cow Index were approximately 0.40.

The magnitude of any relationship between efficiency and milk production is dependent on the definition of efficiency used. Workers in New Zealand have considered efficiency as the proportion of ME partitioned to the udder which is secreted as milk. Using this definition, Trigg and Parr (1981) compared Jersey lines of different genetic merit for milk production, and were unable to detect any association between predicted genetic merit and partial efficiency of ME conversion to milk or ME conversion to body tissue. It has been reported by Bryant and Trigg (1981) and Davey et al (1983) that animals of high genetic merit for milk partition energy differently than animals of low genetic merit. Apparently the differences between animals of different genetic merit for milk production are primarily in the partitioning of energy within the body, and not in efficiencies of energy utilization by productive functions.

3.4.1.5 Other sources of variation. Flatt et al (1970) found stage of lactation effects highly significant in affecting ME utilization for lactation in Holsteins. Broster et al (1969) also saw indications of a stage of lactation effect, although its magnitude was somewhat masked by an interaction with ration in the design of their trial. Body weight changes have been known for a long time to be related to stage of lactation. Hooven et al (1968) found body weight changes to be significant in affecting efficiency. They computed a genetic correlation of -0.17 between body weight and efficiency of lactation. It must be remembered that this is a between animal correlation, and doesn't indicate the effect of weight change within a lactation on efficiency.

3.4.2 Review of endocrine pathways

The hormonal actions and interactions which influence energy partitioning and efficiency of energy utilization are exceedingly complex. Many of these hormonal effects remain unclear and are being researched. However, some of the effects of several key hormones have been determined and will be briefly discussed here, focusing upon their influence on lactation.

3.4.2.1 Insulin. Insulin concentration in the serum of cows has been observed in numerous studies to have an inverse relationship to milk production during a lactation (Hart et al, 1978). Perplexingly, however, insulin concentrations are generally lower in low milk producers than in high producers. The insulin concentration has also been found to be low in animals experiencing energy deficit (Hove, 1974; Schwalm and Schultz, 1976). Level of feeding has not been found to influence insulin levels. Two primary known effects of insulin in cows are to inhibit gluconeogenesis and to facilitate increased glucose uptake and utilization (Kipnis, 1973).

3.4.2.2 Growth Hormone. Growth hormone (GH) concentrations in serum are higher in high producing than in low producing cows. (Johnson et al, 1976; Hart et al, 1978). Exogenous GH has been shown to increase milk yield in cattle (Eppard et al, 1985; Bauman et al, 1985b) indicating that increased yield is attributable at least partly to high serum concentrations of GH, rather than merely a coincidental genetic correlation. Efficiency of milk production, measured as production per unit of feed intake, is also improved when exogenous GH is administered (Machlin, 1973; Peel et al, 1981), although Tyrrell et al (1982a) have shown that this increase does not correspond to an increase in the partial efficiency of ME utilization for milk production. It has been theorized that GH plays a central role in the control of metabolites, especially glucose and non-esterified fatty acids which are precursors to lactation. It also has been speculated that in energy deficient ruminants, GH may increase the rate of fat mobilization from adipose tissue, which makes it an important factor in improving efficiency and level of production during early lactation. Furthermore, GH has been implicated in a mechanism which preferentially partitions energy toward the mammary gland (Davis et al, 1983).

3.4.2.3 Prolactin. Once a lactation has been initiated, prolactin appears to have little effect on level of milk production in ruminants (Hart et al, 1978). After parturition, prolactin concentrations can be markedly reduced without affecting milk production (Karg et al, 1972; Hart 1973). Further, no differences have been found between high- and low-producing cattle in their serum prolactin concentrations, either during lactation or dry period (Hart, 1978). Season, however, has been found to have significant effect on prolactin concentrations (Schams, 1972; Koprowski and Tucker, 1973). Suckling stimulus also causes a temporary increase in serum prolactin (Tucker 1981). The effect of prolactin on the efficiency of milk production has not yet been determined.

3.4.2.4 Thyroxin. The effect of thyroxin on level of milk production is still unclear. There have been several studies which failed to find significant differences in serum thyroxin concentrations between levels of high- and low-producing cows (Bodoh et al, 1972; Hart et al 1978).

However, other studies have shown that thyroxin concentrations are higher in lactating than non-lactating cows, and that concentration is inversely related to level of milk production (Heitzmann and Mallinson, 1972; Vanjonack and Johnson, 1975). Exogenous administration of thyroxin has been shown to cause increased milk production (Blaxter et al, 1949), but a corresponding increase in efficiency does not occur, as more energy intake is required (Thomas, 1953).

The above discussion of four key hormones involved in lactation serves only as an introduction to the vast area of research concerning endocrine control of lactation in the ruminant. The field is far too extensive to be adequately discussed here. An abundance of excellent review articles have appeared in recent years, such as Hart et al (1978), Tucker (1979,1981), Baldwin et al (1980), Bauman and Currie (1980), Bauman and Elliot (1983), Hart (1983), Collier et al (1984), and Bauman et al (1985a).

3.4.3 Summary of reported efficiencies for lactation

Many researchers have published their evaluations of the partial efficiency of ME utilization for lactation. Although they use many different methods to deriving their figures, the results are remarkably consistent, as illustrated in Table II.5.

4. Review of models and modeling in ruminant energetics

A model is the backbone upon which statistical inferences for both quantitative and qualitative relationships are supported. As such, correct specification of a model is paramount to adequately evaluate

Table II.5. Summary of reported partial efficiencies of Metabolizable Energy utilization for lactation in cattle.

Source	Number of animals	Efficiency
Coppock (1964)	103	75%
Coppock et al (1964)	6	54% - 65%
Flatt et al (1970)	*	67%
Kirchgessner et al (1982)	*	61% - 64%
Moe et al (1970)	350	63% - 65%
Moe et al (1972)	*	61% - 64%
Reid (1962)	59	70%
Tyrell et al (1982a)	*	61% - 62%
van Es and Nijkamp (1969)	41	54% - 58%

* Not available

research data and form useful conclusions. Many models have been proposed to explain the relationships between inputs and outputs in ruminant energetics. These can be divided into two functional types: (1) statistical models, which are often used to determine the existence or magnitude of various relationships among independent and dependent variables, based on experimental data; and (2) systems models, which can be used to describe the interrelationships between measured rates of inputs and outputs in a system working through a time period. This section will review several published models of each type which have been used in the study of ruminant energetics.

4.1 Statistical models

The statistical method used most frequently to analyze ruminant energetics has been multiple regression using linear models. Descriptions of previously undefined terms in the models to be reviewed are listed below.

MEI = Daily metabolizable energy intake
MBW = Daily metabolic body weight (generally $BW^{.75}$)
E_{milk} = Energy contained in milk produced daily
Milk = Daily milk production
$E_{+wt\ chg}$ = Energy required for daily body weight gain
$E_{-wt\ chg}$ = Energy produced during daily body weight loss

Moe and Flatt (1969) used the models

$$\begin{aligned} \text{MEI/MBW} &= b_0 + b_1(\text{Milk/MBW}) + b_2(E_{-wt\ chg}/\text{MBW}) \qquad (1)\\ &= -137 + 1.468(\ \text{"}\ ) + 1.262(\ \text{"}\ ) \end{aligned}$$

and

$$\begin{aligned} \text{Milk/MBW} &= b_0 + b_1(\text{MEI/MBW}) + b_2(E_{-wt\ chg}/\text{MBW}) \qquad (2)\\ &= -79.7 + 0.632(\ \text{"}\ ) - 0.840(\ \text{"}\ ) \end{aligned}$$

to examine the use of body tissue reserves for milk production during periods of negative energy balance in dairy cows. Their solutions for each regression coefficient are shown. Model (1) considers required energy input to the animal as a function of output, while model (2) uses energy output from the udder as dependent on sources of energy to the udder. The results from the second model are easier to interpret, as the regression coefficients are the partial efficiencies of conversion of ME to milk and body tissue to milk.

Note that each of the terms in both models, with the exception of the intercept, are on a per-unit-MBW basis. Constructing the models in this way provided two benefits, one statistical and one conceptual. The statistical advantage stems from maintenance being considered a function of MBW. A model could be written without an intercept and including major metabolic functions requiring energy:

$$\text{MEI} = b_1(\text{MBW}) + b_2(\text{Milk}) + b_3(E_{-\text{wt chg}})$$

While correct biologically, such a model would be difficult to analyze statistically because of the absence of an intercept term. If each variable in the model is divided by MBW, however, we can regain the intercept. We must assume that MBW is constant throughout lactation if the models are to be exactly identical. Because MBW tends to vary about ± 10% throughout lactation, it is hoped that the consequences of violating this assumption are small. Conceptually, comparing the results from such a model across cows of different sizes is made easier, since all variables, and hence solutions, are reported per unit of MBW.

Moe et al (1970) developed another set of multiple regression models to study the requirements of maintenance and partial efficiencies of production. Using lactating and dry cows in positive and negative energy balance, their models and solutions for regression coefficients were:

$$\begin{aligned}\text{MEI} &= b_0 + b_1(\text{MBW}) + b_2(E_{\text{milk}}) + b_3(E_{-\text{wt chg}}) \\ &= -2.889 + 0.153(\text{"}\ ) + 1.512(\text{"}\ ) + 1.270(\ \text{"}\ )\end{aligned} \quad (3)$$

$$\begin{aligned}\text{MEI} &= b_0 + b_1(\text{MBW}) + b_2(E_{\text{milk}}) + b_3(E_{+\text{wt chg}}) \\ &= -1.889 + 0.135(\text{"}\ ) + 1.576(\text{"}\ ) + 1.378(\ \text{"}\ )\end{aligned} \quad (4)$$

$$\begin{aligned} MEI &= b_0 + b_1(MBW) + b_2(E_{-wt\ chg}) \\ &= 6.781 + 0.050('' \ ) + 0.990(\ '' \ ) \end{aligned} \quad (5)$$

$$\begin{aligned} MEI &= b_0 + b_1(MBW) + b_2(E_{+wt\ chg}) \\ &= 1.401 + 0.089('' \ ) + 1.703(\ '' \ ) \end{aligned} \quad (6)$$

Equations (3) and (4) were applied to lactating cows in negative and positive energy balance, respectively, while (5) and (6) were for dry cows in negative and positive balance respectively. Because the units for the regression coefficients are energy input per unit output, the partial energy efficiencies of production can be found by inverting the respective regression coefficients. For example, model (3) resulted in a partial energy efficiency for milk production of 1/1.512 or 66%.

The above 6 models were applied to data from 350 animals in energy chambers at Beltsville. There has not been a large-scale study which addresses the question of efficiency using animals maintained in normal herd conditions due to the requirements of MEI and body weight measures.

4.2 Systems models

Using statistical methods, a researcher determines the magnitude and significance of sources of variation. Systems analysis permits modeling the behavior of system outputs in response to measurable inputs. The primary tools in this technique are modeling and simulation. The process of modeling develops a set of mathematical equations to predict changes in the real world, while simulation is the use of modeling to study the dynamics of a system (Mertens, 1977). A sequence of steps has evolved which traces the modeling process (Brown et al, 1981), as depicted in Figure II.2.

There are many more reports of statistical analyses than systems

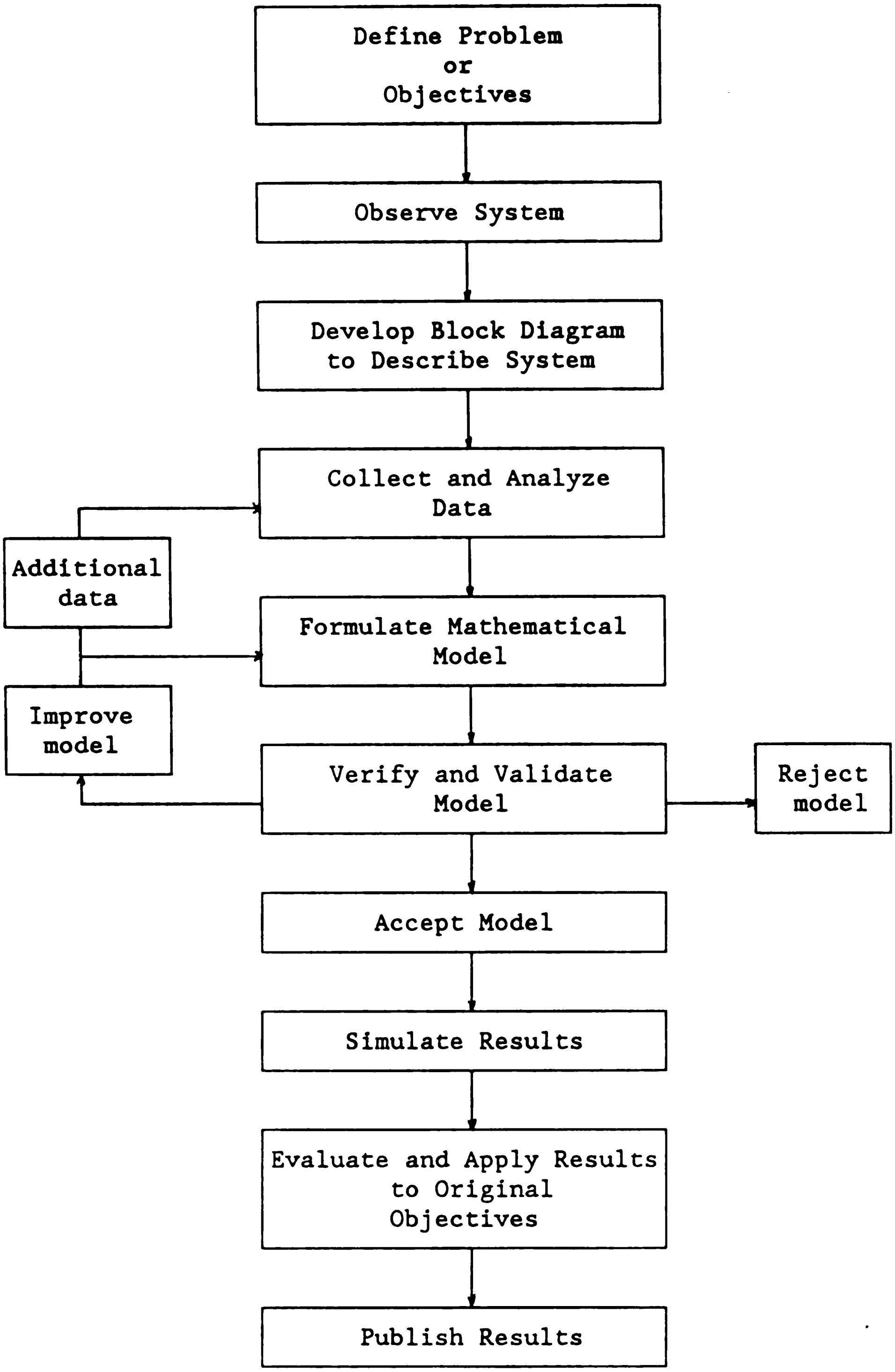

Figure II.2 Steps involved in the modeling process (Brown et al, 1981) analyses in ruminant energetics. Application of systems analysis in this area involves complex computerized modeling of the ruminant digestive and endocrine systems. Two applications will be discussed to illustrate the ability of systems modeling to simulate actual biological events and predict response of a process to certain stimuli. The first is the modeling of feed intake in cattle, and the second is the simulation of energy exchange and growth.

4.2.1 Systems modeling of feed intake in cattle

One of the earliest efforts to develop a model for predicting feed intake in cattle was by Monteiro (1972). He used changes in milk production and body weight throughout a lactation to predict the daily voluntary feed intake by a cow. He relied on a statistical model to obtain his prediction equation. The static nature of the relationships among variables in his equation, however, could not account for the observed slow increase in intake during early lactation. To better fit his observations, Monteiro added a lag parameter which made his model cow produce less milk early in lactation than was observed in experimental cows. Forbes (1977) used the data from Monteiro (1972) and formulated a dynamic model of feed intake in which metabolically controlled intake (MI) was compared with physically controlled intake (PI), and the smaller amount considered to be the animal's intake. This approach is considered dynamic because a change in MI at a given time t led to increased intake at time t which in turn resulted in a change in PI and MI at time t+1. Forbes later (1983) extended his model to predict feeding frequency, producing in effect a minute-by-minute model of the factors which are thought to control feed intake. A block diagram of his cow model is shown in Figure II.3.

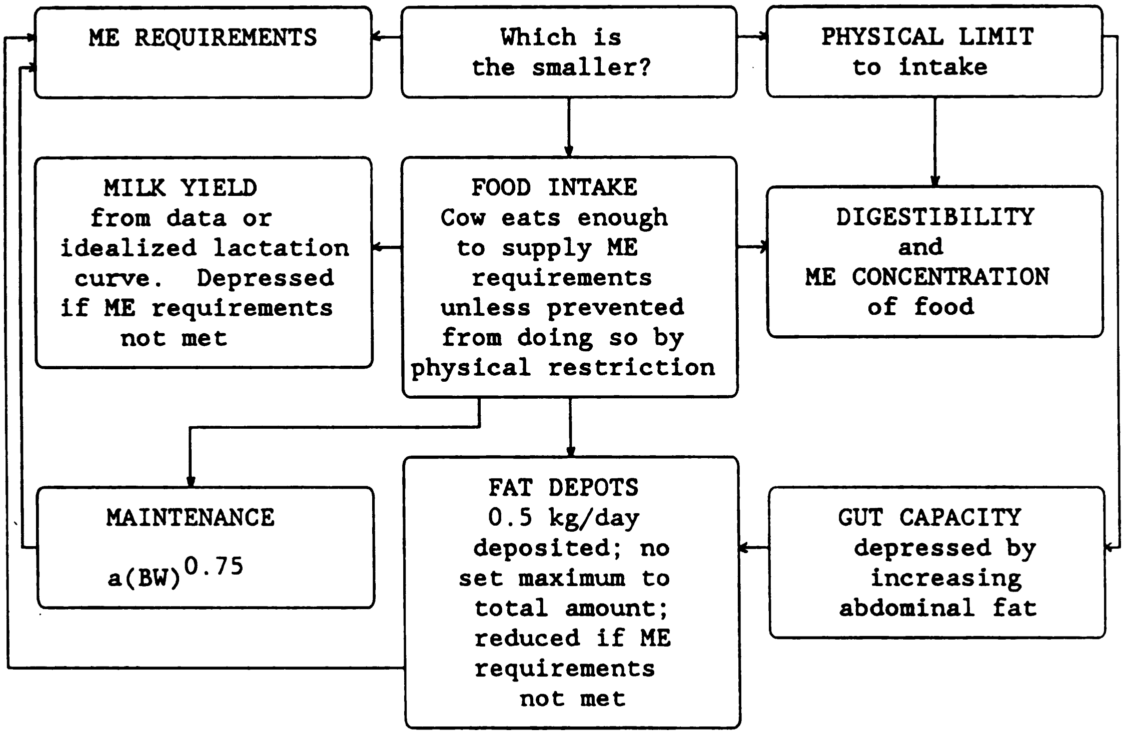

Figure II.3. Block diagram of cow model (from Forbes, 1983)

Bywater (1984) extended the performance of feed intake models by including rumen function in his simulation. This addition considers digestion rate, fluid turnover, and particle breakdown rate for their influence on MI. Bywater claims that his model determines the lag in the effect of metabolizable energy status on feed intake more effectively than prior published models. However, he admitted that there was a systematic error in predicting intake, especially early in lactation, thought to be attributed to inadequacies of the lag function he used. In fact, all models put forth to date share this difficulty of accurately predicting feed intake during the early part of lactation. It is apparent that for feed intake models, the delay function plays an important role in maintaining accurate correspondence between requirements and intake.

4.2.2 Systems modeling of energy exchange and growth in cattle

Unlike the models discussed above, modeling of energy exchange in cattle might be termed 'micromodeling', because it deals with events which occur along biochemical pathways within the digestive and endocrine systems. As such, to fully understand such models, a working knowledge of biochemistry is required. However, a simplified presentation of research conducted in this area will be instructive in showing a representation of digestion which is frequently ignored in higher-level models of ruminant energetics.

Smith et al (1980) discussed the stages involved in developing a model of metabolism in the ruminant. They began by specifying, in block diagram form, the main pathways of energy transformation (Figure II.4). Note that they combined four subsystems (liver, adipose, mammary and peripheral tissues) which together with the blood as transport mechanism and gut as input source made up the complete system for study. After evaluating the behavior of this model, however, they decided that the adipose subsystem did not adequately reflect existing concepts or explain available data. As a result, they developed a complex series of chemical kinetic equations which represented the transformation of sugars and acetate into carbon dioxide, fatty acids, and glyceride glycerol.

The modeling of adipose tissue metabolism is a complicated task, whose results must be continuously compared to existing data to ensure an accurate simulation. Schulz (1980) proposed a system of energy accounting as glucose is continually converted into fatty acids or oxidized. Although his method appeared to accurately determine energy contents of feeds over a wide range of intakes, no mechanism was included to monitor the rates of reaction, and hence it would be difficult to incorporate his model into a system which required delays in this process.

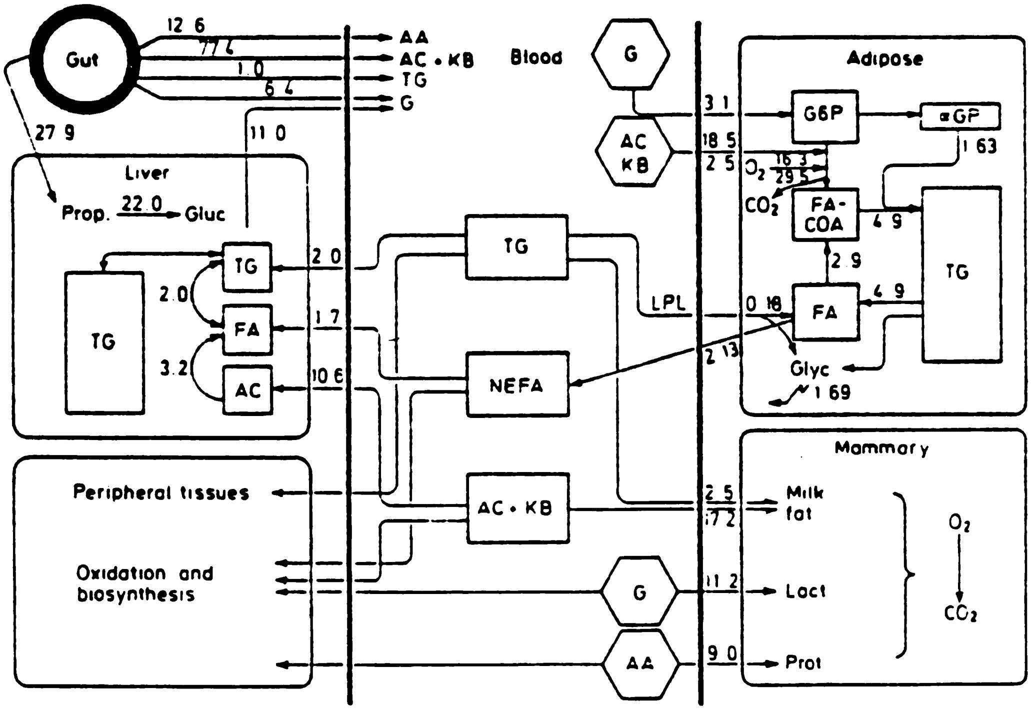

Figure II.4 Block diagram of energy metabolism in a lactating dairy cow (Smith et al, 1979)

Reichl (1980) described a computer program of his design which required as inputs measured intakes of digestible protein, digestible fat and digestible carbohydrates and the desired retentions of proteins and fat. The output from the program includes heat production, ATP balance, oxygen consumption, carbon dioxide, methane and urea production, yield of microbes in the rumen tract and a series of efficiencies of digestion. The system which his program simulated was composed of six submodels on three different levels. These submodels were (1) general outputs and (2) metabolic pathways on the whole animal level, (3) flux rates and (4) pool sizes on the individual tissue level, and (5) redox states and (6) membranes on the level of subcellular fractions. The purpose of his model was to examine the characteristics of a steady state resulting from given inputs rather than simulate the effect of a sequence of inputs through time on rate of nutrient and energy transfer.

In summary, then, both statistical analysis and systems modeling have been used to study the metabolism of dairy cows. Statistical methods are best applied to answer questions about linear relationships among the data, while systems analysis is better able to describe intricate interactions among the rates of change of variables through time. A second difference between the two methods is that statistical procedures are better equipped to directly estimate the probabilities of hypotheses, while systems science system requires that any hypotheses be tested only by examining the performance of a complete systems model. The determination of which means of analysis to use in a study is one which should be made by the researcher, considering the availability of data, his knowledge of the both qualitative and quantitative relationships among the data, and the questions he wishes to investigate.

III. METHODS OF ANALYSIS

1. Description of data

Data were supplied by the Lilly Research Laboratory of Eli Lilly and Co. of Greenfield, Indiana. Several variables were measured throughout one lactation for each of 405 cows of various ages. The cows were distributed in seven herds: two commercial dairies in California and Pennsylvania and five institutional herds: the Lilly Research farm in Greenfield, and herds at Michigan State University, Southern Illinois University, Western Kentucky University and a penitentiary in North Carolina. The data had been collected to test the efficacy of an experimental compound, Actaplanin, on production and feed intake. One of four dosages of the drug was administered to each cow throughout a lactation. The influence of the drug was not a central concern to this study, therefore it was treated as a nuisance variable.

Four rations were formulated to meet the requirements of high-producing, medium-producing and low-producing cows, and heifers. All heifers, regardless of production, were fed identically composed Heifer rations. To determine the appropriate ration to be fed each of the remaining cows, Lilly considered average milk production during the first three weeks. Cows which produced less than 62 lb per day over the first three weeks were classified Low, between 62 and 75 lb/day Medium, and those over 75 were considered High producers.

To facilitate blocking of animals for the Actaplanin trial, a calving group was also recorded for each cow. The number of groups varied among herds, and was based on the cows' calving order within a herd. A calving group variable was not considered in the present study.

Production data were recorded at regular intervals and included daily milk weights in lb and biweekly percentages of milkfat, protein, lactose, and solids-not-fat. Milk data were corrected for solids to an energy value of 340 kcal per lb using a formula published by Tyrrell and Reid (1965):

$$SCM = 12.3 * Fat + 6.56 * SNF - 0.0752 * Milk \qquad (1)$$

where SCM is daily solids-corrected milk yield, Fat is daily fat production, SNF is daily production of solids-not-fat and Milk is milk yield. All quantities are in units of weight, e.g. lb or kg. The weights of Fat and SNF needed for this equation were computed from linear interpolations between biweekly measurements of fat and SNF percentages, and daily milk yield data.

Feed intake was measured daily: dry matter intake (DMI) in lb and net energy intake (NEI) in Mcal. Net energy of a ration was determined using tables published by the National Research Council (NRC, 1978). Additionally, body weights were taken according to the following protocol: four measurements the first month, one measurement every two months for the next eight, and one on each of days 300 and 301 of lactation. The dates of all of the above observations were also recorded.

Breeding dates throughout the lactation were available, as was some calving information, such as weight, sex and condition of the calf, for many but not all cows. Dates of calving both before and after the recorded lactation were reported for many cows. When available, the date of calving after the lactation was used to create a variable, $Preg_i$, consisting of the estimated weight of the fetus and placental tissue in kg on day i. A formula published by Jakobsen (1957) was used for computing Preg:

$$Preg_i = e^{.0174*i}$$

Dam and sire identification were not included on the supplied magnetic tape, but were available in printed form from Lilly. Neither identification was required for this research.

Before proceeding with statistical analysis, a preliminary tabulation was performed. A summary of this tabulation is presented in Appendix I. The data were then reformatted to eliminate redundant and erroneous information, which reduced the number of cows from 405 to 391.

2. Partitioning of energy intake into forms of output

During a lactation, a cow may partition energy into several forms of production: maintenance (including heat production), lactation, support of pregnancy and fetal growth, and tissue metabolism and catabolism. If the quantity of energy partitioned into a certain product is only a small fraction of the total energy consumed, then differences between animals in the efficiency of creating that product will not affect overall efficiency greatly. To understand the relative energy requirements of various forms of production, energy intake was partitioned according to the amount of gross energy output by each product over several time periods. The time periods chosen were the whole lactation, and durations of positive and negative energy balance.

Two methods of measuring energy intake are net energy for lactation (NE) and metabolizable energy (ME). Empirical observation of feeding tables published by the NRC (1978) reveals that the relationship between ME and NE concentrations (Mcal/kg DM) in a feed is

$$NE = (ME + 0.2473) / 1.8315$$

for many common feeds. Applying this equation to estimate daily metabolizable energy intake (MEI) from daily net energy intake for lactation yields

$$MEI = NEI * 1.8315 - 0.2473 * DMI \qquad (2)$$

where DMI is measured in lb and all energy measures are in Mcal. Equation (2) was used throughout this research to estimate MEI. The difference between the NE and ME content of feeds is that ME includes energy which is converted to heat during the production process in addition to the energy required for milk, maintenance and body tissue production, while NE does not include energy spent as heat. It must be remembered that by using equation (2) to convert NEI and DMI into MEI, the variation among cows in efficiency of conversion of feed to energy is reduced. There was little alternative, however, since true MEI can only be measured on an animal within an energy chamber or wearing respiration apparatus which can monitor body heat.

For each cow, the fraction of energy apportioned to the various products was computed. The process was repeated using MEI and NEI as energy sources, and over all three time periods. Products considered from MEI were solids-corrected-milk, body tissue, maintenance and heat of production. NEI accounted for solids-corrected-milk, maintenance requirements and body tissue gain or loss.

3.

pr

ou

ha

fr

da

de

wi

ac

f

3

m

y

m

3. Regression procedures

To examine the relationship between feed energy and energy of products during a lactation, a series of regressions of energy intake on output was performed. Many models were considered, each postulated to have a meaningful biological interpretation. The coefficient solutions from each model were compared to corresponding published estimates from data collected on animals in energy chambers. Before these models are described, however, several procedures common to most or all of them will be explained. The following techniques used within each model adjusted the data to more accurately reflect the underlying biological functions of lactation, digestion and weight change.

3.1. Procedures for data manipulation within regression

Several variables in the data set required adjustment to make them more useful in the regressions. One example, the formula for estimating MEI, has already been presented. Three more techniques were used to modify the data before regression. These were:

(1) adjustment of milk secretion data to estimate rates of milk synthesis;

(2) a distributed delay to estimate the continuum of energy in the bloodstream of a cow from discrete intake measures; and

(3) producing a continuous curve for estimating body weight from a small number of measurements taken at intervals throughout lactation.

Appendix II describes the algorithms used to perform the above adjustments, along with segments of FORTRAN code implementing the algorithms.

3.1.1. Adjustment of milk weights to approximate milk synthesis rates

Milking an animal until all milk is removed is not economical per unit of milking time and can cause health problems. Current management practices recommend removing about 75%-85% of milk in the udder at each milking (Bath et al, 1978). The residual milk is retained by the udder until the subsequent letdown, when most of it is secreted. The amount of energy required daily for milk production is a function of daily milk synthesized within the udder rather than daily milk yield. Because not all of the milk synthesized by the udder is secreted at each milking, we must distinguish between these two quantities. Also, milk synthesis is a continuous process while daily milk yields are discrete measures which may vary considerably in magnitude from day to day. Adjusting daily milk records to a basis of milk produced daily in the udder can eliminate some of the large differences between consecutive days which may have been caused by inconsistent milking practices. For example, the judgment of different milkers with respect to proper duration for leaving milking apparatus attached to the udder may vary, depending also on the milking rates of other cows in a parlor at the time.

The following algorithm was used to obtain estimates of daily rates of milk synthesis from production data. All cows in the study were milked twice daily, and for simplification each of the two milk yields was considered exactly half the day's production.

Let: dm_i = milk yield on day i

$m_{i,1}$ = milk yield at first milking on day i
= $0.5 * dm_i$

$m_{i,2}$ = milk yield at second milking on day i
= $0.5 * dm_i$

ds_i = milk synthesized on day i

s_i = milk synthesized during one-half of day i
= $0.5 * ds_i$

f = fraction of total udder capacity yielded at one milking

fd = fraction of milk synthesized and secreted per day

Now, for the first day, if we assume $f = 0.83$,

$$m_{1,1} = f*s_1$$

$$m_{1,2} = f*s_1 + f*(1-f)*s_1$$

$$dm_i = m_{1,1} + m_{1,2}$$

$$= [0.83 * s_1 + 0.83 * s_1 + 0.83 * 0.17 * s_1] / 2$$

$$= 1.8 * s_1 = 0.9 * ds_1$$

Therefore, $fd = 0.9$, indicating that if residual milk is 17% of the udder capacity at each milking, daily residual milk is 10%. In other words, 90% of the milk synthesized on day i is secreted on the same day. In general, for any day i of lactation,

$$dm_i = 0.9 * ds_i + 0.09 * ds_{i-1} + 0.009 * ds_{i-2} + \ldots \qquad (3)$$

This study required the computation of daily milk synthesized (ds_i) for each day i. Notice that, for day i-1,

$$dm_{i-1} = 0.9 * ds_{i-1} + 0.09 * ds_{i-2} + 0.009 * ds_{i-3} + \ldots \qquad (4)$$

Now if we multiply equation (3) by 10 and subtract from it equation (4),

$$10 * dm_i - dm_{i-1} = 9 * ds_i$$

with all other terms dropping out. Then, to obtain the quantity of milk synthesized on day i,

$$ds_i = [10 * dm_i - dm_{i-1}] / 9 \qquad (5)$$

Equation (5) was applied to all milk yield data except for the first day. On day 1, the amount of milk synthesized was set to 110% of the yield. To examine the effect on efficiency estimates of this adjustment, two preliminary analyses were run in which the daily proportion of residual milk was varied between 0% and 25%.

The first procedure was to compute simple phenotypic correlations between daily milk synthesized and daily energy available in the bloodstream. One correlation was computed for each cow, and the mean of the resulting 391 correlations determined. As this parameter was increased from 0% to 15% and then to 25%, the correlation to daily available energy decreased slightly.

The second analysis fit the model

$$\mathrm{NEI} = b_0 + b_1(\mathrm{SCM}) + b_2(\mathrm{WtChg}) + e$$

where NEI is the daily energy available in the bloodstream (Mcal), discussed in III.3.1.2, and WtChg is the daily weight gain or loss (lb) computed as described in III.3.1.3. SCM is the solids-corrected milk synthesized daily in the udder (lb), and varied depending on the fraction of residual milk used in the model. This parameter took each of three values: 0%, 13% and 25%. Data from a single cow were fit, and regression coefficients obtained. Little difference was observed among resulting efficiencies, regardless of the percentage used to compute residual milk. Following this trial, a 10% residual milk weighting was used for all further regressions.

3.1.2. Distributed delay for estimating energy availability

The data included daily DMI and NEI, which were estimated from measures of feed disappearance. These data provide discrete measures of energy available for production. However, the measure of energy required in this study is the daily energy available for production, rather than daily energy consumed. The two are related through time, as energy consumed is gradually digested and made available to the metabolism. Using NEI and MEI without correcting for this delay in availability would require several assumptions:

(1) that feed disappearance correctly predicts the cow's internal energy status,

(2) that the cow consumed her daily energy at a single point in time each day, and

(3) that the energy was instantly available for use in production or maintenance.

In fact, these assumptions in general can not be supported. Variations in daily feed disappearance weighings may be due to factors other than daily consumption, such as wastage or human error. A cow may consume feed at several times throughout the day. Finally, it takes some time for the energy in the feed to become available to the cow in the bloodstream.

A delay function was used to simulate the ongoing process of digestion. In addition, this function could reduce the effect of large differences in intake on consecutive days. The resulting rates of energy available in the bloodstream would be more continuous, i.e., not as subject to large daily variation. The input to the process was daily energy intake, and its output was the daily energy available in the bloodstream. The most critical parameter used by a delay function is the half-life of the process. In this study, the half-life is the time it takes for half the feed energy ingested by a cow over the course of a day to reach the bloodstream. This parameter must consider that feed is consumed over a 24 hour period and is constantly being digested. Research has indicated that the half-life is related to the quality of feed consumed, with high quality corresponding to a shorter half-life (Bath et al, 1978). Typical values for the parameter ranged from 8 to 20 hr (Colucci et al, 1981).

Choosing a reasonable half-life for this analysis involved a compromise. Reported estimates of the half-lives for many typical rations were about 12 hr (Colucci et al, 1981). On the other hand longer delays, on the order of 24 hr, improved the ability of the function to produce a smoother output. A value of 18 hr was chosen as a reasonable compromise. Two analyses described in III.3.1.1 were performed to determine the effect of varying the half-life on resulting efficiency estimates and on correlations between daily milk synthesis and energy availability. The parameter was varied among 0, 18, 24 and 36 hr in both procedures. For both analyses, the differences among results from using different half-lives were negligible. For the remainder of the research, 18 hr was used as the half-life.

3.1.3. Estimation of continuous body weight curve from discrete weights

A serious shortcoming of the data was the paucity of body weight measures. Animals recorded for a complete lactation were weighed only 10 times, and the distribution was such that weights were taken only every two months from day 22 through day 299 of lactation. Body weight is an important indicator of whether a cow is adding to or mobilizing body tissue, which is a requirement for or source of energy, respectively. Without adequate body weight information, the additional energy supplied by the cow in negative energy balance can not be considered, nor can the additional requirement for weight gain later in lactation during pregnancy.

Several methods were available which would generate estimates for body weights during periods between existing measurements:

(1) linear interpolation between data points;

(2) fitting a spline curve to the data; or

(3) computing a least-squares polynomial equation to fit the data.

The former two methods would produce curves which exactly include existing data points. This is undesirable, for it was not uncommon in the data to find a difference of 50 lb between body weights taken on consecutive days. Much of this difference was likely to be caused by differing gut fill rather than change in empty liveweight. Because splining causes the resulting weight curve to be continuously differentiable, when applied to weights recorded on consecutive days it could cause unrealistically large rates of change for several days before and after the consecutive measures. Interpolation has the disadvantage that it results in identical rates of daily weight change for up to 60 consecutive days. The method would create ten different rates of weight change throughout the lactation from the ten different body weights per animal.

None of these disadvantages are shared by polynomial regression, provided that an appropriate polynomial is chosen. The choice of which degree of polynomial to use is a difficult one. Polynomials of higher degree result in better fit of the curve to data, but there is a danger of error due to insufficient precision on most computers when the degree exceeds about six. Within this limitation the degree should be chosen as high as possible without fitting random variation, or noise. This decision is frequently subjective.

Regressions were performed using polynomials of varying degree on body weight measurements from several representative cows. Visual examination of the fits indicated that a 4th degree polynomial was adequate to reflect major inflections in the weight curve throughout lactation without fitting the noise associated with measures on consecutive days described above. Therefore, for all cows with lactation lengths of at least 250 days, daily body weights were estimated by a 4th degree polynomial fit to actual weights. Care was taken to ensure that cows included were weighed at least seven times before applying the polynomial regression to their body weight data. If the degree of a polynomial approaches the number of observations being fit, wild fluctuations may occur in its curve which can make it unsuitable for estimating weights between observations. Although the regression line would continue to fit the data with minimum residual variance, predictions of weights at times between weighings may have a much larger error component than if the analysis had more degrees of freedom for error.

Polynomial regressions were performed on the body weight records from 244 cows having a lactation length of at least 250 days. From the solutions for each cow, daily body weights were estimated for each day of lactation. Daily metabolic body weights (MBW) were computed by raising daily weight estimates to the 0.75 power as recommended by the NRC (1978). A WtChg variable was also obtained from estimated daily body weights. On day i, $WtChg_i$ was computed as the difference between body weights on day i and i-1. $WtChg_1$ was set to zero.

For the remainder of this study, the terms NEI and MEI will refer to daily energy available within the bloodstream, i.e. after the delay has been applied to the energy intake data. Similarly, SCM will refer to the amount of solids-corrected milk synthesized daily, rather than amount of SCM secreted per day.

3.2 Multiple regressions to analyze energy utilization by various products

One of the assumptions required by multiple regression is that independent variables are measured without error. Although it is seldom, if ever, completely satisfied when observing biological systems, several variables in this study may be in serious violation of this assumption. These variables, and the effects of their errors in measurement, merit further discussion.

All recorded independent variables in the models to follow contained a degree of uncertainty. For example, daily solids-corrected milk records were not found by analyzing and correcting every unit of milk for its energy content, but by applying equations from Tyrrell and Reid (1965) involving milk and components yield. However two independent variables, WtChg and Preg, were subject to much larger measurement error than SCM or NEI. The source of error in WtChg was the fourth degree polynomial approximation of body weight as a function of day of lactation. Though in general the polynomial fit body weight rather well over the length of lactation, the 56 day interval between measures during middle and late lactation prevented accurate estimation of day-by-day changes. The variable Preg, weight of fetal and maternal support tissues, was also subject to error. The formula of Jakobsen et al (1957) generalized the fetal growth curve, although fit of the curve was not as precise during the second half of gestation as during the first half. It appeared that the fit of the curve was within about 20% of most measured fetal and tissue weights during the second half of gestation for the investigation of Jakobsen et al (1957). With varying sizes of dam and weights of fetuses, it is reasonable to expect that similar inaccuracies occurred in the data for this study.

In a simple regression, the estimated regression coefficient is the ratio of covariance between independent and dependent variables and variance of independent variable. The presence of measurement error in an independent variable, such as WtChg and Preg, could increase the variance of the variable. If we assume that on average the covariance between each variable and NEI is unaffected, then in the case of simple regression the estimated regression coefficient would be smaller than the true parameter. A similar effect may arise in multiple regression models. Therefore any assertions of the significance of a regression estimate are likely to be on the conservative side.

Twelve multiple regression models were examined which involved either NEI or MEI as the measure of energy intake. Table III.1 illustrates the terms in each model and the relationships among models.

Table III.1. Summary of multiple regression models fit (model number in parentheses) and relationships among them

	dependent variable			
	Net energy		Metabolizable energy	
independent variables	linear	per unit MBW	linear	per unit MBW
MBW,SCM	(1)	(4)	(7)	(10)
MBW,SCM,WtChg	(2)	(5)	(8)	(11)
MBW,SCM,WtChg,Preg	(3)	(6)	(9)	(12)

A more specific description of each model, identified by number in Table III.1, is shown below. The subscript i indicates measurements on day i, where i is from 1 through the final day of milk production.

(1) $NEI_i = b_0 + b_1SCM_i + e_i$

(2) $NEI_i = b_0 + b_1SCM_i + b_2WtChg_i + e_i$

(3) $NEI_i = b_0 + b_1SCM_i + b_2WtChg_i + b_3Preg_i + e_i$

(4) $NEI_i/MBW_i = b_0 + b_1(SCM_i/MBW_i) + e_i$

(5) $NEI_i/MBW_i = b_0 + b_1(SCM_i/MBW_i) + b_2(WtChg_i/MBW_i) + e_i$

(6) $NEI_i/MBW_i = b_0 + b_1(SCM_i/MBW_i) + b_2(WtChg_i/MBW_i) + b_3(Preg_i/MBW_i) + e_i$

(7) $MEI_i = b_0 + b_1NE_{SCM,i} + e_i$

(8) $MEI_i = b_0 + b_1NE_{SCM,i} + b_2NE_{WtChg,i} + e_i$

(9) $MEI_i = b_0 + b_1NE_{SCM,i} + b_2NE_{WtChg,i} + b_3NE_{Preg,i} + e_i$

(10) $MEI_i/MBW_i = b_0 + b_1(NE_{SCM,i}/MBW_i) + e_i$

(11) $MEI_i/MBW_i = b_0 + b_1(NE_{SCM,i}/MBW_i) + b_2(NE_{WtChg,i}/MBW_i) + e_i$

(12) $MEI_i/MBW_i = b_0 + b_1(NE_{SCM,i}/MBW_i) + b_2(NE_{WtChg,i}/MBW_i) + b_3(Preg_i/MBW_i) + e_i$

Because each model is independent from the others, b_0, b_1, b_2, b_3 and e_i

were different from model to model. The random residual term, e_i, was assumed to be normally distributed with mean 0 and homogeneous variance in all models. No covariances were assumed among observations. These assumptions have been applied in most published studies of energy utilization by regression. However, the sequential nature of the data through time suggests that autocorrelated errors may occur. Section III.3.3.4 will describe the techniques used to examine the effects of autocorrelation.

Models (3) through (6) and (10) through (12) are transformations of models without intercepts, with each variable measured on a per-unit-MBW basis. This can be seen through multiplication by MBW_i. A transformation consisting of dividing each daily variable by MBW_i was performed because of the statistical difficulties of interpreting a model when no intercept term is included. As an indication of the problem, R^2 values can assume any real values when no intercept is in the model, compared with theoretical bounds of 0 and 1 when an intercept is fit. After a model without intercept is transformed, R^2 values could be directly compared with those from models having an intercept. However, residual variances could not be compared because the transformation changed the scale of the dependent variable. The preferable estimator of residual variance would untransform the data and compute a residual sum of squares. This would have a substantial computational cost, but an economical approximation was calculated by estimating the residual variance of the transformed model and multiplying by the square of the mean divisor of the transformation. For example, if data were transformed by dividing by MBW, then the resulting residual variance was computed by multiplying residual variance from the transformed model by the square of mean MBW.

Each regression model was fit to 357 cows having a lactation length of at least 250 days. Each model was fit for each cow over the entire lactation, over the period of positive energy balance, and over the period of negative energy balance. The energy balance of an animal during a lactation was determined by daily body weight change. When the change was positive, she was considered to be in positive energy balance, while negative balance was indicated by a daily weight loss (Figure III.1). Because of the polynomial regression technique used to estimate body weights throughout lactation, this method of energy balance determination was more free of day-to-day errors due to degree of gut fill, body water content or mismeasurement. It was also highly unlikely to produce a daily body weight change of exactly zero.

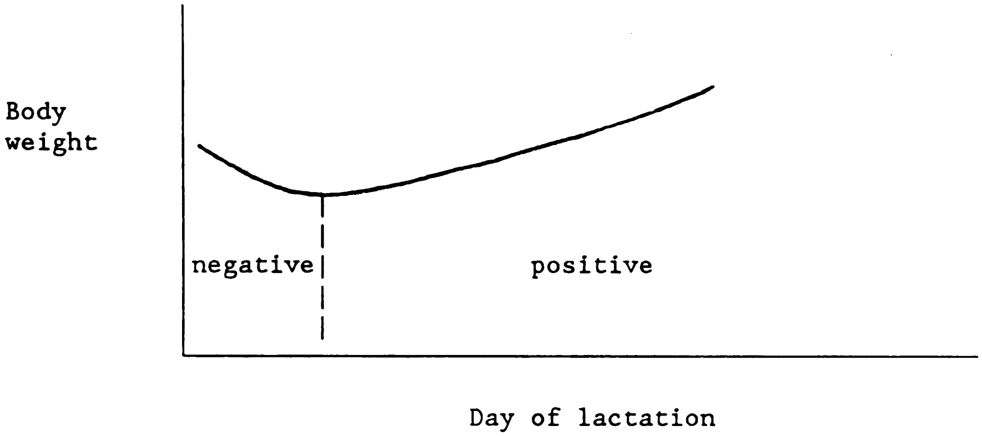

Figure III.1. Determination of periods of positive and negative energy balance by weight change throughout lactation

3.3. Two-stage regressions using net energy as a measure of energy intake

A two-stage regression procedure was developed to produce more biologically reasonable solutions for coefficients of variables requiring the majority of energy expenditure. The technique used was:

Stage 1: The quantity of energy required by all except one independent variable, as estimated using parameters published by NRC (1978), was collectively considered as a new independent variable whose coefficient had expectation 1.0. A multiple linear regression of NEI on the remaining variable and the new composite variable was then performed.

Stage 2: Energy required by the fitted variable was computed using the regression coefficient estimated in stage 1. This energy was subtracted from the original NEI and a multiple regression performed of the difference on the remaining variables.

The two-stage models used are listed below. For each model, an analysis was performed over periods of positive and negative energy balance, as well as over the entire lactation, for each of the 357 cows having a lactation length of at least 250 days.

(13) Stage 1: $NEI_i/MBW_i = b_0 + b_1(\text{Reqt for } SCM_i + WtChg_i)/MBW_i + e_i$

Stage 2: $(NEI_i - b_0 MBW_i)/SCM_i = b_0' + b_1' WtChg_i/SCM_i + e_i'$

(14) Stage 1: $NEI_i/SCM_i = b_0 + b_1(\text{Reqt for } MBW_i + WtChg_i)/SCM_i + e_i$

Stage 2: $(NEI_i - b_0 SCM_i)/MBW_i = b_0' + b_1' WtChg_i/MBW_i + e_i'$

Note that both (13) and (14) are per-unit-MBW models as described in III.3.2. Also, performing the regressions in two stages produces coefficient estimates which are not best in the sense of minimizing residual variance. The sole justification for using this method is that it could produce coefficients within biologically reasonable bounds.

3.4. Regressions considering autocorrelation among residuals

Because the data for each cow are sequential through time, it is likely that residuals are autocorrelated. Four models were used to examine the effects of including an autoregression term on coefficient estimates. These models are described below.

(15) $(\mathrm{NEI}_i - \mathrm{NE\ Reqt\ for\ MBW}_i + \mathrm{WtChg}_i)/\mathrm{SCM}_i = b_0 + e_i$,

where $e_i \sim (0,\sigma^2)$

(16) $(\mathrm{NEI}_i - \mathrm{NE\ Reqt\ for\ MBW}_i + \mathrm{WtChg}_i)/\mathrm{SCM}_i = b_0 + e_i$,

where $e_i = \rho * e_{i-1} + u_i$, $u \sim (0,\sigma_u^2)$

(17) $(\mathrm{MEI}_i - \mathrm{ME\ Reqt\ for\ MBW}_i + \mathrm{WtChg}_i)/\mathrm{SCM}_i = b_0 + e_i$,

where $e_i \sim (0,\sigma^2)$

(18) $(\mathrm{MEI}_i - \mathrm{ME\ Reqt\ for\ MBW}_i + \mathrm{WtChg}_i)/\mathrm{SCM}_i = b_0 + e_i$,

where $e_i = \rho * e_{i-1} + u_i$, $u \sim (0,\sigma_u^2)$

Models (15) through (18) are simple per-unit-MBW models to facilitate comparisons among solutions for b_0 and among estimates of ρ, the autocorrelation coefficient. An algorithm was developed which enabled efficient iteration for computing ρ. A complete description of the algorithm with a FORTRAN implementation is presented in Appendix III. This algorithm did not guarantee estimates of ρ within the parameter space of (-1,1), but in application fewer than ten of 357 estimates from each model were out of the parameter space.

Autoregression models were applied to 357 cows with at least 250 day lactations, over three durations: the entire lactation, and periods of positive and negative energy balance.

4. Analyses of variance on estimated coefficients from selected models

Four models, (7), (10), (14) and (16) were selected and their coefficients used in analyses of variance to determine the contribution of various factors to the variance of regression coefficients. The models were representative of those examined in this study: one was a two-stage model, one included an autocorrelation coefficient, and the remaining two were multiple regression models. The coefficients used were from the period of the entire lactation rather than positive or negative energy balance. Analyses of variance were performed on a total of nine coefficients from the four models.

The analysis of variance (ANOVA) model is shown on the next page:

$$y_{ijklm} = \mu + HS_i + R_j + T_k + A_l + b_1 \, Milk_{ijklm} + b_2 \, Milk^2_{ijklm} + e_{ijklm}$$

where:

		degrees of freedom
y_{ijklm}	- regression coefficient for a cow	
μ	- constant	1
HS_i	- effect of ith Herd-Season	24
R_j	- effect of jth Ration	3
T_k	- effect of kth Treatment	3
A_l	- effect of lth Parity group	2
$Milk_{ijklm}$	- covariate of Milk production from entire lactation	1
$Milk^2_{ijklm}$	- covariate of squared milk production	1
e_{ijklm}	- random residual $\sim(0,\sigma^2)$	322
		357 observations

Only main effects were included in the ANOVA, along with covariates of milk and milk squared. The covariates were considered to examine the belief that much variation in efficiency can be accounted for by differences in production. Four seasons were obtained by month of initiation of lactation, with January through March denoted season 1, and so forth in three month groupings. Several herds had no cows initiating lactations in one or more seasons, hence the herd-season effect has only 24, rather than 28, degrees of freedom. Parity was considered as first, second, third, and all later parities. Confounding between the heifer ration and first parity reduced the number of degrees of freedom for Parity to 2.

IV. RESULTS AND DISCUSSION

1. Partitioning energy intake into forms of output

The results of partitioning energy input into useful product are shown in Tables IV.1 and IV.2. Table IV.1 displays the utilization of NE intake while ME intake is considered in Table IV.2. Requirements for the various outputs were obtained from the National Research Council (NRC, 1978) recommendations.

Several observations apply to both tables:

(1) The proportion of energy required by milk production is higher during periods of negative energy balance than positive energy balance. This was expected, because during negative energy balance the energy available from feed is supplemented by energy gained from metabolized body tissue.

(2) There are negligible differences in energy used for maintenance between negative and positive energy balance.

(3) The energy required for pregnancy support at any time during the lactation is very small in comparison to that required for other purposes. This is an indication that the influence of pregnancy on our efficiency studies may be small.

Table IV.1. Percentage of net energy intake used for various purposes, during periods of negative and positive energy balance and over the entire lactation

Period	Maint	Milk	Weight Change	Pregnancy	Other
Negative energy balance	30.98	67.46	-8.54	0.08	10.02
Positive energy balance	29.70	58.99	9.19	0.14	1.97
Overall lactation	29.94	60.58	5.88	0.13	3.48

Table IV.2. Percentage of metabolizable energy intake used for various purposes, during periods of negative and positive energy balance and over the entire lactation

Period	Maint	Milk	Weight Change	Pregnancy	Heat Increment
Negative energy balance	20.81	45.31	-5.74	0.05	39.56
Positive energy balance	19.95	39.68	6.18	0.09	34.09
Overall lactation	20.11	40.73	3.95	0.09	35.12

The category Other in Table IV.1 contains excess NE intake which cannot be accounted for by the four production functions. One could speculate that the NRC (1978) recommendation of constant maintenance requirements throughout lactation with respect to metabolic body weight may underestimate maintenance needs during negative balance. Another part of its large value of 10.02% in negative energy balance may be caused by an overestimation of energy metabolized by weight loss. There are only about three body weight measurements during negative balance, and that variable may therefore be more subject to error than either milk or maintenance.

Table IV.2 indicates that the energy gained from the difference in WtChg between negative and positive balance is divided rather evenly between heat increment and milk production. Because the relative amounts of energy expended on milk production and heat increment are about the same, the even partitioning of extra energy from tissue might be expected.

For all periods it is clear that milk production and maintenance are the productive functions which require the most energy throughout the lactation. Heat increment, though not a productive function, accounts for a large percentage of ME throughout lactation, while the energy needs for body weight change and pregnancy are relatively small.

2. Effect of half-life of energy absorption and percentage of daily residual milk on energy utilization

Two different methods were used to examine the effect of varying the rate of energy absorption through digestion, as well as the daily amount of residual milk. Table IV.3 shows the correlations between NE available in the bloodstream and daily solids-corrected milk synthesized by the udder, when various half-lives are applied to energy intake and several percentages of daily residual milk are assumed for milk production. Table IV.4 presents results of several analyses, each using the same model, for which only the percentage of residual milk and half-life of energy availability were varied. Not all combinations of energy half-lives and residual percentages were examined, but only those most likely to show contrast.

Both Tables IV.3 and IV.4 indicate little effect of varying either the half-life of energy or the percentage of residual milk on the relationship between energy input and energy utilization. Note that the values in Table IV.4 are mean coefficients computed from only seven cows. However, the most extreme differences in parameters (between half-life=0, residual=100% and half-life=1.5, residual=75%) produced changes in coefficients of less than 10% in each of the seven cows and three coefficients. For reasons described in III.3.1.2 and III.3.1.3, ensuing regressions used a half-life for energy absorption of 0.75 days and a 10% value for daily residual milk.

3. Determination of predicted coefficient values from literature

One of the objectives of this research was to develop models which would use field-collected data to produce estimates comparable to those from energy-chamber data. However, most of the models used in this study have not been applied to energy-chamber data. Therefore, some published coefficient estimates required adjustments to enable their comparison to the solutions obtained in this study.

Table IV.3. Correlations between estimated NE available in bloodstream and daily SCM synthesis for various half-lives of energy absorption and various percentages of daily residual milk

Half-life of energy absorption in days	Percentage of daily residual milk 0%	15%	25%	50%
0	.44	.43	.40	.40
0.75	.44	.43	.39	.39
1.0	.44	.43	.39	.39
1.5	.43	.42	.39	.39

Table IV.4. Comparison of mean estimated regression coefficients* using various half-lives of energy absorption and various percentages of daily residual SCM

Half-life of energy absorption in days	Percentage of daily residual milk								
	0%			13%			25%		
	b_0	b_1	b_2	b_0	b_1	b_2	b_0	b_1	b_2
0	19.7	.152	.266		-		19.3	.159	.278
0.75	19.7	.152	.265	19.5	.157	.271	19.3	.160	.276
1.0		-			-		19.3	.160	.274
1.5		-			-		19.3	.160	.272

* model: $NEI = b_0 + b_1SCM + b_2WtChg + e$

Four uses of energy were considered in this study: maintenance, SCM production, pregnancy and body weight change. Published reports have assumed that the amounts of energy required by these functions are additive, as will this investigation. That is, the amount of energy required by a cow is simply the sum of requirements for each of the four functions. The computation of predicted values for each of the four functions will be described. The average relationship between NE and ME in this data set was

$$NE = .6717 * ME,$$

which is dependent on the energy concentration (NE per kg dry matter) of the ration as inferred by equation (2) in section III.2. This relationship was used to adjust all NE requirements to ME requirements. The following four sections will describe the computation of predicted estimates of coefficients. All weights in the equations have units of kg, and all energy measurements are in Mcal.

Maintenance. The NRC (1978) estimated NE requirements for maintenance (NE_{Maint}) by

$$NE_{Maint} = 0.073 * MBW,$$

where MBW is metabolic body weight, or body weight to the three-fourths power, as described in section III.3.1.3. Predicted metabolic energy requirements for maintenance (ME_{Maint}) were computed by

$$\begin{aligned} ME_{Maint} &= NE_{Maint} / 0.6717 \\ &= 0.109 * MBW . \end{aligned}$$

Models which have an intercept obtain mean total daily maintenance requirements, rather than requirements per unit MBW, as the estimate for b_0.

The mean MBW ($\overline{MBW}$) for all cows was 121.7 $kg^{.75}$. Therefore predicted value for this coefficient is

$$\begin{aligned} NE_{Maint} &= 0.073 * \overline{MBW} \\ &= 0.073 * 121.7 = 8.89 \text{ Mcal} \end{aligned}$$

$$\begin{aligned} ME_{Maint} &= 0.109 * \overline{MBW} \\ &= 0.109 * 121.7 = 13.27 \text{ Mcal} \end{aligned}$$

Solids-corrected milk production. NE requirement for SCM production (NE_{SCM}) is

$$NE_{SCM} = 0.340 * SCM,$$

since milk production has been solids-corrected to 340 kcal/lb (NRC, 1978; Flatt and Reid, 1965). ME requirement for SCM production (ME_{SCM}) is

$$\begin{aligned} ME_{SCM} &= NE_{SCM} \ / \ 0.6717 \\ &= 0.506 * SCM \ . \end{aligned}$$

The relationship between ME intake used for milk and net energy produced as milk is the reciprocal of efficiency, or 1.0 / 0.65.

Pregnancy. As described in section III.1, the variable $Preg_t$ represents the weight of fetal tissues ($e^{.0174t}$) on day t of pregnancy. Moe et al (1970) computed NE requirements for pregnancy (NE_{Preg}) of

$$NE_{Preg} = 0.065 * Preg \ .$$

The predicted ME requirements (ME_{Preg}) are

$$\begin{aligned} ME_{Preg} &= NE_{Preg} \ / \ 0.6717 \\ &= 0.097 * Preg \ . \end{aligned}$$

Bod

gai

res

ME

The

in

of

pro

the

eff

mob

the

0.8

for

the

4.

est

Thr

1

Body weight change. NRC (1978) estimates the NE requirements for weight gain (NE_{+WtChg}) and weight loss (NE_{-WtChg}) during lactation as:

$$NE_{+WtChg} = 5.12 * WtChg \text{ , and}$$

$$NE_{-WtChg} = 4.92 * WtChg,$$

respectively. These correspond to ME requirements (ME_{+WtChg} and ME_{-WtChg}) of

$$ME_{+WtChg} = 7.62 * WtChg \text{ , and}$$

$$ME_{-WtChg} = 7.32 * WtChg \text{ .}$$

The relationship between NE used for tissue gain or loss and the energy in that tissue can be expressed in two ways: for tissue gain, the ratio of tissue energy deposited per unit NE input; for tissue loss, NE produced per unit of tissue energy metabolized. Because the ratio is in the form of output per unit input, it can be interpreted as an efficiency. For weight gain, this efficiency is 0.75, while for tissue mobilization it is 0.82 (Moe et al, 1970). Thus, the net efficiency of the complete process of tissue deposition and metabolization is 0.75 x 0.82 = 62%. The same efficiencies were used to compute ME utilization for weight change, since the average relationship between ME and NE was the constant multiple 0.6717.

4. Results from regression analyses

Eighteen regression models were examined, and their coefficient estimates will be presented in tables grouping similar models together. Three types of comparisons can be made within each table:

1) Estimates for each coefficient can be compared to those for other coefficients. For example, b_1 can be contrasted with b_2, and so forth.

2) Corresponding coefficients from different models can be compared. If independent variables were completely uncorrelated, the expected value of b_0, for example, remains the same regardless of model used.

3) Estimates obtained from the same period of lactation may be compared. For example, estimates obtained from data recorded during negative energy balance may be contrasted to those from the entire lactation, or positive balance.

The index numbers (1) through (18) will be used to refer to each of the 18 models presented in section III. The number of animals included in regressions depended on which period was being analyzed. For a cow to be considered in a period of either positive or negative energy balance, she was required to have at least 50 days gaining or losing weight, repectively. This criterion was adopted to prevent cows only marginally gaining or losing weight from unduly influencing mean estimates. It eliminated 181 cows from being considered for negative energy balance, although none were restricted from positive balance. The number of cows included in a regression for any period were:

negative energy balance: n = 176;
positive energy balance: n = 357; and
entire lactation : n = 357.

Few cows were reported pregnant during negative energy balance. For this reason, no coefficient estimates are listed for models including a pregnancy term for periods of negative energy balance.

4.1. Multiple regression models

Tables IV.5 through IV.8 present mean coefficient estimates for models (1) through (12), which are shown below. The subscript i indicates day of observation.

(1) $NEI_i = b_0 + b_1SCM_i + e_i$

(2) $NEI_i = b_0 + b_1SCM_i + b_2WtChg_i + e_i$

(3) $NEI_i = b_0 + b_1SCM_i + b_2WtChg_i + b_3Preg_i + e_i$

(4) $NEI_i/MBW_i = b_0 + b_1(SCM_i/MBW_i) + e_i$

(5) $NEI_i/MBW_i = b_0 + b_1(SCM_i/MBW_i) + b_2(WtChg_i/MBW_i) + e_i$

(6) $NEI_i/MBW_i = b_0 + b_1(SCM_i/MBW_i) + b_2(WtChg_i/MBW_i) + b_3(Preg_i/MBW_i) + e_i$

(7) $MEI_i = b_0 + b_1NE_{SCM,i} + e_i$

(8) $MEI_i = b_0 + b_1NE_{SCM,i} + b_2NE_{WtChg,i} + e_i$

(9) $MEI_i = b_0 + b_1NE_{SCM,i} + b_2NE_{WtChg,i} + b_3NE_{Preg,i} + e_i$

(10) $MEI_i/MBW_i = b_0 + b_1(NE_{SCM,i}/MBW_i) + e_i$

(11) $MEI_i/MBW_i = b_0 + b_1(NE_{SCM,i}/MBW_i) + b_2(NE_{WtChg,i}/MBW_i) + e_i$

(12) $MEI_i/MBW_i = b_0 +b_1(NE_{SCM,i}/MBW_i) +b_2(NE_{WtChg,i}/MBW_i) +b_3(Preg_i/MBW_i) +e_i$

Models are grouped by method of energy intake measurement (ME or NE) and whether they are adjusted per unit MBW. Before considering each separately, some observations can be made which apply to all four tables.

Within each table, for all combinations of models and periods, the estimates of intercept were higher than predicted. Mean coefficients for b_1, corresponding to SCM, were low compared to values reported in the literature. Estimates of coefficients for WtChg, b_2, were variable but mostly positive, with larger coefficients of variation than b_0 or b_1. Finally, b_3, the coefficient for Preg, is generally negative. The

negative coefficient implies that supporting pregnancy generates rather than requires energy, which is not biologically reasonable. The standard deviation of mean coefficients tends to be largest when estimates are made during negative energy balance, smaller for positive energy balance, and smallest over the entire lactation. This is attributable to the greater numbers of observations on each cow in the latter two periods, compared to negative energy balance.

Table IV.5 contains results of regressions using models (1) through (3). Comparing results among models, there appears to be little change in b_1 or b_0 when the WtChg term is added to the model. Adding a pregnancy term causes slightly greater changes in the coefficients. Changes in coefficients estimated from different periods are not great for either b_0 or b_1. Differences between periods are larger for the coefficients of WtChg and Preg (b_2 and b_3), accompanied by larger coefficients of variation than either b_0 or b_1.

Table IV.6 presents coefficients from models (4) through (6), whose variables have been adjusted to a per-unit-MBW basis. If metabolic weight were constant throughout lactation, estimates of the intercept would be expected to differ from estimates using models (1) through (3), while other coefficients would be identical. In practice, MBW was not constant within animals, although its coefficient of variation was the smallest among the four independent variables considered. Therefore the coefficients for b_1 through b_3 all differ slightly from the first three models.

In contrast to the first six models, models (7) to (12) measured

Table IV.5 Mean regression coefficients in models with dependent variable measured as Net Energy, over periods of negative energy balance (-), positive energy balance (+), and over entire lactation (A). Corresponding standard deviations are parenthesized.

	b_0			b_1 [SCM]			b_2 [WtChg]			b_3 [Preg]		
Model	-	+	A	-	+	A	-	+	A	-	+	A
(1)	20.244	21.091	21.116	.153	.159	.151						
	(.950)	(.392)	(.365)	(.018)	(.008)	(.008)						
(2)	21.305	20.949	19.647	.155	.158	.170	4.461	.581	1.920			
	(.817)	(.471)	(.400)	(.015)	(.009)	(.008)	(1.202)	(.353)	(.293)			
(3)		22.934	22.133		.123	.131		.991	2.320		-.191	-.277
		(.558)	(.492)		(.009)	(.009)		(.507)	(.429)		(.117)	(.084)
Reported		8.52			.34			4.92			.007	

Table IV.6 Mean regression coefficients for models adjusted to a per-unit-MBW basis, with dependent variable measured as NEI/MBW, over periods of negative energy balance (-), positive energy balance (+), and over entire lactation (A). Corresponding standard deviations of means in parentheses.

	b_0			b_1 [SCM/MBW]			b_2 [WtChg/MBW]			b_3 [Preg/MBW]		
Model	-	+	A	-	+	A	-	+	A	-	+	A
(4)	.160	.152	.154	.168	.211	.199						
	(.005)	(.003)	(.003)	(.017)	(.008)	(.008)						
(5)	.170	.157	.147	.171	.201	.212	4.466	-.001	1.468			
	(.007)	(.004)	(.004)	(.015)	(.008)	(.008)	(1.209)	(.508)	(.466)			
(6)		.185	.177		.143	.151		1.089	2.182		-.394	-.392
		(.005)	(.004)		(.009)	(.009)		(.619)	(.556)		(.116)	(.090)
Reported		0.073			.34		4.92	5.12			.007	

independent variables in units of energy required for production, rather than quantity of production. The reciprocal of any regression coefficient except for the intercept indicated the efficiency of conversion of metabolizable energy into an output.

Results from using models (7) through (9) are shown in Table IV.7. Coefficients pertaining to milk production (b_1) were less than unity, which implies greater than 100% efficiency. Therefore this model was unacceptable for estimating efficiency of ME conversion to SCM. Likewise, accurate estimation of the efficiency of energy conversion to weight change and fetal growth was difficult. With the exception of estimates from negative energy balance, b_2 was computed as less than unity. Estimates of b_3, the energy required per Mcal increase in energy content of fetal tissues, were all less than zero. Generally, when Preg was included in the model, it adversely affected both the accuracy and the precision of the remainder of the coefficients.

Table IV.8 contains mean coefficient estimates and standard deviations of means from models (10) through (12). These models are similar to models (7) through (9), but have been adjusted to a per-unit-MBW basis. Regression coefficients for SCM and WtChg in models (7) through (12) are expressed as ME intake per unit NE used for maintenance or products. Reciprocals of these regression coefficients, that is, NE output per unit ME intake, were interpreted as the partial efficiencies of meeting the requirements of independent variables. Because a valid efficiency cannot exceed 100%, coefficients producing efficiencies greater than 100% were not regarded as biologically reasonable.

Coefficients for maintenance were about twice what has been

Table IV.7 Mean regression coefficients in models with dependent variable measured as ME, over periods of negative energy balance (-), positive energy balance (+), and over entire lactation (A). Corresponding standard deviations are parenthesized.

	b_0			b_1 [NE_{SCM}]			b_2 [NE_{WtChg}]			b_3 [NE_{Preg}]		
Model	-	+	A	-	+	A	-	+	A	-	+	A
(7)	29.509	30.619	30.631	.706	.741	.706						
	(1.426)	(.586)	(.547)	(.078)	(.036)	(.034)						
(8)	31.073	30.421	28.484	.718	.735	.789	1.380	.174	.579			
	(1.234)	(.706)	(.602)	(.067)	(.038)	(.036)	(.367)	(.107)	(.089)			
(9)		33.506	32.330		.572	.611		.300	.706		-.294	-.420
		(.839)	(.737)		(.040)	(.038)		(.155)	(.130)		(.125)	(.127)
Reported		13.11			1.54			1.20			.07	

Table IV.8 Mean regression coefficients in models adjusted to per-unit-MBW basis, with dependent variable measured as ME/MBW, over periods of negative energy balance (-), positive energy balance (+), and over entire lactation (A). Corresponding standard deviations are parenthesized.

	b_0			b_1 [NE_{SCM}/MBW]			b_2 [NE_{WtChg}/MBW]			b_3 [Preg/MBW]		
Model	-	+	A	-	+	A	-	+	A	-	+	A
(10)	.233 (.012)	.221 (.004)	.223 (.004)	.771 (.075)	.962 (.035)	.911 (.034)						
(11)	.249 (.010)	.228 (.006)	.212 (.005)	.786 (.067)	.921 (.037)	.969 (.036)	1.385 (.370)	-.001 (.154)	.444 (.141)			
(12)		.269 (.007)	.259 (.007)		.663 (.041)	.696 (.040)		.327 (.187)	.662 (.168)		-.588 (.174)	-.588 (.135)
Reported		.108			1.54			1.20			.07	

reported, increasing with the number of terms in the model. Estimates of intercepts were closer to predicted for periods having more observations, such as over the whole lactation, than for those having few observations, as during negative energy balance. The coefficients for SCM (b_2) also grew progressively worse as more variables were included in the model and when fewer observations were used to obtain estimates. Mean estimates of coefficients for WtChg (b_3) and Preg (b_4) are also given in Table IV.8. Although when computed from periods of negative energy balance they approach estimates reported in the literature, on the whole these estimates are less than unity, and often less than zero. Coupled with the adverse effects of including WtChg and especially Preg variables on intercept and SCM coefficients, there is little benefit to including these two variables in the model.

4.2. Two-stage multiple regression analyses

Two-stage models used in this research are shown below.

(13) Stage 1: $NEI_i/MBW_i = b_0 + b_1(NE_{SCM,i} + NE_{WtChg,i})/MBW_i + e_i$

Stage 2: $(NEI_i - b_0 MBW_i)/SCM_i = b_0' + b_1' WtChg_i/SCM_i + e_i'$

(14) Stage 1: $NEI_i/SCM_i = b_0 + b_1(NE_{Maint,i} + NE_{WtChg,i})/SCM_i + e_i$

Stage 2: $(NEI_i - b_0 SCM_i)/MBW_i = b_0' + b_1' WtChg_i/MBW_i + e_i'$

The results from two-stage regression are shown in Table IV.9, which follows the same format as the previous four tables of this section. Although the method of analysis differed from that of previous models, the expectations of coefficients from literature reports, made under the same assumption of independence among independent variables are identical to models (4) through (6).

Table IV.9 Mean regression coefficients in two-stage models with dependent variable measured as NE, over periods of negative energy balance (-), positive energy balance (+), and over entire lactation (A). Corresponding standard deviations are parenthesized.

	b_1 [MBW]			b_2 [SCM]			b_3 [WtChg]		
Model	-	+	A	-	+	A	-	+	A
(13)	.158	.151	.151	.184	.203	.193	4.621	.920	1.996
	(.006)	(.004)	(.003)	(.013)	(.009)	(.007)	(1.120)	(.243)	(.353)
(14)	.101	.103	.085	.336	.313	.352	4.153	1.864	2.483
	(.007)	(.003)	(.003)	(.017)	(.008)	(.009)	(1.234)	(.354)	(.333)
Reported		0.073			.34		4.92	5.12	

Model (13), as was found with each of the previous models, overestimated requirements for maintenance and underestimated those for SCM. Mean coefficient estimate of WtChg varied greatly with the stage of lactation, but had much higher standard deviations than those for either maintenance or SCM coefficients, whose standard deviations were in fact rather small.

Model (14) produced results closer to reported than any of the other models examined to this point. The coefficient for maintenance, though still 40% higher than reported values, differs by less than any other difference produced from previous models. Part of this smaller difference may be accounted for by some correlation between MBW and WtChg, as the coefficient for WtChg (b_3) was smaller than expected. Finally, the b_2 coefficient mean estimate, corresponding to NE required per pound of SCM produced, matched almost exactly previously reported research results. It was further encouraging that the standard deviation of the mean coefficients for MBW and SCM were rather small. This indicated that not only were the mean estimates of these coefficients reasonable, but the coefficients measured for most of the individual cows were reasonable as well. This property, that solutions for most cows be biologically meaningful, had not been satisfied by any of the previous thirteen models, and is important if we wish to estimate biological efficiency for animals without requiring energy chambers.

4.3 Consideration of serial autocorrelation of residuals

The last type of model considered was designed to compare the effects of an autoregressive residual term on estimates of energy utilization for milk production. Models (15) through (18), used to investigate the effect autocorrelated residuals, are listed below.

(15) $(NEI_i - \text{NE Reqt for } MBW_i + WtChg_i)/SCM_i = b_0 + e_i$,

$\quad$ where $e_i \sim (0,\sigma^2)$

(16) $(NEI_i - \text{NE Reqt for } MBW_i + WtChg_i)/SCM_i = b_0 + e_i$,

$\quad$ where $e_i = \rho * e_{i-1} + u_i$, $u \sim (0,\sigma_u^2)$

(17) $(MEI_i - \text{ME Reqt for } MBW_i + WtChg_i)/SCM_i = b_0 + e_i$,

$\quad$ where $e_i \sim (0,\sigma^2)$

(18) $(MEI_i - \text{ME Reqt for } MBW_i + WtChg_i)/SCM_i = b_0 + e_i$,

$\quad$ where $e_i = \rho * e_{i-1} + u_i$, $u \sim (0,\sigma_u^2)$

Two measures of energy intake were used, NE and ME. In each case, requirements for maintenance and weight change were held constant over all cows, so that only the coefficient for milk production was estimated. Regression coefficients obtained with and without the assumption of autocorrelation among residuals were compared.

Table IV.10 presents results from models using NE as the measure of energy intake. The regression coefficient is larger than reported regardless of whether the model is autoregressive, although b_1 values estimated without autocorrelation approached literature values more closely. Table IV.11 shows results from models which used ME as the measure of energy intake and held energy requirements for maintenance and weight change constant. The reciprocal of b_1 was taken as a measure of efficiency of conversion of ME to SCM. As before, regression coefficients were slightly higher than expected, resulting in computed efficiencies of 55% to 60%. Again, though, inclusion of an autoregressive residual term had more effect on the standard deviations of coefficient means than on the means themselves.

Table IV.10 Mean regression coefficients from models with and without autocorrelation coefficient, adjusted on a per-unit-MBW basis with dependent variable measured as NE, over periods of negative energy balance (-), positive energy balance (+), and over entire lactation (A). Corresponding standard deviations are parenthesized.

	b_1 [SCM]			autoregression coefficient (ρ)		
Model	-	+	A	-	+	A
(15)	.424 (.010)	.363 (.004)	.376 (.004)			
(16)	.500 (.061)	.415 (.041)	.392 (.013)	.685 (.013)	.751 (.006)	.769 (.006)
Reported		0.34				

Table IV.11 Mean regression coefficients from models assuming autocorrelation of residual terms adjusted to per-unit-MBW basis with dependent variable measured as ME, over periods of negative energy balance (-), positive energy balance (+), and over entire lactation (A). Corresponding standard deviations are parenthesized.

	b_1 [NE_{SCM}]			autoregression coefficient (ρ)		
Model	-	+	A	-	+	A
(17)	1.838 (.040)	1.665 (.016)	1.704 (.016)	.	.	.
(18)	1.692 (.168)	1.833 (.161)	1.732 (.022)	.629 (.014)	.689 (.006)	.713 (.006)
Reported		1.54			-	

By fitting an autoregressive model, we would expect that the variance of within lactation prediction error would decrease. Figures IV.1 and IV.2 illustrate differences in daily predicted ME intake throughout the lactation of a particular cow, from models with and without autoregression terms to actual data. The autoregressive model succeeds in reducing the correlations among consecutive residuals, and better follows the curve of daily energy intake. However, these figures also suggest the primary difficulty with applying results from using this type of model. To accurately estimate the energy required on day t requires measures of production such as SCM, WtChg, and MBW which are available. The autoregressive model also needs the residual from day t-1, which cannot be available until a lactation is completed and coefficients for regression and autocorrelation are computed. This dilemma might be at least partially resolved as data sets with more than one lactation per cow become available. The repeatabilities of autocorrelation and regression coefficients may be high enough to permit their estimation by an earlier lactation and use within later ones.

The second shortcoming with the autoregression models as implemented in this research concerns the inability of any iterative algorithm, such as the modified Cochrane-Orcutt (1949) algorithm used in this study, to guarantee globally best estimates of the autocorrelation coefficient or even ensure estimates within the parameter space (-1,1). When autoregression parameters greater than unity are estimated, regression coefficients frequently are so large or small in magnitude as to be rendered useless. As a result, population estimates can be greatly affected by the number of individuals whose autocorrelation coefficients are greater than unity. For example, Table IV.12 indicates

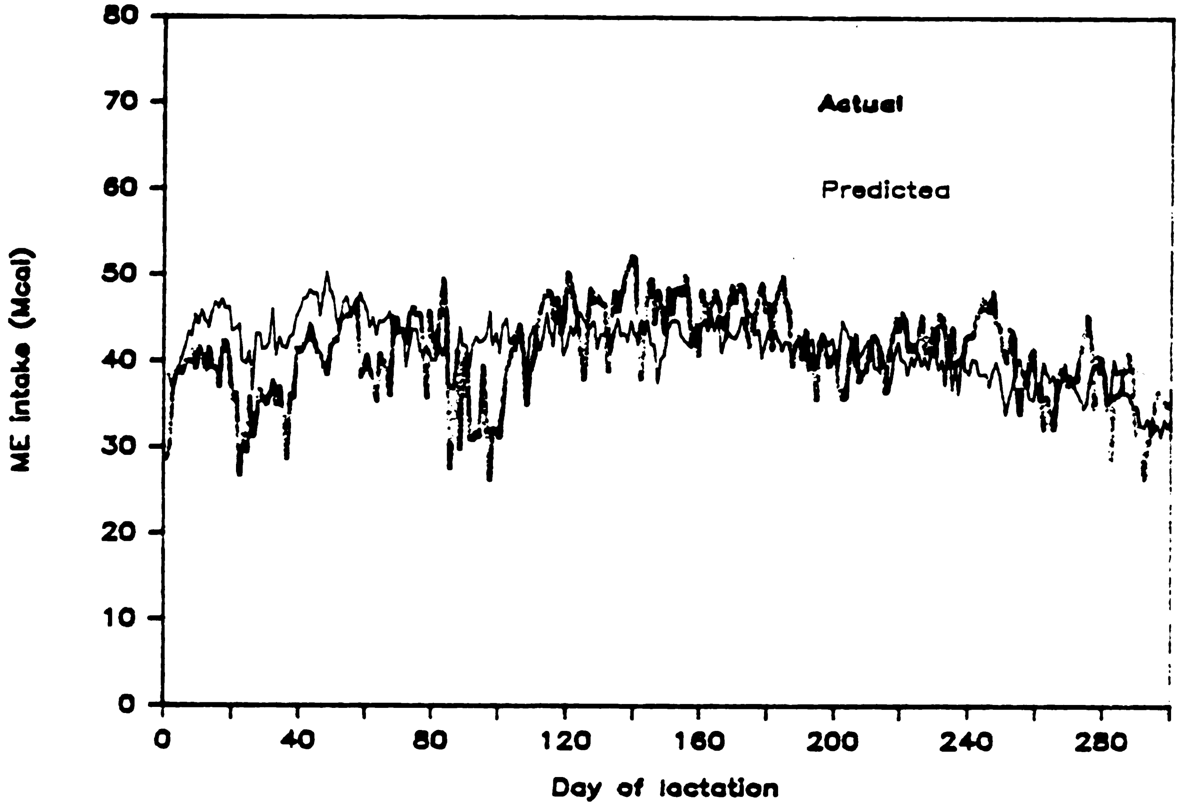

Figure IV.1 Predicted vs actual metabolizable energy intake in models without an autocorrelation coefficient

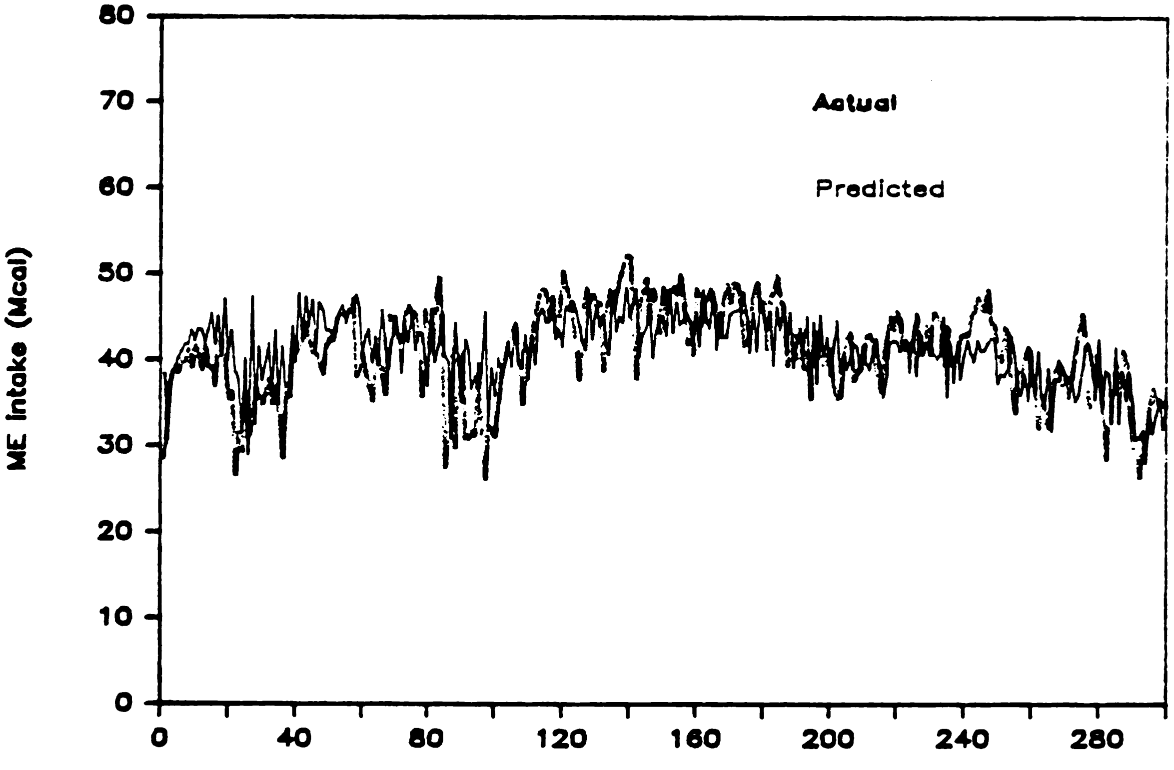

Figure IV.2 Predicted vs actual metabolizable energy intake in models with an autocorrelation coefficient the changes in population estimates for coefficients when cows having extreme ρ's are progressively eliminated from the data set. Clearly, the biggest change in estimates is obtained when cows with ρ greater than unity are eliminated. Limitations of $\rho < .95$ or $\rho < .90$ have comparatively small effects thereafter. Especially apparent is the large reduction in the standard deviation of the mean estimates, due to eliminating extreme animals, when those with $\rho > 1.0$ are deleted.

Table IV.12 Effect of eliminating cows having extreme autocorrelation coefficients on means and standard deviations of means for b_0 and autocorrelation coefficient obtained over entire lactation

Model (16)

Cows eliminated	Mean ρ	Mean b_1
None	$.769 \pm .006$	$.392 \pm .013$
$\rho > 1.0$	$.768 \pm .006$	$.379 \pm .004$
$\rho > .95$	$.767 \pm .005$	$.380 \pm .004$
$\rho > .90$	$.754 \pm .005$	$.376 \pm .004$

Model (18)

Cows eliminated	Mean ρ	Mean b_1
None	$.713 \pm .006$	$1.732 \pm .022$
$\rho > 1.0$	$.712 \pm .006$	$1.718 \pm .018$
$\rho > .95$	$.711 \pm .006$	$1.715 \pm .017$
$\rho > .90$	$.705 \pm .006$	$1.706 \pm .016$

4.4 Summary of estimates of partial efficiencies

Table IV.13 summarizes mean estimates of the partial energy efficiencies of maintenance and lactation obtained from each of the 18 models. All estimates were computed over the period of the entire lactation. The efficiency of converting ME to milk or maintenance is nearly the same, and reported as 65% by NRC

(1978). Only model (14) produced reasonable estimates of partial efficiencies of both maintenance and lactation. Models (15) through (18), while not designed to estimate partial efficiency for maintenance, produced reasonable estimates of efficiency of lactation. Values greater than unity, produced by models (1) through (13), are not reasonable as true efficiency estimates. Their relative value may still be useful to rank cows for partial efficiency of lactation, although this question was not further investigated.

Table IV.13 Summary table of estimates of partial efficiencies of lactation (k_ℓ) and maintenance (k_m)

Multiple regression models	k_m	k_ℓ
(1)	.271	1.52
(2)	.292	1.35
(3)	.259	1.75
(4)	.318	1.15
(5)	.334	1.08
(6)	.277	1.51
(7)	.287	1.47
(8)	.309	1.32
(9)	.272	1.69
(10)	.325	1.14
(11)	.342	1.06
(12)	.280	1.49

Two-stage models	k_m	k_ℓ
(13)	.325	1.18
(14)	.578	.649

Autocorrelation models	k_ℓ
(15)	.601
(16)	.581
(17)	.588
(18)	.578

Reported value = 0.65

5. Analyses of variance on regression coefficients from selected models

The results from eighteen regression models have been presented and discussed. From them, four models were selected and used in analyses of variance (ANOVA) to determine the effects of various factors present in the data on coefficients for individual cows. The models were chosen to be representative of the various combinations of independent and dependent variables; one was a two-stage model, one included autocorrelated residuals, and the remaining two were simultaneous multiple regression models. The models chosen are listed below:

$$\text{(7)} \qquad ME = b_0 + b_1\, E_{SCM} + e$$

$$\text{(10)} \qquad ME = b_1\, E_{MBW} + b_2\, E_{SCM} + e$$

$$\text{(14)} \qquad \text{Stage 1:} \quad NE = b_2\, SCM + b'\, E_{MBW+WtChg} + e$$

$$\text{Stage 2:} \quad NE - b_2\, SCM = b_1\, MBW + b_3\, WtChg + e$$

$$\text{(16)} \qquad NE_t - NE_{Maint,t} - NE_{WtChg,t} = b_1\, SCM_t + e_t$$

$$\text{where } e_t = \rho\, e_{t-1} + u_t\,, \quad u_t \sim (0, \sigma_u^2)$$

The coefficients used were computed over the entire lactation rather than only during positive or negative energy balance, to best reflect the cows' overall efficiencies.

Factors in the ANOVA model were described in section III.4. They were herd-season, ration, treatment with Actaplanin, parity, and covariates of total milk over the lactation and total milk squared. No two-way or higher interactions were included.

Complete tabular results from the analyses of variance are included in Appendix IV. A summary of these tables is presented in Table IV.14, which allows the comparison of factors of significance across models.

Most evident from Table IV.13 is the importance of herd-season on nearly all coefficients. Many possible reasons for influence of herd-season exist, ranging from different qualities of feedstuffs throughout the year and across herds, to temperature variation (possibly affecting maintenance requirements), and varying care in measuring or recording data among herds.

Table IV.13 Summary of significance of various factors on regression coefficients from selected models

	Model (7)		Model (10)		Model (14)			Model (16)	
	b_0	b_1	b_1	b_2	b_1	b_2	b_3	rho	b_0
Herd-Season	**	**	**	**	**	**	ns	**	ns
Ration	ns	ns	ns	*	ns	*	ns	**	*
Treatment	ns	ns	*	ns	ns	ns	ns	ns	ns
Parity	ns	ns	ns	ns	ns	ns	ns	ns	ns
Milk & Milk^2	ns	ns	*	ns	ns	**	ns	ns	ns

** : $\alpha < .01$
* : $\alpha < .05$
ns : $\alpha > .05$ (not significant)

The ration factor, which acts to partially block cows by production level, significantly affects coefficients in four of nine analyses. Although from this table it appears that the relationship between coefficients and milk production is not strong enough to warrant covariate terms, perhaps a simple blocking of production level into low, medium, or high groups would be effective in explaining variance.

Finally, neither treatment with Actaplanin nor parity appeared to have much effect on coefficients. We would expect the consequences of ignoring these two factors to be small when studying differences in coefficients among cows.

V. CONCLUSIONS

Data from Lilly Research laboratories was examined by 18 regression models. The data consisted of measurements on milk production, component percentages, body weights and intake through complete lactations of 405 cows. Cows were distributed in seven herds, and fed one of four rations by determined by production level and parity. A nuisance treatment, dosage of the pharmaceutical Actaplanin, was also recorded. Models were investigated for their ability to yield energy utilization coefficients approaching those obtained using data from animals in energy chambers.

Tabulation of the data revealed that an average of over 90% of net energy during lactation goes into meeting requirements of milk production and maintenance. Of all metabolic needs for energy during lactation, pregnancy support was found to require the least amount of energy, less than 1% in nearly all cases. The energy requirements for gain or energy yield from loss of body tissue were also smaller than those for either milk production or maintenance, generally in the range of ± 15% of net energy intake.

Multiple linear regression models were used to compute coefficient estimates describing energy conversion into useful product. Compared to previously published results, this method produced consistently higher efficiencies for satisfying maintenance requirements, and lower for meeting the needs of milk production. The efficiencies computed for pregnancy and weight change were more widely variable across cows than those computed for milk production and maintenance. Adjustment of variables to a per-unit-MBW basis did not improve estimates compared to those predicted from energy chamber work. Likewise, considering energy as Net Energy versus Metabolizable Energy had only a modest effect on the relative magnitudes of partial efficiencies for milk production and maintenance. Finally, increasing the number of output products considered as a function of energy inputs in a model adversely affected the correspondence of resulting coefficients to published values from energy chamber research.

A two-stage multiple regression procedure which fit milk alone in the first stage, followed by maintenance and weight change in the second, was superior to all other models in the comparison of computed regression coefficients to published values. Further, the estimates of partial efficiencies for the various forms of production were biologically reasonable for nearly all cows. However, when maintenance was fit first followed by milk and weight change, the fit was no better than for the multiple regression described in the previous paragraph.

Finally, the effect of assuming autocorrelated residuals was examined. The main advantage to using an autoregressive model appeared to be in its accuracy of predicting daily feed intakes from previous days' productions and intakes. However, estimates for energy efficiencies were somewhat poorer than from models without autoregression, compared to reported values. A second difficulty was the periodic occurence of autocorrelation coefficients outside the parameter space, specifically greater than unity. This problem affected a small number of cows, and could be overcome using more elaborate computational techniques.

Analyses of variance were performed on resultant coefficients from several models to ascertain common significant sources of variation. Herd-season was found to be highly significant for one or more coefficients from every model. Several coefficients were moderately to highly affected by Ration, but not to the degree of Herd-season. The nuisance variable of Treatment, as well as Parity and covariates of Milk and $Milk^2$ were, in general, not found to be significant sources of variation.

This research has shown that estimating parameters of production efficiency from data collected on-farm has the potential to supplement expensive, limited energy chamber studies. Before widespread application of these findings, however, several further questions must be addressed:

1. The results and comparisons reported in this study deal only with mean parameter estimates. Research must be conducted to show that estimates for individual animals obtained from data collected on-farm correspond to those from data collected on the same cows in energy chambers. Examination of this question might require gathering data for analysis from a small number of animals in energy chambers, and using a subset of that data to emulate an on-farm collection scheme. This subset would be analyzed as I have described in this paper.

2. One of the shortcomings of the data set was the infrequency of body weights on individuals. The effect of more frequent weighings should be examined, and a weighing schedule developed which would

specify the number and days of weight measurements that optimize estimation of a body weight curve. In this way, measurement error for body weight change would be reduced, and daily energy balance could be more accurately estimated.

3. The data for this research did not include observations from subsequent lactations, nor from dry periods. Observations from more than one lactation would enable the computation of repeatabilities, while data from the dry periods could yield better estimates of energy utilization for pregnancy, weight change, and maintenance without the simultaneous influence of milk production.

Application of this research may be seen to benefit many facets of the dairy industry. As automated feeding and data-collection systems become more common on commercial dairy farms, a body of data could be developed which would enable scientists to compute genetic parameters of partial efficiencies. As the quantity of data grows, sire evaluation for efficiency measures would become feasible. At the same time, the genetic relationship between efficiency and milk production or conformation could be computed.

To estimate coefficients of energy conversion into products on a routine basis at the commercial dairy level, certain data must be collected regularly. Minimally these include energy intake, milk production, butterfat test, and body weight. The minimum necessary frequency of data collection has not been addressed by this research and may vary depending on the variable observed. The importance of frequent body weighings, for use in computing rate of tissue gain or loss, should be emphasized.

The application of efficiency data collected on a commercial herd may produce immediate benefits to the herd itself. Because of the logistics and expense of putting a commercial herd through an energy chamber to collect data, little research has been reported concerning the effects of differences in efficiency on animal health. Also, the effects of additives (such as growth hormone or antibiotics) or management techniques (such as three- or four-times-per-day milking) have not been studied within commercial herds. If these findings make such research possible, tomorrow's dairy farmer may be able to tailor his management of individual cows to maximize the profitability of each one, and obtain the most profit, rather than simply the most milk, that his herd can produce.

APPENDICES

Appendix I.

Tabulation of data

Table I.1. Distribution of cows among numbers of recorded milk weights

	number of recorded milk weights						
	<200	201-225	226-250	251-275	276-300	301-325	>325
N of cows	36	4	12	52	233	68	0

Table I.2. Distribution of cows among parities

	parity								
	1	2	3	4	5	6	7	8	other
N of cows	106	147	68	26	18	9	4	6	21

Table I.3. Distribution of cows among calving groups

	calving group								
	1	2	3	4	5	6	7	8	other
N of cows	107	97	81	45	28	20	10	3	14

Table I.4. Distribution of cows among daily milk production averages

	average milk production (lbs/day)										
	<35	35-40	40-45	45-50	50-55	55-60	60-65	65-70	70-75	75-80	>80
N of cows	11	21	50	58	94	80	45	19	10	8	9

Table I.5. Distribution of cows among months of initiation of lactation

	month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
N of cows	31	38	24	12	8	11	35	38	50	69	50	39

Table I.6. Distribution of cows among treatments with Actaplanin

	dosage code				
	BN	CN	DN	EN	error
N of cows	96	99	99	97	14

Table I.7. Distribution of cows among herds

Herd location	N of cows
Greenfield, IN	71
Western Kentucky	44
Pennsylvania	62
Southern Illinois	44
California	61
Michigan	64
North Carolina	59

Table I.8. Distribution of cows among milk levels

	milk level				
	Heifer	Low	Medium	High	error
N of cows	105	65	143	78	14

Appendix II.

Descriptions of algorithms used to modify variables

A. Adjustment of milk weights for actual daily milk produced

This adjustment must be used when the cow secretes on day i some fraction p of the milk that she actually produces on day i. The actual algorithm for adjusting milk secreted to milk produced on day i is:

$$\text{Milk produced}_i = \sum_{i=1}^{301-i} p^i(\text{Milk secreted}_i)$$

for example, when p=0.75, the milk produced on day 10 would be computed by:

$$0.75(\text{milk}_{10}) + 0.75^2(\text{milk}_{11}) + 0.75^3(\text{milk}_{12}) \ . \ . \ .$$

where milk_i = milk secreted on day i. However, this method is rather expensive to use computationally. A numerical approximation used in this research was

$$\text{Milk produced}_i = \sum_{i=1}^{i} p^i(\text{Milk secreted}_i)$$

Because of the relatively small daily change in milk producing ability and the comparatively large distortion in milk produced caused by residuals, this technique will approximate the first method quite well. Its advantage is in computational simplifications, where daily milk produced can be computed using the algorithm:

```
      MILKP=MILK(1)
      DO 1 I=1,NDAYS
      MILKP = P*MILK(I) + (1.-P)*MILKP
         .
         .
         .
 1    CONTINUE
```

where the first MILKP is milk produced on the current day, the second is the previous day's milk produced, MILK(I) is milk secreted on current day, and P is the fraction of milk produced on one day which is secreted the same day.

B. Distributed delay for estimating energy availability

A delay routine is used to account for feed intake not being instantaneously converted to energy, but rather gradually digested and absorbed. Llewelllyn (1965) provided a source for a subroutine which simulates such a delay.

```
      SUBROUTINE DELDT(RINR,ROUTR,CROUTR,DEL,IDT,DT,K)
      DIMENSION CROUTR(K)
C
C definition of variables:
C     RINR = input rate
C     ROUTR = output rate
C     CROUTR = array holding intermediate rates
C     DEL = delay half-life; i.e. time for 1/2 input to be output
C     IDT = # of internal "micro-delays" to produce smoother output
C     DT = distance between inputs (i.e. 1 day)
C     K = length of CROUTR
C
      DEL1=DEL*FLOAT(IDT)/(FLOAT(K)*DT)
      ROUTR=0.
      DO 2 J=1,IDT
          RIN=RINR/FLOAT(IDT)
          DO 1 I=1,K
              ABC=CROUTR(I)
              CROUTR(I)=ABC+(RIN-ABC)/DEL1
              RIN=ABC
1             CONTINUE
          ROUTR=ROUTR+CROUTR(K)
2         CONTINUE
      RETURN
      END
```

To use such a routine, CROUTR is initialized to the first input rate, and the subroutine is then called at regular intervals, with RINR as input, and ROUTR as desired output.

C. Estimation of body weight curve from discrete weights

For purposes of this research, a fourth-degree polynomial was fit, but the procedure is applicable to polynomials of any degree. There is a danger, when using too high a degree, of obtaining a nearly singular incidence matrix which introduces inaccuracies into the solutions. In our case, the 60-bit single precision of a CDC Cyber series mainframe computer combined with no more than quartic equations produced reliable results for estimating weights to more than 5 digits. This was sufficient for our purposes.

```
      SUBROUTINE WTCURV(WEIGHT,N,B)
      DIMENSION WEIGHT(N),B(5)
C
C description of variables:
C     WEIGHT = array of weighing days in col 1 and weights in col 2
C     B = solutions to 4th degree equation (output)
C     N = # of observations in WEIGHT
C
      ...initialize X'X and X'y to 0...(not shown)

      X(1)=1.
      DO 1 I=1,N
          T=WEIGHT(I,1)
          DO 2 I=2,5
              X(K)=T*X(K-1)
 2            CONTINUE
          Y=WEIGHT(I,2)

          ...add X and y to X'X and X'y equations...(not shown)

 1        CONTINUE

      ...solve equation X'Xb = X'y...(not shown)

      RETURN
      END
```

Appendix III.

Single pass algorithm of Cochrane-Orcutt procedure for analyzing regression models containing autocorrelated residuals

Ordinary multiple regression has the form

$$\begin{pmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \\ \cdot \\ \cdot \\ \cdot \\ y_n \end{pmatrix} = \begin{pmatrix} 1 & x_{1,1} & x_{1,2} & x_{1,3} & x_{1,4} & \cdots & x_{1,m} \\ 1 & x_{2,1} & x_{2,2} & x_{2,3} & x_{2,4} & \cdots & x_{2,m} \\ 1 & x_{3,1} & x_{3,2} & x_{3,3} & x_{3,4} & \cdots & x_{3,m} \\ 1 & x_{4,1} & x_{4,2} & x_{4,3} & x_{4,4} & \cdots & x_{4,m} \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \\ 1 & x_{n,1} & x_{n,2} & x_{n,3} & x_{n,4} & \cdots & x_{n,m} \end{pmatrix} \begin{pmatrix} b_0 \\ b_1 \\ b_2 \\ b_3 \\ b_4 \\ \cdot \\ \cdot \\ b_m \end{pmatrix} + \begin{pmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \\ \cdot \\ \cdot \\ \cdot \\ e_n \end{pmatrix}$$

$$= \begin{pmatrix} x_1' \\ x_2' \\ x_3' \\ x_4' \\ \cdot \\ \cdot \\ \cdot \\ x_n' \end{pmatrix} b + \begin{pmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \\ \cdot \\ \cdot \\ \cdot \\ e_n \end{pmatrix}$$

$$y = X \quad b + e$$

However, when residuals are autocorrelated, the error structure is

$$e_t = \rho e_{t-1} + u_t, \text{ where } \mathbf{u} \sim N(\mathbf{0}, \sigma^2_u \mathbf{I})$$

and

$$V(\mathbf{e}) = \begin{bmatrix} 1 & \rho & \rho^2 & \rho^3 & \rho^4 & . & . & . \\ \rho & 1 & \rho & \rho^2 & \rho^3 & . & . & . \\ \rho^2 & \rho & 1 & \rho & \rho^2 & . & . & . \\ \rho^3 & \rho^2 & \rho & 1 & \rho & . & . & . \\ \rho^4 & \rho^3 & \rho^2 & \rho & 1 & & & \\ . & . & . & . & & . & & \\ . & . & . & . & & & . & \\ . & . & . & . & & & & . \end{bmatrix}$$

At time t,

$$y_t = \mathbf{x}_t'\mathbf{b} + e_t = \mathbf{x}_t'\mathbf{b} + \rho e_{t-1} + u_t \qquad (1)$$

and at time t-1,

$$y_{t-1} = \mathbf{x}'_{t-1}\mathbf{b} + e_{t-1} \,. \qquad (2)$$

Multiplying (2) by ρ and subtracting from (1) yields

$$y_t - y_{t-1} = (\mathbf{x}_t' - \rho\mathbf{x}_{t-1}')\ \mathbf{b} + u_t$$

which can be expanded

$$\begin{bmatrix} y_2 - \rho y_1 \\ y_3 - \rho y_2 \\ y_4 - \rho y_3 \\ y_5 - \rho y_4 \\ \cdot \\ \cdot \\ \cdot \\ y_n - \rho y_{n-1} \end{bmatrix} = \begin{bmatrix} x_2' - \rho x_1' \\ x_3' - \rho x_2' \\ x_4' - \rho x_3' \\ x_5' - \rho x_4' \\ \cdot \quad \cdot \\ \cdot \\ \cdot \\ x_n' - \rho x_{n-1}' \end{bmatrix} b + u$$

or

$$y^* = X^* b + u \ .$$

Setting up the normal equations and solving,

$$\hat{b} = (X^{*\prime}X^*)^{-1}X^{*\prime}y^* \ .$$

Terms on the right hand side of this equation can be expressed as

$$X^{*\prime}X^* = \{a_{ij}\} = \sum_{k=2}^{n} (x_{ki} - \rho x_{k-1,i})(x_{kj} - \rho x_{k-1,j})$$

$$= \sum_{k=2}^{n} x_{ki}x_{kj} - \rho \sum_{k=2}^{n} x_{ki}x_{k-1,j} - \rho \sum_{k=2}^{n} x_{k-1,i}x_{kj} + \rho^2 \sum_{k=2}^{n} x_{k-1,i}x_{k-1,j} \tag{3}$$

and

$$X^{*\prime}y^* = \{c_i\} = \sum_{k=2}^{n} (x_{ki} - \rho x_{k-1,i})(y_k - \rho y_{k-1})$$

$$= \sum_{k=2}^{n} x_{ki}y_k - \rho \sum_{k=2}^{n} x_{k-1,i}y_k - \rho \sum_{k=2}^{n} x_{ki}y_{k-1} + \rho^2 \sum_{k=2}^{n} x_{k-1,i}y_{k-1} \ . \tag{4}$$

Note that each summation in (3) and (4) is constant with respect to ρ and so needs only to be computed once and recalled for each iteration when converging on ρ. Thus, **b** and ρ can be computed iteratively while requiring only one pass through the data.

On each iteration, $\hat{\rho}$ is computed using the relationship between consecutive residuals:

$$\hat{e}_t = \rho\, \hat{e}_{t-1} + u_t$$

and

$$\hat{\mathbf{e}} = \mathbf{y} - \mathbf{X}\hat{\mathbf{b}} \quad .$$

Therefore

$$\hat{\rho} = \frac{\sum_{k=2}^{n} \hat{e}_{t-1}\hat{e}_t}{\sum_{k=2}^{n} \hat{e}_t^2} \quad . \tag{5}$$

Numerator and denominator in (5) are computed by

$$\begin{aligned}\sum_{k=2}^{n} \hat{e}_{t-1}\hat{e}_t &= \sum_{k=2}^{n} (y_{k-1} - \mathbf{x}_{k-1}\hat{\mathbf{b}})(y_k - \mathbf{x}_k\hat{\mathbf{b}}) \\ &= \sum_{k=2}^{n} y_{k-1}y_k - \sum_{i=0}^{m} \hat{b}_i \left(\sum_{k=2}^{n} x_{k-1,i}y_k \right) - \sum_{i=0}^{m} \hat{b}_i \left(\sum_{k=2}^{n} x_{kj}y_{k-1} \right) \\ &\quad + \sum_{i=0}^{m} \sum_{j=0}^{m} \hat{b}_i\hat{b}_j \left(\sum_{k=2}^{n} x_{k-1,i}x_{kj} \right)\end{aligned} \tag{6}$$

and

$$\begin{aligned}\sum_{k=2}^{n} \hat{e}_t^2 &= \sum_{k=2}^{n} (y_k - \mathbf{x}_k\hat{\mathbf{b}})(y_k - \mathbf{x}_k\hat{\mathbf{b}}) \\ &= \sum_{k=2}^{n} y_k y_k - 2 \sum_{i=0}^{m} \hat{b}_i \left(\sum_{k=2}^{n} x_{ki}y_k \right) + \sum_{i=0}^{m} \sum_{j=0}^{m} \hat{b}_i\hat{b}_j \left(\sum_{k=2}^{n} x_{ki}x_{kj} \right)\end{aligned} \tag{7}$$

respectively. Note that each inner summation over n in (6) and (7) is invariant to **b** and ρ, which enables computation on one pass through the data.

Appendix IV.

Analyses of variance on coefficients from selected models

Table A.IV.1 Analyses of variance on estimates obtained over the complete lactation from model (7):

$$ME = b_0 + b_1 NE_{SCM} + e$$

(a) ANOVA for b_0

Factor	df	Partial SSQ	MS	F test	
Herd-Season	24	8870.3098	369.5962	4.7060	**
Ration	3	369.6157	123.2052	1.5687	
Treatment	3	401.6214	133.8738	1.7046	
Age	2	59.8698	29.9349	0.3812	
Milk + Milk^2	2	277.5130	138.7565	1.7668	
Residual	322	25289.1151	78.5376		
Total	356	37999.6875			

(b) ANOVA for b_1

Factor	df	Partial SSQ	MS	F test	
Herd-Season	24	51.0875	2.1286	7.7611	**
Ration	3	1.5732	0.5244	1.9120	
Treatment	3	0.5695	0.1898	0.6921	
Age	2	0.0546	0.0273	0.0995	
Milk + Milk^2	2	0.1237	0.0619	0.2255	
Residual	322	88.3154	0.2743		
Total	356	147.5734			

Critical values:		$\alpha = .05$	$\alpha = .01$
	$F_{24,322} =$	1.55	1.83
	$F_{3,322} =$	2.62	3.84
	$F_{2,322} =$	3.02	4.66

Table A.IV.2 Analyses of variance on estimates obtained over the complete lactation from model (10)

$$ME/MBW = b_0 + b_1\ NE_{SCM}/MBW + e$$

(a) ANOVA for b_1

Factor	df	Partial SSQ	MS	F test
Herd-Season	24	0.5660	0.0236	5.4752 **
Ration	3	0.0034	0.0011	0.2592
Treatment	3	0.0394	0.0131	3.0468 *
Age	2	0.0008	0.0004	0.0963
Milk + Milk^2	2	0.0319	0.0160	3.7077 *
Residual	322	1.3870	0.0043	
Total	356	2.2018		

(b) ANOVA for b_2

Factor	df	Partial SSQ	MS	F test
Herd-Season	24	52.1432	2.1726	9.0831 **
Ration	3	2.1370	0.7123	2.9781 *
Treatment	3	0.8797	0.2932	1.2259
Age	2	0.0815	0.0408	0.1704
Milk + Milk^2	2	1.0528	0.5264	2.2007
Residual	322	77.0205	0.2392	
Total	356	145.6503		

Critical values:	$\alpha = .05$	$\alpha = .01$
$F_{24,322}$ =	1.55	1.83
$F_{3,322}$ =	2.62	3.84
$F_{2,322}$ =	3.02	4.66

Table A.IV.3 Analyses of variance on estimates obtained from two-stage model (14)

Stage 1: $NE/SCM = b_1 + b' (NE_{MBW}+NE_{WtChg})/SCM + e$

Stage 2: $(NE - b_1 SCM)/MBW = b_0 + b_2 WtChg/MBW + e$

(a) ANOVA for b_0

Factor	df	Partial SSQ	MS	F test
Herd-Season	24	0.1891	0.0079	2.6277 **
Ration	3	0.0136	0.0045	1.5071
Treatment	3	0.0056	0.0019	0.6257
Age	2	0.0008	0.0004	0.1250
Milk + Milk^2	2	0.0113	0.0057	1.8839
Residual	322	0.9657	0.0030	
Total	356			

(b) ANOVA for b_1

Factor	df	Partial SSQ	MS	F test
Herd-Season	24	2.1084	0.0879	4.4247 **
Ration	3	0.1823	0.0608	3.0606 *
Treatment	3	0.0273	0.0091	0.4583
Age	2	0.0278	0.0139	0.7001
Milk + Milk^2	2	0.3265	0.1633	8.2223 **
Residual	322	6.3931	0.0199	
Total	356	9.2522		

(c) ANOVA for b_2

Factor	df	Partial SSQ	MS	F test
Herd-Season	24	499.5187	20.8133	0.5165
Ration	3	46.6595	15.5532	0.3860
Treatment	3	200.4571	66.8190	1.6581
Age	2	64.5340	32.2670	0.8007
Milk + Milk^2	2	139.7847	69.8924	1.7344
Residual	322	12976.0263	40.2982	
Total	356	14118.7647		

Critical values:		$\alpha = .05$	$\alpha = .01$
	$F_{24,322}$ =	1.55	1.83
	$F_{3,322}$ =	2.62	3.84
	$F_{2,322}$ =	3.02	4.66

Table A.IV.4 Analyses of variance on estimates including autocorrelation coefficient obtained over the complete lactation from model (16):

$$(NE_t - NE_{Maint,t} - NE_{WtChg,t})/SCM = b_0 + e_t$$

$$\text{where } e_t = \rho \, e_{t-1} + u_t \, , \; u_t \sim N(0,\sigma_u^2)$$

(a) ANOVA for ρ

Factor	df	Partial SSQ	MS	F test
Herd-Season	24	0.7110	0.0296	3.2602 **
Ration	3	0.1174	0.0391	4.3049 **
Treatment	3	0.0381	0.0127	1.3975
Age	2	0.0040	0.0020	0.2190
Milk + Milk^2	2	0.0214	0.0107	1.1786
Residual	322	2.9261	0.0091	
Total	356	3.9029		

(b) ANOVA for b_0

Factor	df	Partial SSQ	MS	F test
Herd-Season	24	0.8773	0.0366	0.6149
Ration	3	0.6687	0.2229	3.7495 *
Treatment	3	0.1728	0.0576	0.9691
Age	2	0.2668	0.1334	2.2439
Milk + Milk^2	2	0.3211	0.1605	2.7002
Residual	322	19.1432	0.0595	
Total	356	21.2083		

Critical values:	$\alpha = .05$	$\alpha = .01$
$F_{24,322}$ =	1.55	1.83
$F_{3,322}$ =	2.62	3.84
$F_{2,322}$ =	3.02	4.66

LIST OF REFERENCES

A
l

B
A

B
p
S

B
P

B
P
a

B
l
B

B
p
a

B
S
e

B
t
a

B
P

B
r

B
e

B
s

LIST OF REFERENCES

Agricultural Research Council. 1965. The nutrient requirements of farm livestock. No. 2. Ruminants. Agric. Res. Counc., London.

Baldwin, RL, AC Bywater. 1984. Nutritional energetics of animals. Ann. Rev. Nutr. 4:101.

Baldwin, RL, NE Smith, J Taylor, M Sharp. 1980. Manipulating metabolic parameters to improve growth rate and milk secretion. J. Anim. Sci. 51:1416.

Bath, DL, FN Dickenson, HA Tucker, RD Appleman. 1978. Dairy Cattle: Principles, Practices, Problems, Profits. Lea & Febiger, Philadelphia.

Bauman, DE, WB Currie. 1980. Partitioning of nutrients during prognancy and lactation: A review of mechanisms involving homeostasis and homeorhesis. J. Dairy Sci. 63:1514.

Bauman, DE, JM Elliot. 1983. Control of nutrient partitioning in lactating ruminants. In: Biochemistry of Lactation, Mepham, TB (Ed.). Elsevier Sci. Publ. B.V. pp 437-468.

Bauman, DE, PJ Eppard, MJ DeGeeter, GA Lanza. 1985a. Responses of high-producing dairy cows to long-term treatment with pituitary somatotropin and recombinant somatotropin. J. Dairy Sci. 68:1352.

Bauman, DE, SN McCutcheon, WD Steinhour, PJ Eppard, SJ Sechen. 1985b. Sources of variation and prospects for improvement of productive efficiency in the dairy cow: a review. J. Anim. Sci. 60:583.

Blaxter, KL, EP Reineke, FW Crampton, WE Peterson. 1949. The role of thyroidal materials and synthetic goitrogens in animal production and an appraisal of their practical use. J. Anim. Sci. 8:307.

Blaxter, KL. 1961. The utilization of the energy of food by ruminants. Proc. 2nd Symp. Energy Metab. EAAP Publ. 10:211.

Blaxter, KL. 1974. Metabolizable energy and feeding systems for ruminants. In: H Swan and D Lewis (Eds.) Nutrition conference for feed manufacturers, No. 7, pp 3-26.

Blaxter, KL, NMcC Graham. 1955. Plane of nutrition and starch equivalents. J. Agric. Sci., Camb. 46:292.

Blaxter, KL, FW Wainman. 1964. Use of energy of different rations by sheep and cattle. J. Agric. Sci., Camb. 63:113.

Blaxter,KL, AW Boyne. 1978. The estimation of the nutritive value of feeds as energy sources for ruminants and the derivation of feeding systems. J. Agric. Sci., Camb. 90:47.

Bodoh, CW, WJ Tyler, LH Schultz, GE Shook. 1972. Thyroid activities of Holstein cows selected for high or average milk production. J. Dairy Sci. 55:682.

Brody, S, WC Hall. 1932. Mo. Res. Bull. #180.

Brody, S. 1945. Bioenergetics and growth. New York:Reinhold.

Broster, WH, VJ Broster, T Smith. 1969. Experiments on the nutrition of the dairy heifer. VIII. Effect on milk production of feeding at two stages of lactation. J. Agric. Sci., Camb. 72:229.

Broster, WH, VJ Broster, T Smith, JW Siviter. 1975. Experiments on the nutrition of the dairy heifer IX. Food utilisation in lactation. J. Agric. Sci., Camb., 84:173.

Brown LD. 1966. Influence of intake on feed utilization. J. Dairy Sci. 49:223.

Brown, CA, CC Stallings, SW Telega. 1981. Nutritional modeling and its impact on manegerial goals in dairy production. J. Dairy Sci. 64:2083.

Bryant, AM, TE Trigg. 1981.Progress report on the performance of Jersey cows differing in breeding index. Proc. New Zealand Soc. Anim. Prod. 41:39

Byers, FM, RE Rompala. 1980. Level of energy effects on patterns and energetic efficxiency of tissue deposition in small or large mature size beef cattle. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:141.

Bywater, AC. 1984. A generalized model of feed intake and digestion in lactating cows. Agric. Sys. 13:167.

Cochrane, D, GH Orcutt. 1949. Application of least squares regressions to relationships containing autocorrelated error terms. J. Am. Stat. Assoc. 44:32.

Collier, RJ, JP McNamara, CR Wallace, MH Dehoff. 1984. A review of endocrine regulation of metabolism during lactation. J. Anim. Sci. 59:498.

Colovos, NF, JB Holter, RM Clark, WE Urban Jr, HH Hayes. 1970. Energy expenditure in physical activity of cattle. Proc. 5th Symp. Energy Metab. EAAP Publ. 13:89.

Colucci, PE, LE Chase, PJ Van Soest. 1982. Feed intake, apparent diet digestibility, and rate of particulate passage in dairy cattle. J. Dairy Sci. 65:1445.

Coppock, CE. 1964. The utilization of metabolizable energy for milk production by dairy cows. Ph.D. thesis, University of Maryland.

Coppock, CE, WP Flatt, LA 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, AA, RW Blake, PF Dahm, TC Cartwright, GT Schelling, CE Coppock. 1983. Relationships between measures of feed efficiency and transmitting ability for milk of Holstein cows. J. Dairy Sci. 66:1937.

Davey, AWF, C Grainger, DDS MacKenzie, DS Flux, GF Wilson, IM Brookes, CW 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.

Davis,SR, RJ Collier, JP McNamara, HH Head. 1983. Effect of growth hormone and thyroxine treatment of dairy cows on milk production, cardiac output and mammary blood flow. Proc. New Zealand Soc. Endocr. 26:31.

DeBrabander, DL, PM Ghekiere, JV Aerts, FX Buysse, RJ Moermans. 1982. Tests of 6 energy evaluation systems for dairy cows. Livestock Prod. Sci. 9:457.

Eppard, PJ, DE Bauman, SN McCutcheon. 1985. Effect of dose of bovine growth hormone on lactation of dairy cows. J. Dairy Sci. 68:1109.

Flatt, WP, PW Moe. 1971. Partition of nutrients between lactation and body weight gain in dairy cattle. In: D. Falconer (ed), Lactation. Butterworth, London, pp 341-347.

Flatt, WP, PW Moe AW Munson, T Cooper. 1970. Energy utilization by high-producing dairy cows II. Summary of energy balance experiments with lactating Holstein cows. Proc. 5th Symp. Energy Metab. EAAP Publ. 13:89.

Forbes, JM. 1977. Development of a model of voluntary food intake and energy balance in lactating cows. Anim Prod. 24:203.

Forbes, JM. 1983. Models for the prediction of food intake and energy balance in dairy cows. Livestock Prod. Sci. 10:149.

Garrett, N. 1980. Energy utilization by growing cattle as determined in 72 comparative slaughter experiments. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:3.

Garrett, WN, DE Johnson. 1983. Nutritional energetics of ruminants. J. Anim. Sci. 57 (Supp 2):478.

Geay, Y, J Robelin, M Vermorel. 1980. Influence of the metabolizable energy contenet of the diet on energy utilization for growth in bulls and heifers. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:9.

Geers, R, H Michels. 1982. Metabolic body size: A biological and/or a mathematical concept? Proc. 9th Symp. Energy Metab. EAAP Publ. 29:135.

Graham, NMcC. 1982. Energy feeding standards: A methodological problem. Proc. 9th Symp. Energy Metab. EAAP Publ. 29:108.

Grieve, DG, GK MacLeod, TR Batra, EB Burnside, JB 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.

Hart, IC. 1973. Effect of 2-Br-alpha-ergocryptine on milk yield and the level of prolactin and growth hormone in the blood of the goat at milking. J. Endocr. 57:179.

Hart, IC, JA Bines, SV Morant, JL Ridley. 1978. Endocrine control of energy metabolism in the cow: comparison of the levels of hormones (prolactin, growth hormone, insulin and thyroxine) and metabolites in the plasma of high- and low-yielding cows at various stages of lactation. J. Endocr. 77:333.

Hashizume, T, H Morimoto, T Masubuchi, M Abe, T Hamada. 1965. Some aspects of energy utilization by cows during gestation and lactation. Proc. 3rd Symp. Energy Metab. EAAP Publ. 11:111.

Heaney, GP, GA Lodge. 1974. Energy metabolism during late pregnancy in the ewe. Proc. 6th Symp. Energy Metab. EAAP Publ. 14:123.

Heitzmann, RJ, CB Mallinson. 1972. A comparison of thyroxine levels in the plasma of healthy, starved and acetonaemic dairy cows. Res. in Vetr. Sci. 13:591.

Hooven NW Jr., RH Miller, RD Plowman. 1968. Genetic and environmental relationships among efficiency, yield, consumption and weight of Holstein cows. J. Dairy Sci. 51:1409.

Hove, K. 1974. Nocturnal plasma insulin levels in cows with varying levels of plasma ketone bodies; relations to plasma sugar and acetoacetate. Acta Endocr. 76:513.

Iwasaki, K, T Haryu, K Kameoka. 1980. Energy utilization by Japanese black cattle in late pregnancy. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:307.

Jakobsen, PE, PH Sorensen, H Larsen. 1957. Energy investigations as related to fetus formation in cattle. Acta Agric. Scand. 7:103.

Joanning, SW, DE Johnson, BP Barry. 1981. Nutrient digestibility depressions in corn silage-corn grain mixtures fed to steers. J. Anim. Sci. 53:1095.

Johnson, MD, O DeDios, AC Lippincott. 1976. Environmental stress, TRH and lactation effects on plasma growth hormone of cattle. In: IAEA/FAO Symp. on Nuclear Tech. in Anim. Prod. and Health. pp 555-562.

Karg, H, D Schams, V Reinhardt. 1972. Effects of 2-Br-alpha-ergocryptine on plasma prolactin level and milk yield in cows. Experientia 28:574.

Kipnis, DM. 1973. In: Methods in investigative and diagnostic endocrinology, pp 827-835. SA Berson, RS Yalow (Eds.) New York: American Elsevier; Amsterdam and London: North Holland.

Kirchgessner, M, HL Mueller, FJ Schwarz. 1982. Experimental studies on the feeding frequencies of dairy cows. Proc. 9th Symp. on energy metabolism, EAAP Publ. 29:30.

Koprowski, JA, HA Tucker. 1973. Serum prolactin during various physiological states and its relationship to milk production in the bovine. Endocr. 92:1480.

Kronfeld, DS, S Donoghue, JM Naylor, K Johnson, CA Bradley. 1980. Metabolic effects of feeding protected tallow to dairy cows. J. Dairy Sci. 63:545.

Kromann,RP. 1973. Evaluation of net energy systems. J. Anim. Sci. 37:200.

Langlands, JP, HAM Sutherland. 1968. An estimate of the nutrients utilized for pregnancy by Merino sheep. Br. J. Nutr. 22:217.

Lingvall,P, PG Knutsson, J Bertilsson. 1978. EAAP 29th annual meeting, Stockholm.

Llewellyn, RW. 1965. FORDYN--An industrial dynamics simulator. Raleigh: North Carolina State University.

Lofgreen, GP, WN Garrett. 1968. A system for expressing net energy requirements and feed values for growing and finishing cattle. J. Anim. Sci. 27:793.

Machlin, LJ. 1973. Effect of growth hormone on milk production and feed utilization in dairy cows. J. Dairy Sci. 56:575.

Meeh, K. 1879. Zeit. Biol. 15:425.

Meissner, HH. 1982. Genotype-dietary interaction in growth and efficiency of beef bulls. Proc. 9th Symp. Energy Metab. EAAP Publ. 29:132.

Menke, KH. 1980. A system for predicition of retention of protein and fat in growing animals. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:175.

Mertens, DR. 1977. Principles of modeling and simulation in teaching and research. J. Dairy Sci. 60:1176.

Ministry of Agriculture Food and Fisheries. 1975. Technical Bulletin 33.

Moe, PW. 1981. Energy metabolism of dairy cattle. J. Dairy Sci. 64:1120.

Moe, PW, WP Flatt. 1969. Use of body tissue reserves for milk production by the dairy cow. J. Dairy Sci. 52(Supp 1):928.

Moe, PW, WP Flatt, HP Tyrrell. 1972. Net energy value of feeds for dairy cattle. J. Dairy Sci. 55:945.

Moe, PW, JT Reid, HF Tyrrell. 1965. Effect of level of intake on digestibility of dietary energy by high producing cows. J. Dairy Sci. 48:1053.

Moe, PW, HF Tyrrell. 1972. Metabolizable energy requirement of pregnant dairy cows. J. Dairy Sci. 55:480.

Moe, PW, HF Tyrrell, WP Flatt. 1970. Partial efficiency of energy use for maintenance, lactation, body gain and gestation in the dairy cow. Proc. 5th Symp. Energy Metab. EAAP Publ. 13:65.

Moe, PW, HF Tyrrell, WP Flatt. 1971. Energetics of body tissue mobilisation. J. Dairy Sci. 54:548.

Monteiro, LS. 1972. The control of appetite in lactating cows. Anim. Prod. 14:263.

National Research Council. 1966. Glossary of terms. Pub. No. 1411. Nat. Acad. Sci.-Nat. Res. Counc., Washington, DC.

National Research Council. 1978. Nutrient requirements of domestic animals. No. 3. Nutrient requirements of dairy cattle. 5th rev. ed. Nat. Acad. Sci. Washington, DC.

Neilson, DR, CT Whittemore, M Lewis, JC Alliston, DJ Roberts, LS Hodgson-Jones, J Mills, H Parkinson, JHD Prescott. 1983. Production characyteristics of high-yielding dairy cows. Anim. Prod. 36:321.

Patle, BR, VD Mudgal. 1977. Utilization of dietary energy for maintenance, milk production and lipogenesis by lactating crossbred cows during their midstage of lactation. Br. J. Nutr. 37:23.

Peel, CJ, DE Bauman, RC Gorewit, CJ Sniffen. 1981. Effect of exogenous growth hormone on lactational performance in high-yielding dairy cows. J. Nutr. 111:1662.

Peterson, LA, EE Hatfield, US Garrigus. 1973. Influence of concentration of dietary energy on protein needs of growing-finishing cattle. J. Anim. Sci. 36:772.

Rattray, PV, WN Garrett, NE East, N Hinman. 1974. Efficiency of utilization of metabolisable energy during pregnancy and the energy requirements for pregnancy in sheep. J. Anim. Sci. 38:383.

Rattray, PV, TE Trigg, CF Urlich. 1980. Energy exchanges in twin-pregnant ewes. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:325.

Reichl, JR. 1980. Simulation models for energy metabolism in monogastric and ruminating animals. Proc. 8th Symp. on energy metabolism, EAAP Publ. 26:203.

Reid, JT, J Robb. 1971. Relationship of body composition to energy intake and energetic efficiency. J. Dairy. Sci. 54:553.

Reid, JT, OD White, R Anrique, A Fortin. 1980. Nutritional energetics of livestock: Some present boundaries of knowledge and future research needs. J. Anim. Sci. 51:1393.

Roux, CZ, HS Hofmeyr, E Jordaan. 1982. The problem of multicolinearity in the estimation of partial efficiencies of protein and fat by regression methods. Proc. 9th Symp. Energy Metab. EAAP Publ. 29:138.

Rubner. 1883. Die Gesetze des Energie verbrauchs bei der Ernahung. Zeit. Bil. 19:313

Schams, D. 1972. Prolactin levels in bovine blood, influence by milking manipulation, genital stimulation and oxytocin administration with specific consideration of the seasonal variations. Acta Endocr. 71:684.

Schneider, W, D Fritz, JR Reichl, KH Menke. 1980. Effect of protein content and metabolizability of the diet on the efficiency of utilization of metabolizable energy in dairy cows. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:341.

Schulz, AR. 1980. Development of a computer program for simulation of energy metabolism in the whole animal. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:199.

Schwalm, JD, LH Schultz. 1976. Relationship of insulin concentration to blood metabolites in the dairy cow. J. Dairy Sci. 59:255.

Smith, NE, RL Baldwin, WM Sharp. 1980. Models of tissue and animal metabolism. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:193.

Sundstøl, F, A Ekern, P Lingvall, E Lindgren, J Bertilsson. 1980. Energy utilization in sheep fed grass silage and hay. Proc. 8th Symp. on energy metabolism, EAAP Publ. 26:17.

Sutton, JD, IC Hart, WH Broster. 1982. The effect of feeding frequency on energy metabolism in milking cows given low-roughage diets. Proc. 9th Symp. on Energy Metab. EAAP Publ. 29:26.

Sykes, AR, AC Field. 1972. Effects of dietary deficiencies of energy, protein and calcium on the pregnant ewee. J. agric. Sci., Camb. 78:127.

Taylor, StCS, HG Turner, GB Young. 1981. Genetic control of equilibrium maintenance efficiency in cattle. Anim. Prod. 33:179.

Theriez, M, M Tissier, JP Brun. 1980. Effects of metabolizable energy content of diet and feediong level on the efficiency of energy utilization by young growing lambs. Proc. 8th Symp. on Energy Metab. EAAP Publ. 26:69.

Thomas, JW. 1953. The use of thyroprotein for milk production. Natl. Res. Counc. Publ. 266:47.

Thonney, ML, RW Touchberry, RD Goodrich, JC Meiske. 1976. Intraspecies relationship between fasting heat production and body weight: A reevaluation of $W^{.75}$. J. Anim. Sci. 43:692.

Tissier, M, M Theriez, A Purroy, A Brelurut. 1980. Energy utilization by ewes during pregnancy and lactation. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:329.

Trigg, TE, KE Jury, AM Bryant, CR Parr. 1980. The energy metabolism of dairy cows underfed in early lactation. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:345.

Trigg, TE, CW Parr. 1981. Aspects of energy metabolism of Jersey cowsdiffering in breeding index. Proc. New Zealand Soc. Anim. Prod. 41:44.

Tucker, HA. 1979. Endocrinology of lactation. Seminars in Perinatology 3:199.

Tucker, HA. 1981. Physiological control of mammary growth, lactogenesis, and lactation. J. Dairy Sci. 64:1403.

Tyrrell, HF, ACG Brown, PJ Reynolds, GL Haaland, CJ Peel, DE Bauman, WC Steinhour. 1982a. Effect of growth hormone on utilization of energy by lactating Holstein cows. Proc. 9th Symp. Energy Metab. EAAP Publ. 29:466.

Tyrrell, HF, GL Haaland, PW Moe, ACG Brown. 1982b. Effect of level and solubility of dietary protein on the energy value of rations fed to lactating dairy cows. Proc. 9th Symp. Energy Metab. EAAP Publ. 29:14.

Tyrrell, HF, PW Moe. 1980. Energetics of growth in cattle. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:227.

Tyrrell, HF, PW Moe, RR Oltjen. 1974. Energetics of growth and fattening compared to lactation in cattle. Proc. 6th Symp. Energy Metab. EAAP Publ. 14:205.
Tyrrell, HF, JT Reid. 1965. Prediction of the energy value of cow's milk. J. Dairy Sci. 48:1215.

Tyrrell, HF, JT Reid, PW Moe. 1966. Further observations on the effect of level of intake on digestibility of dietary energy by high-producing cows. J. Dairy Sci. 49:739.

van der Honing, Y, A Steg. 1980. Calculation of energy values of feedstuffs for milk production: Comparison of various feed evaluation systems. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:23.

van der Honing, Y, A Steg, AJH van Es. 1976. Feed evaluation for dairy cows: tests on the system proposed in the Netherlands. Livestock Prod. Sci. 4, 57-67.

van Es, AJH. 1961. Between animal variation in the amount of energy required for the maintenance of dairy cows. Ph.D. dissertation. State Agric. Univ., Wageningen, The Netherlands.

van Es, AJH. 1976. Factors influencing the efficiency of energy utilization by beef and dairy cattle. In: H. Swan and WH Broster (eds.), Principles of Cattle Production. Butterworth, London, pp 237-253.

van Es, AJH. 1980. Feed evaluation: a survey. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:85.

van Es, AJH, HJ Nijkamp. 1969. Energy, carbon, and nitrogen balance experiments with lactating cows. Proc. 4th Symp. Energy Metab. EAAP Publ. 12:209.

Vanjonack, WJ, HD Johnson. 1975. Effects of moderate heat and milk yield on plasma thyroxine in dairy cattle. J. Dairy Sci. 58:507.

Vercoe, JE, JE Frisch. 1974. Fasting metabolism, liveweight and voluntary feed intake of different breeds of cattle. Proc. 6th Symp. Energy Metab. EAAP Publ. 14:131.

Vermorel, M, JC Bouvier, Y Geay. 1980. Energy utilization by growing calves: Effects of age, milk intake and feeding level. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:49.

Vermorel, M, Y Geay, J Robelin. 1982. Energy utilization by growing bulls, variations with genotype, liveweight, feeding level and between animals. Proc. 9th Symp. Energy Metab. EAAP Publ. 29:88.

Wainman, FW, JS Smith, PJS Dewey. 1980. The predicted and observed metabolizable enrgy values of mixtures of maize silage and barley fed to cattle. Proc. 8th Symp. Energy Metab. EAAP Publ. 26:55.

Webster, AJF. 1980. The energetic efficiency of growth. Livestock Prod. Sci. 7:243.

Webster, AJF. 1981. The energetic efficiency of metabolism. Proc. Nutr. Soc. 40:121.

Webster, AJF, JM Brockway, JS Smith. 1974a. Energy changes during growth in cattle. Proc. 6th Symp. Energy Metab. EAAP Publ. 14:135.

Webster, AJF, JM Brockway, JS Smith. 1974b. Prediction of the energy requirements for growth in beef cattle. 1. The irrelevance of fasting metabolism. Anim. Prod. 19:127.

Webster, AJF, JS Smith, RM Crabtree, GS Mollison. 1976. Production of the energy requirements for growth in beef cattle. Anim. Prod. 23:329.

MICHIGAN STATE UNIV. LIBRARIES
31293010702318