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GENETIC PARAMETERS FOR PARTITIONED USES OF ENERGY INTAKE ESTIMATED FROM FIELD COLLECTED AND CALORIMETRIC DATA ON THE SAME LACTATING HOLSTEIN COWS

presented by

PETER MALACHI SAAMA

has been accepted towards fulfillment of the requirements for

M.S. degree in Animal Science

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Major professor

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BY

PETER MALACHI SAAMA

A THESIS

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

MASTER OF SCIENCE

Department of Animal Science

ABSTRACT

GENETIC PARAMETERS FOR PARTITIONED USES OF ENERGY INTAKE ESTIMATED FROM FIELD COLLECTED AND CALORIMETRIC DATA ON THE SAME LACTATING HOLSTEIN COWS

By

Peter Malachi Saama

Energy balance trials were conducted on 34 multiparous Holstein cows at the University of New Hampshire, Durham, at wk 6, 10, and 14 postpartum during 1980-1985. Diet, parity, and season effects were found to be non-significant sources of variation in gross energy consumed, fecal, urinary, methane, heat, milk, and maintenance energy, and tissue energy balance and their ratios. Milk energy as a covariate was highly significant in these variables except energy for heat production and that for maintenance. The effect of maintenance interacted with periods. Field estimates on gross efficiency were obtained from intake and production data recorded during wk 5, 7, 9, 11, 13, and 15 postpartum. All energy and gross efficiency estimates from field data closely approximated measures of the same traits from energy chamber data. This approximation was better at postpeak lactation. An additional data set of 37 cows was procured from energy balance trials conducted during 1987-1989. Animal models were used to estimate partial energy requirements and genetic parameters for energy usage traits. Estimation and prediction was by a derivative-free REML algorithm. Omitting animal effects did not affect solutions for covariates. Genetic and phenotypic variations and heritability estimates in energy intake variables, at postpeak lactation, were similar for chamber and field data.

DEDICATION

To Beatrice Mary Namuyomba and Cyprian Kikunyi Bamwoze

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1 INTRODUCTION

The main purpose of raising livestock is to convert feeds into food products desirable to humans. The animal industry plays a major role in maximizing food for human consumption from the available feedstuffs and other inputs. The nutrients or resources that are needed for an animal to achieve its potential have been described. Emmans and Oldham (1988) suggest that a number of functions will become important when resources and nutrients are limiting. They are: 1) maintenance of essential metabolic processes and tissue integrity; 2) maintenance of established pregnancy; 3) maximal rate of secretion of milk constituents as determined by genotype, stage of lactation, and perhaps age and parity; 4) achievement of an upper limit to body protein mass at a particular stage of maturity; 5) achievement of a desired fat mass in relation to protein mass or stage of maturity.

High peak milk yields and an extension of the high yield phase of lactation are occurring in dairy cattle due to continued improvements in genetics, adoption of new management and feed systems, and biotechnological advances. Nutrient requirements of the cow increase with milk yield (NRC, 1989).

During early lactation, cows are often in negative energy and N balance because maximal DMI does not occur until peak milk production. Therefore, cows mobilize energy and protein from body tissue to support milk production. Energy and amino acids are the two nutritional factors most likely to limit milk production. The relationship between N and energy requirements for cows is complex because there

are two requirments to be met: one for the host animal and another for the ruminal microbes.

The ultimate goal of any animal related agricultural enterprise is to provide the most acceptable, properly balanced, and least expensive ration that can be fed to a given species of animals. This is so because the provision of feed to animals constitues a major component of farm expenditure. Since all of the organic nutrients contained in a feed can serve as a source of energy, a measure of energy value of a feed is desirable.

Several attempts at defining an over-all energy unit of measurement which is easily determined, accurate and readily reproducible have been made and continue to be made by scientists in the US and elsewhere. Four different methods are used in the US to determined the useful energy of livestock feeds. They are the determination of total digestible nutients, digestible energy, metabolizable energy, and net energy. Net energy is the most scientifically acceptable method of expressing the energy value of a feed (Moe and Tyrrell, 1973). Whence, the energy value of a feed is defined as the increase in energy retention which occurs per unit increment of a feed given.

In this study, "efficiency" is defined as the ratio of energy in the product to the product of energy partitioning from which it was formed. Efficiency of energy use and energy requirements have been identified more precisely. Progressively more intensive experimentation has described physiological and biochemical bases for an ever increasing body of knowledge concerning variation in energy use. In most cases, the laboratory techniques are too expensive or impractical to be used on a routine

basis.

In the long run, methods to predict quantities of nutrients absorbed from the gut will permit a more flexible and accurate method of evaluating diets, predicting animal performance and estimating the genetic potential for animal feed and energetic efficiency.

In general, there are two ways in which the net energy value of feed may be estimated: a) by regression of total energy balance on DMI, and b) by assuming a maintenance requirement in terms of either energy intake or energy balance and either subtracting the metabolizable energy requirement for maintenance from the actual metabolizable energy intake or adding the net energy required for maintenance to the actual energy balance (Moe and Tyrrell, 1972). Whenever either of these approaches is used, it is important to ask how accurate the approximations are and whether this accuracy holds in other production conditions. An initial attempt to address these issues was made by Walter and Mao (1989) when they compared estimates of energy requirements from barn data with reported values. Consequently, the use of field collected data to predict enery requirements of dairy cattle was considered a plausible source of data for generating databases for quantititative analyses. However verification of this assertion has not been made.

This study represents an unprecedented effort at making comparisons of various measures energy utilization and energetic efficiency as well as genetic parameter estimates for energy intake from field collected and energy chamber data on the same cows.

2 OBJECTIVES

- To examine sources of variation in partitioned uses of energy intake using energy chamber data.
- 2) To compare energy intake and gross efficiency measures from calorimetric and field data on the same pluriparous lactating cows.
- To compare genetic parameters for energy intake traits estimated from respiration chamber data and field data on the same primiparous lactating cows.

3 REVIEW OF LITERATURE

3.1 Dietary sources of energy and fiber

Adequate dietary energy and fiber are essential for high producing dairy cows during early lactation. The three main dietary sources of energy and fiber are protein, carbohydrate, and lipid.

3.2 Protein

Adequate intake of protein is needed to provide the proper amount of total protein to the small intestine for digestion and absorption. Due to limited body reserves (Andrew, 1990), protein deficient diets quickly influence the nutritional and productive status of cows in early lactation (Wohlt, 1978^a; Wohlt, 1978^b). The quantity and quality of amino acids reaching the small intestine are the result of microbial synthesis in the rumen and the extent to which feed proteins escape ruminal degradation. However, the amount of protein supplied by microbial synthesis in the rumen is not adequate to meet the needs of high producing cows (NRC, 1989). In lieu of this, dietary undegradable protein (UIP) is often required (Satter, 1986; Robinson, 1991).

Milk yield responses to increasing the UIP content of rations have been observed (Cardoniga, 1988; Rogers, 1987); however, the amino acid profile of bypass protein must be of high quality, supplying required nutrients (Satter, 1986; Susmel, 1989). Effects of supplemental fat and UIP on milk yield were additive

(Ferguson, 1988; Wolht, 1991; Wilks, 1991). Fish meal has been reported to be less degradable in the rumen than soybean meal (Sniffen, 1987; Atwal, 1992).

3.2.1 Carbohydrate

Carbohydrates are the major components in plant tissues and they comprise up to 50% of the dry matter in forages, although higher concentrations (up to 80%) may be found in some seeds, especially cereal grains (Church, 1982). The primary function of carbohydrates in animal nutrition is to serve as a source of energy for normal life processes. Type of dietary carbohydrate and level of carbohydrate intake are factors which often determine level of performance of lactating dairy cattle.

Forages that are high in digestibility and that can be consumed in large amounts are an essential diet component for high producing dairy cattle. Alfalfa is a widely used source of energy, fiber, and protein for dairy cows. The high solubility and degradability of alfalfa protein, however, may result in N wastage in the rumen. Additional sources of feed protein, a portion of which will pass out of the rumen undegraded, may be necessary to supplement the protein in alfalfa forage. Increasing dietary crude protein (CP) levels from 13.8% to 17.5% by the use of cottonseed meal (CSM) was beneficial to cows consuming alfalfa-based diets in early lactation (Grings, 1991).

Because of its oil content, whole cotton seed (WCS) his considered a high energy ingredient. Feeding WCS supplements increased yields (Anderson, 1979) and resulted in higher milk fat percentage (DePeters, 1985) but depressed milk protein percentage (Smith, 1981; DePeters, 1985).

Increased grain in the diet has been shown to be responsible for an increase in milk production (Hoffman, 1991; Kesler, 1962), higher protein percentage (Yousef, 1970). Nonetheless, some studies have shown a decrease in milk fat percentage as grain increases (Donker, 1982; Macleod, 1983). Increasing energy in diets using cereal grain supplements necessitates greater reductions in forage levels than if supplemental fat is fed. However, production response to added fat primarily depends on the nature of the diet, form of added fat, and availability of the fat to the rumen microbes and to the animal postruminally (Chalupa, 1986; Jenkins, 1982).

3.2.2 Lipid

Energy requirements at peak lactation exceed the energy intake thus creating a deficit. Consequently feeding supplemental fat is utilized as a means of increasing the ration energy density. Feeding supplemental fat increased milk yield (Hoffman, 1991; Palmquist, 1978). Cows fed supplemental fat also had higher BW, and weight gain was significant with time (Hoffman, 1991). Dietary fat supplements increase the energy density of the diet as well as total tract apparent digestion of N (Ohajuruka, 1991) but dietary fats can have a negative impact on milk protein (DePeters, 1987), rumen fermentation and fiber digestibility (Palmquist, 1978; Palmquist, 1980). Thus, fat supplements must be relatively inert in the rumen to reduce these detrimental effects (Ferretti, 1990).

Calcium salts of long-chain fatty acids (Ca-LCFA) of palm-oil are chemically

bound dietary fats that do not adversely affect rumen fermentation (Chalupa, 1986) or fiber digestibility (Schauff, 1989) in lactating cows. Strategic feeding of regimens including use of Ca-LCFA (Kent, 1988; Schneider, 1988) have been used as a method to alleviate a portion of the dietary energy deficit experienced by early postpartum dairy cows (Bauman, 1980; Coppock, 1985). The net energy of Ca-LCFA from palmoil has been determined in mature holstein cows (Andrew, 1990).

3.3 Energy metabolism

Dietary energy can be partitioned several ways. The flow of energy in the lactating cow, as described by NRC (1989) is shown in Figure 1. Intake of dietary energy is the gross energy (GE) of the food consumed. A substantial portion of GE is lost from the animal as fecal energy (FE) and the difference (GE-FE) is termed the apparent digestible energy (DE). Portions of the DE are voided as urinary energy (UE) and gaseous energy in the form of methane (CH₄). The remainder of GE-FE-UE is metabolizable energy (ME). An increase in heat production (HP) following consumption of food is termed heat increment (HI) and includes heat of fermentation, heat of product formation, thermal regulation, waste formation and excretion, voluntary activity, and basal metabolism. The difference (ME-HI) is net energy (NE). The NE can be recovered as a useful product such as maintenance (MNT), milk energy (MKE), body gain or loss, and conceptus energy (CE). What is left over is termed tissue energy balance (EB). This bioenergetics framework can be expanded to include many of the intermediate steps of metabolism involved and each component

can be divided into component parts. For example the ability of the food consumed to meet the NE requirement for maintenance is expressed as NE_m . It is important to recognize that dietary energy is not used with equal efficiency for all physiological functions. Approximate ranges for the efficiency use of ME are described by Moe et al. (1973).



Figure 1. Framework of energy metabolism in the lactating dairy cow.

3.3.1 Energy partitioning by indirect-calorimetry

Many techniques used to study energy metabolism have been discussed in detail recently by Blaxter (1989). In general, measurement of the overall energy transformations in an animal in terms of free energy is not possible for technical reasons. Therefore, measurements of energy exchanges in dairy cattle are made simply in terms of the changes in heat on complete oxidation. The heat produced in oxidation of food is measured by techniques of calorimetry. The heat of combution of food, whether in vitro or in vivo, is carried out by the technique of calorimetry. For instance, the heat of combustion of food is carried out by adiabatic bomb calorimetry.

The method of indirect calorimetry (Bursztein, 1989) provides a unique process by which the type and rate of subtrate oxidation and heat production are measured in vivo starting from gaseous exchange measurements. The use of gas exchange for indirect calorimetry is based on assumptions that go back to the investigations of Lavoisier in the late 18th century (Holmes, 1985). The standard gas equations are reviewed by Bursztein (1989). These gas equations treat O_2 and CO_2 as ideal gases. Johnson (1980) argues that this is incorrect for O_2 and N_2 , but is only partially true for CO_2 , thus introducing a small error. A more important potential error is related to water vapor, where the expired air is assumed to be saturated and complete drying is required for use of the gas equations, although neither of these conditions may be totally correct. Respiration apparatus for indirect calorimetry are of two main types: open circuit and closed circuit.

In the open circuit respiration apparatus, outdoor air is passed through the

chamber of the instrument and the changes in its oxygen, methane and carbon dioxide content are measured. The total amounts of carbon dioxide and methane produced and of oxygen consumed can be determined if the amount of air which passes through the apparatus and the incremental changes in gas concentrations are known (or fixed). The general principle of an open circuit apparatus is illustrated in Figure 2.



Figure 2. General principle of open circuit apparutus (Blaxter, 1989).

the spirometer A. The flow through the chamber is measured and sample is taken and stored in spirometer B. A further sample is deflected through an absorption system to determine the proportion of CO_2 and CH_4 . Analyses of the air samples in the gas meter provide a measure of the O_2 consumption. Formulae for performing routine calculations of respiration trial data in dairy cattle have been presented (Flatt, 1961).

and stored in

In the closed circuit system (Blaxter, 1989), air is circulated continuously through absorbents which remove carbon dioxide and water vapor; the air freed of these gases returns to the chamber. A fall in the pressure in the whole apparatus occurs as a result of the absorption of oxygen by the animal, and oxygen admitted to the system in proportion to this fall in pressure. By weighing the absorbents, the amount of carbon dioxide produced can be measured directly, and the amount of oxygen can be measured either by weight or volume. Technical problems with closed circuit systems, as discussed by Wainman and Blaxter (1958), present some practical difficulties.

Implementation of indirect calorimetry apparutus by Armsby (1904), Ritzman and Benedict (1929), Ritzman and Colovos (1932), Mitchell et al. (1932), Kleiber (1936), USDA-ARS, as described by Flatt et al. (1958), and others has provided a more complete and scientifically sound basis of feed evaluation as well as a more thorough knowledge of the energy requirements of dairy cattle and a basic understanding of factors affecting the energy metabolism of dairy cattle.

3.3.2 Energy use for maintenance

The cow has certain obligatory needs for nutrients, which by definition must be met to maintain life and functional processes. The partitioning of nutrients to various body tissues involves two types of regulation, homeostatis and homeorhesis (Bauman and Currie 1980). Homeostatic control involves maintenance of physiological equillibrium or constant conditions in the internal environment. This includes regulation to maintain constancy of body temperature (Kennedy, 1967) and the intake of food and partitioning of nutrients in the absorptive and postabsorptive periods (Tepperman and Tepperman, 1970). The co-ordination of metabolism in various tissues to support a physiological state, such as pregnancy, is under homeorhetic

control (Kennedy, 1967). The informative study by Mertz and Van den Bergh (1977) illustrates the relationship between homeostasis and homeorhesis.

3.3.2.1 Sources of variation in maintenance energy

Ritzman and Benedict (1938) found that the basal metabolism of their cows was rather variable. Brouwer, et al. (1961) found evidence for variation in the maintenance requirement per 500 kg of BW of a cow. Significant variation exists in the maintenance requirement of animals when comparisons are made across a range of species and ages (Reid, 1974; Reid et al., 1980). This includes differences due to type of diet and physiological state, which are known to affect maintainenance requirements (Garrett and Johnson, 1983). Significant effects of breed, breed size, age, and feeding level on maintenance were observed by Taylor et al. (1986).

3.3.2.2 Efficiency of energy utilization for maintenance

The efficiency of ME use for maintenance (k_m) and for gain (k_g) are related to the source of ME. Studies in which steam volatile fatty acids, glucose and protein were given as the sole energy source, suggest that k_m is in the range of 80-85%, is constant for widely different foods and is predicatable from physiological experiments in which the end products of fermentation have been given as the sole source of energy (Blaxter, 1961). These results supported the conclusion of Ritzman and Benedict (1938) from earlier calorimetric studies. However, Blaxter and Wainman (1964) observed that k_m was not constant, but appeared to increase with the feed quality.

Van Es and Nijkamp (1969) reported similar results from 41 balance trials with lactating cows consuming mixed diets of concentrate, silage, and variable amounts of hay. More recently, Blaxter and Boyne (1978) reported that k_m is affected by types of feed.

3.3.2.3 Estimation of maintenance energy

In animal calorimetry, heat production attributable to maintenance metabolism can be distinguished from HI by measuring the fasting heat production (FHP). The total heat produced less FHP would be considered as HI (Holter, 1974).

There are several ways of estimating k_m . Brody's (1945) scaling of energy maintenance to BW^{.73} subsequently rounded by Kleiber (1965) to a scaling of BW.⁷⁵, as useful estimate of FHP has gained widespread use. According to NRC (1989), k_m was calculated as .086 Mcal/kg^{.75} of BW. Table1, from the results of Van Kampen (1987), shows that in animals with the same metabolic level or with equal amounts of heat produced per kg BW^{.75}, there is a positive relationship between BW and HP expressed per animal. However, expressing HP/kg BW results in a negative relationship.

TABLE 1. The effect of body weight on heat production.				
Body Weight	HP/animal	HP/kg BW	HP/m ²	HP/kg BW.75
— kg —	kJ			
.1	89	890	4134	500
1	500	500	5000	500
10	2810	281	6050	500
100	15810	158	7327	500
1000	88915	89	8871	500

- 1 - 1 - 4 • . • .•

Generally, k_m is estimated by measuring fasting metabolism or by regressing EB on ME (Moe and Tyrrell, 1973). In the latter case, the intercept is taken as k_m but is expressed in production units (NE_{mit}). Summarizing 332 energy balance trials, Moe et al. (1972) reported a maintenance requirement of 73 kcal NEmik/kg BW.75. National Research Council (1989) uses 80 kcal NE_{mik}/kg BW.75 for maintenance taking into account usual physical actitivity of cows.

With respect to fasting metabolism of dry cows, Holter (1976) reported 103.4 ± 2.8 kcal/kg BW^{.75} 98.6 ± 3.5 kcal/kg BW^{.75} at 1 and 31 days after lactation, respectively, while Flatt et al. (1965) observed a fasting metabolic rate of 73.5 kcal/kg BW.75 in dry cows.

There seems to be little agreement concerning the maintenance requirement of lactating cows. It has been assumed (Moe and Tyrrell, 1973; Tyrrell and Moe, 1972) that FHP in cattle numerically is greater than NEmik determined by regression procedure.

3.3.2.4 Genetic aspects for maintenance energy

Taylor et al. (1986) have discussed the role of genetics in influencing efficiency of maintenance requirements per unit metabolic body weight (MBW); estimated by BW^{.75}. They computed a coefficient of phenotypic variation in MNT of 6.4% and a repeatability of .70 for 2-year periods. Van Es (1961) obtained an estimate of amongcow coefficient of variation of 4-8% (in dry cows) and 5-10% (dairy cows and steers) in 237 energy balance trials that he reviewed.

The results of Andersen (1980) showed within-breed variation in maintenance requirements for beef bulls. A heritability of .31 was calculated from these data. Taylor et al. (1986) suggested genetic differences in maintenance requirement may be due largely to genetic differences in HI. In agreement with this postulate, Vercoe (1970) found that genetic differences in level of production require different k_m to convert NE_{milk} to ME for maintenance (ME_{milk}). Davey et al. (1983) concluded the maintenance requirement of cows was not influenced by genetic merit for milk production.

3.3.3 Energy use for milk production

The utilization of energy for milk yield has major economic implications. Energy sources making up ME can influence the product of energy partitioning. Flatt et al. (1969) observed that MKE increased and tissue energy decreased, as alfalfa was substituted for concentrate. Tyrrell et al. (1973) noted a shift in NE from tissue deposition to MKE as equal feed-energy increments were changed from corn to beetpulp.

3.3.3.1 Sources of variation in milk energy

Bauman (1985) indicated, based on literature, that little variation exists among animals in the efficiency with which ME is utilized for milk. A slight increase in efficiency of ME use for milk production was attributable to metabolizability of the diet (Van Es and Nijkamp, 1969). Extensive analyses by Moe (1981) of results from energy balance trials performed by Flatt et al. (1969) showed that 1) use of ME for milk or body tissue gain was unaffected by milk yield, amount of body tissue gain (or loss), and stage of lactation; 2) variation among cow was due to the amount of feed consumed. However, an equal digestible DM produced more milk from white clover than from ryegrass (Rogers et al., 1979). Other sources of variation in k_i have been observed.

Kirchgessner et al. (1982) found that k_i increased as frequency of feeding increased. The influence of cold temperatures on the energy requirement of lactating cows was minimal (NRC, 1989). This was attributed to the high HP at high feed intakes. Hooven et al. (1968) found that BW change increased as k_i increased.

3.3.3.2 Efficiency of energy utilization for milk

Energy utilization for milk is primarily a function of digestibility (Waldo and Jorgensen, 1981). Van Es and Nijkamp (1969) found no effects of percentage of crude fiber or of crude protein on efficiency of milk production. They concluded that ME was used for milk production (k_i) with and efficiency of 54-58%. Walter and Mao (1989) has summarized the reported partial efficiencies for lactation and observed a range of 54-75%. Multiple regression analyses were used by Moe et al. (1970) and Moe et al. (1971) to derive partial efficiencies for milk production. Partial efficiency of ME for milk were 61-64%. Hashizume et al. (1965) found k_i of 74 and 82% for low and high concentrate diets. Calorimetric studies (Armstrong et al., 1964; Flatt et al., 1965; Moe et al., 1972) have shown that lactating cows, use DE or ME for milk production with a similar degree of efficiency.

3.3.3.3 Estimation of milk energy

The NE requirement for milk (NE₁) is defined as the energy contained in the milk produced (NRC, 1989). The Gaines (1928) equation proposed the use of 4% fatcorrected milk as a measure of NE₁. The inadequacies of this procedure became evident with dietary regimens (Laben, 1963; Van Soest, 1963) aimed at producing lower fat and a higher solids-not-fat (SNF) concentration. The landmark analysis (Tyrrell and Reid, 1965) of 21 different combinations of milk components demonstrated that the most practical equation for the accurate prediction of energy in milk was:

Energy (kcal/kg) = 41.84 (% fat) + 22.29 (% SNF) - 25.58.

In an effort to correct on the basis of SNF, solid-corrected milk (SCM) was computed as:

SCM (kg) = 12.3 (kg fat) + 6.56 (kg SNF) - .0752 (kg Milk).

The SCM equation has been used widely to predict energy in milk (Walter and Mao, 1989; Ngwerume and Mao, 1992) with a high degree of accuracy. NRC (1989) computed NE_1 as:

 NE_1 (Mcal/kg of milk) = .3512 + [.0962 (% fat)].

3.3.3.4 Genetic aspects of milk energy

There is a lack of studies in the literature on the genetic parameters of milk energy due to the following reasons: 1) the number of animals in respiration chambers and energy balance studies was too small, and equipment and labor was too expensive to extend these studies; 2) the studies were carried out mainly by nutritionists who are mostly interested in using uniform animals. In this regard, another caveat is that most studies of genetic differences between animals have focused on the genetic relationship between milk yield and feed efficiency (Custodio et al., 1983; Grieve et al., 1976; Wilmink, 1987). For this reason, present knowledge of genetic parameters for milk energy is limited.

There is a unanimous agreement, in the literature, that direct selection on gross feed efficiency has no advantage because of the high correlation between gross feed efficiency and milk yield (Buttazoni and Mao, 1989; Custodio et al., 1983; Grieve et al., 1976; Freeman, 1967; Korver, 1988). Variation between animals in appetite, digestion, nutrient absorption, maintenance requirement, utilization of ME for MKE, nutrient partitioning and output composition makes gross feed efficiency an imprecise measure of efficiency.

3.3.4 Energy use for live weight gain or loss

Because production of milk during lactation has a high priority in the dairy cow, production of milk may continue to be high despite insufficient DMI. In such situations, the animal must mobilize body tissue to compensate for the energy deficit. On the other hand, excessive intake of energy during late lactation and the dry period can cause BW gain (Morrow, 1976). The composition of the BW gain or loss is important in determining k_g (Garrett, 1980). Some extensive reviews discuss manipulation of growth (Elsley, 1976), energy use for growth (Millward, 1976), and nutrition and genetic effects on body composition (Lister, 1976). Moe et al. (1971) caution that live weight change alone may not provide an accurate measure of EB.

Partial efficiency of ME for body gain (or loss) was 75% (Moe et al. 1970; Moe et al. 1971). Thorbek (1970) found partial efficiencies for protein and fat deposition of 43 and 77%. Protein-deficient diets shifted energy deposition from protein to fat (Black, 1974).

3.4 Canonical correlation analysis

It often happens that we make measurements on several variables. Collectively these variables make up a multivariate system which may be divided a priori into two sets, with each set relating to a particular component of the system and with some idea required of the association between these components. For example, we may take p measurements relating to the yield of alfalfa (e.g.height, dry weight, number of leaves) at each of n sites in a region, and, at the same time, we may have recorded q

variables relating to the weather conditions at each of these sites (e.g. average daily rainfall, humidity, hours of sunshine). The whole system thus consists of n units on each of which (p + q) variables have been measured. The overall (p + q)x(p + q)correlation matrix contains all information on associations between pairs of variables in the system, but attempting to extract from this matrix some idea of the association between the two sets of variables is a difficult task. This is because the correlations between the sets may not have a consistent pattern, and these between set correlations must in any case be adjusted somehow for the within-set correlations. Hotelling (1936) proposed the method of canonical correlation which derives a measure of maximum correlation between linear combinations of the original sets of variables. A rigorous derivation of the canonical correlation model may be found in Anderson (1958). A derivation of computing procedures for canonical correlation used in this project is outlined in Appendix V.

3.5 (Co)variance component estimation

The basis for estimating variance components was established by Fisher (1925); that basis being: equate quadratic forms in the observation vector to their expected values and thereby construct a set of equations with unknown parameters the vector of variance components to be estimated. Whence, the method yields equations linear in the variance components that can be solved and the solutions taken as the estimates but this method was confined to balanced data.

In genetic studies, the data are unbalanced. Henderson (1953) extended the

knowledge of estimation of components of variance to unbalanced data with his Methods I, II, and III. Method I, which computes sums of squares in the standard analysis of variance (ANOVA) with balanced data, equates the mean squares to their expectations and solves for the components, has been used extensively but cannot be used on mixed models. Method II is unbiased by fixed effects. It adjusts for fixed effects (in models having no interaction between fixed and random factors), estimated as if random effects were fixed, then estimates components as in Method I, using the adjusted data. These two methods enabled substantial analyses to be performed. Method III yields estimates of components of variance that are unbiased by fixed effects and their interactions and has contributed relatively more to animal breeding applications. However, the order in which reductions in sums of squares are computed is noteworthy. Reductions in sums of squares using a full model minus reductions in sums of squares from reduced models are equated to their expectations and solved for components. Computing these reductions and their expectations may be difficult for large data sets. Hence other approaches such as the method of maximum likelihood (ML) have been preferred.

3.5.1 ML estimates of (co)variance components

The ML method was applied to the general mixed model by Hartley and Rao (1967). The scope of ML estimation for the estimation of variance components has been reviewed by Edwards (1961) and Harville (1977). In general, for a given statistical model, parameters θ to be estimated, and assumed distribution of the data,

the likelihood function $L(\theta)$ can be derived. The ML estimates are the numerical values of the parameters for which $L(\theta)$ attains its maximum. Maximizing the likelihood leads to estimates that are functions of sufficient statistics, universally most powerful, consistent, asymptotically normal, and often efficient. Large computational requirements restrict the use of ML for estimating variance components. Inherent to ML are some undesirable properties. The first is that the distribution of the data, usually a multivariate normal distribution, is assumed known. Secondly, ML estimators are biased as fixed effects in the model of analysis are treated as if they were known. This bias can be reduced by considering only the part of $L(\theta)$ which is independent of the fixed effects (Patterson and Thompson, 1971) and hence invariant of the location parameter. The latter approach is referred to as restricted maximum likelihood (REML). Under normality the REML estimation is equivalent to both minimum norm quadratic unbiased estimation (MINQUE; Rao, 1971^a) and local minimum variance quadratic estimation (MIVQUE; Rao, 1971^b). Other properties of REML are discussed by Harville (1977).

3.5.2 REML estimates of (co)variance components

Interest in estimation of (co)variance components by REML procedures has increased in recent years since REML: 1) yields estimates less affected by selection bias than Henderson's (1953) Methods I, II and III (Schaeffer, 1979); 2) allows for estimation of genetic parameters after consideration of information on all relatives (Meyer, 1986) without knowledge of true variance covariance components; 3) is

computationally feasible. Several REML algorithms have been used (Meyer, 1990) but most of these are iterative, often leading to repeated re-ordering of the mixed model equations (MME). For instance, the expectation maximization (EM-REML) algorithm requires inversion of the mixed model matrix (MMM), and utilizes information on first or second derivatives in order to obtain estimates that maximize $L(\theta)$. An alternative algorithm which avoids explicit evaluation of first derivatives is the derivative free (DF) algorithm (Graser et al., 1987; Meyer, 1986) generally referred to as derivative-free restricted maximum likelihood (DF-REML).

3.5.2.1 Derivative-free type REML algorithms

The best linear unbiased prediction (BLUP) method (Henderson, 1973) has rapidly become the method of choice for genetic evaluation of animals. The notion of utilizing the numerator relationship matrix in the analysis of BLUP under an animal model (AM) was presented by Henderson (1952). In the AM the order of the MME often exceeds the number of records making inversion of the MMM impractical. Use of DF-REML has become exceedingly attractive with the widespread use of the AM.

The application of BLUP to multiple traits was described by Henderson and Quass (1976). The inclusion of maternal effects and presentation of the reduced animal model were made by Quass and Pollak (1980). The approach of DFREML is suitable for AM including additional random components (Meyer, 1991). The use of a direct sparse matrix solver to obtain $L(\theta)$ can reduce cental processing unit (CPU) time per round of a DF algorithm (Boldman and Van Vleck, 1991). Recently, a
method to approximate sampling variances and confidence intervals for individual parameters in a multi-parameter analysis has been described (Meyer and Hill, 1991).

3.5.2.2 Limitations of DF-type algorithms

The maximum value of L(0) in DF-type algorithms has less significant digits than the maximized function. This condition could lead to false maxima, especially for multilple traits and when correlations are high (Misztal, 1992). Hence, the method of DF-REML, like EM-REML, does not guarantee identification of global maxima in the presence of local maxima. Groenveld and Kovac (1990), using a small data set, explored if multiple solutions could be generated for a multivariate mixed model estimating six covariance components by a DF-type algorithm. Multiple solutions from the DF algorithm suggested existence of local maxima. However, the DF-type algorithm was superior to all other algoritms considered in that study. In terms of CPU time it was faster by a factor of 22 misidentifying only one solution instead of 2 as EM-REML did.

4 Sources of Variation in Partitioned Uses of Energy Intake in Pluriparous Lactating Holstein Cows in Energy Chamber

4.1 ABSTRACT

Data were energy chamber measures on 34 multiparous Holstein cows collected during wk 6, 10, and 14 postpartum. For each period, cows were placed in digestion stalls for a six-day excreta collection followed by two consecutive 11-h methane and heat production measurements. Energy partition averages coincided with conventional values. Sources of variation among cows in gross energy consumed, fecal, urinary, methane, heat, milk, and maintenance energy, and tissue energy balance were analyzed. Also analyzed were heat production, energy balance, milk energy, maintenance energy expressed in ratios to various energy intake measures. A withinperiod model containing fixed effects of treatment, parity, season, and covariates for maintenance and milk energy was used. Neither diet, parity, nor season effects was found to be a significant source of variation in all the variables. Milk energy as a covariate was highly significant in all variables except energy for heat production and that for maintenance. However, the covariate maintenance energy was found to be a significant effect in heat production at wk 10 and 14 postpartum. The effect of maintenance interacted with periods in most energy partition and efficiency measures.

4.2 INTRODUCTION

The fundamental aspects of energy metabolism were described by results from several complete energy balance trials in direct or indirect calorimeters (Knott, 1934;

Moe, 1966; Moe and Tyrrell, 1973; Van Es, 1961). An explanation for the causes of variation in energy efficiency of animals fed different diets was provided by Armstrong and Blaxter (1957; 1957); 1965). They observed that the heat increment of VFA was controlled by the amount of acetate in fattening sheep but had less effect in sheep at maintenance. Thus, it was demonstrated that the end-products of digestion were more important than nutrients consumed in understanding metabolic efficiency in ruminants. Variation in partial efficiency of use of energy of VFA for milk production and maintenance also was shown to be of considerable significance. In addition, the type of ration (Flatt, 1966; Tyrrell et al., 1973), level of intake (Moe, 1966), level of production (Flatt, 1969), stage of lactation (Janicki, 1985), environmental conditions (Young, 1976), and size of the cow (Tyrrell et al., 1973) can affect the partition of the energy consumed. However, effects of variation in amount and type of diet on energy efficiency and energy partition are better explained by a knowledge of amounts and balance of the specific metabolites which are absorbed from the digestive tract.

A plethora of literature exists on the influence of ration composition and level of intake on digestive efficiency, but there is a paucity of data that describe the associated magnitude and sources of variation. Much of the previous work has focused on proportions in partitioned energy intake by a typical, or an average, cow. However, an examination and understanding of variation among cows is much needed. Such an understanding may indicate whether the efficiency of a cow's ability to convert energy intake for production would be a worthwhile criteria for genetic

selection. This study was undertaken to determine the amount of variation and examine specific sources of variation in each of the partitioned energy uses and energy efficiency measures.

4.3 MATERIALS AND METHODS

4.3.1 Experimental Procedure and Data

Measurements were taken on 34 pluriparous cows during the course of three periods, wk 6, 10, and 14 postpartum. Diets were protein supplements, low-protein concentrate, corn-silage treated with urea at ensiling, and wilted grass silage fed individually for ad libitum intake. All ration components were blended and fed twice daily to provide at least 2.3 kg of orts daily as indicated by Holter (1982). Composites of low-protein grain and supplements were ground in a Wiley mill (1mm), mixed thoroughly, subsampled, and analyzed for proximate nutrients, ADF, and combustible energy (Parr adiabatic oxygen bomb calorimeter). Milk samples were collected from each milking, composited over the collection period, and analyzed for combustible energy according to methods described by Janicki and co-workers (1985).

Feces and urine were collected using mechanical separators and weighed daily; a 1% aliquot was taken each day and composited over the 6-d collection period. Following excreta collection, cows were placed in an open circuit, indirect respiration calorimeter to measure heat and CH₄ production for two consecutive 11-h periods. Samples of composite chamber air were analyzed for CO_2 , CH₄, and O_2 concentrations. Thereafter, energy balance was determined by difference between inputs and outputs. Energy partition variables were fecal energy (FE), urinary energy (UE), digestible energy (DE), methane energy, metabolizable energy (ME), heat production (HP), heat increment, net energy (NE), milk energy (MKE), maintenance (MNT) and energy balance (EB). Efficiency values of energy conversion were expressed as ratios of energy in product and the product from which it was formed, namely, MNT/ME, MNT/NE, MKE/ME and MKE/NE.

4.3.2 Model and Analysis algorithm

Within each of the three postpartum periods, crude mean and SD were computed for each of the energy expenditure and efficiency variables. Proportions of partitioned energy intake first were expressed using crude means. Variation among cows was expressed in CV. Variation in energy intake and in each of the partitioned energy measures was analyzed using a within period model:

$$y_{ijkl} = \mu + S_i + T_j + P_k + b_1 X_{1ijkl} + b_2 X_{2ijkl} + \epsilon_{ijkl}$$

where: y_{ijkl} is an energy partition (kcal) or efficiency (%) trait; μ is a constant common to all observations; S_i is fixed effect of season, i=1,2, and 3 where 1 is November through March, 2 is June through August and 3 is other months; T_j is fixed effect of treatment, j=1,...,4; P_k is fixed effect of parity, $k=2,3,\geq4$; X_{1ijkl} is maintenance (kcal) as a covariate; X_{2ijkl} is milk energy (kcal) as a covariate; and ϵ_{ijkl} is random residual error distributed as, $N(0,I\sigma_e^2)$ where σ_e^2 is assumed to be homogenous across all groups. When y_{ijkl} was milk energy or a related trait, X_{1ijkl} was dropped from the model. Similarly, when y_{ijkl} was maintenance or an associated measure, X_{2ijkl} was excluded from the model. All analyses were performed using SAS[•] GLM (1985).

4.4 RESULTS AND DISCUSSION

The partitioning of energy intake was based on raw means of cows over the duration of the energy metabolism study. Figure 3 illustrates the overall means and SD of the energy intake variable expressed as a percentage of gross energy (GE) consumed. The chart depicted the flow of dietary energy through a dairy cow: GE less FE yielded DE, which gave ME after subtracting UE and CH₄ and so on. Utilization of energy for production was more than that for maintenance. The proportion of energy left over as tissue energy balance portrays that the experimental animals were in positive energy balance. These energy partitioning data are consistent with those reported by Flatt (1966). Changes in the postpartum partitioning of ingested energy are discussed in more detail elsewhere (Janicki, 1985).

The within period means and SD for the energy partition traits are given in Table 2. Intake of GE was comparable for the three stages of lactation. Fecal and CH_4 energy, HP, and EB appeared to increase whereas the DE, ME, and MKE decreased over time. These changes in the energy utilization could be attributed to changes in diet and production (Janicki, 1985) as lactation progressed. There was more variation



Figure 3. Overall mean percentages for partitioning of energy intake (n = 34). Values in parentheses are SD for each energy partition trait.

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Trait	Mcan	SE	SD	cv	Mcan	SE	SD	сv	Mcan	SE	SD	cv
	1	cal/d		88		kcal/d .		88		kcal/d		×
Gross energy	83573	1865	10877	13	85039	1768	10309	12	84925	1558	9085	11
Fecal energy	26973	792	4620	17	28597	809	4719	17	29386	645	3761	13
Digestible energy	56600	1239	7227	13	56442	1109	6464	11	55538	1089	6349	11
Urinary energy	1891	8	382	20	2093	76	445	21	2088	20	411	20
Methane energy	3250	143	832	26	3847	107	621	16	4194	70	408	0
Metabolizable energy	51109	1120	6528	13	50162	971	5664	11	48876	1008	5880	12
Heat production	24172	431	2511	10	24423	399	2326	10	24524	564	3290	13
Heat increment	10542	375	2186	21	10835	334	1948	18	10832	515	3004	28
Net energy	40566	892	5198	13	39327	814	4746	12	38044	804	4688	12
Maintenance energy	13280	152	884	٢	13248	146	848	9	13312	139	812	9
Milk energy	26514	883	5146	19	24275	824	4805	8	21701	714	4165	19
Energy balance	772	856	4989	646	1804	629	3666	203	3031	761	4436	146

in the energy used for production than for maintenance. Variation in CH_4 was higher than that for UE. However, with the exception of EB, variation among cows was not very high.

The efficiency of energy utilization is shown in Table 3. Methane loss as a proportion of DE, and HP as a ratio of ME increased by wk 14 postpartum. The increased forage in the diet could account for this trend. Urinary losses were relatively similar in all three periods. Likewise the efficiency of ME and NE for maintenance did not change. Therefore the decrease in efficiency in milk energy from ME and NE over time could be associated with reduced milk yield with time. On the other hand, the use of ME for MNT appeared to be constant across all periods. Consequently, the conversion of ME into tissue energy balance, increased from wk 6 to 14 and represented the highest variation among cows. Postpartum fluctuations in the magnitude of the variation in the efficiency traits are indicative of a substantial amount of variation in the efficiency of GE partitioning during lactation.

The amount of variation in each of the energy conversion traits was partitioned using the within period model. The levels of significance for all fixed effects and partial regression coefficients for the covariates are shown in Tables 4 and 5 for selected traits. Energy in milk was an important source of variation in HP, ME, NE, and EB during the postpartum period (P < .05). The results suggested that variation in the efficiency with which ME or NE are used for HP, MKE, or MNT is independent of diet, season, and parity.

					•		,					•	•			
		S	'erall			Wk	6 pp			Wk	10 pp			Wk	4 pp	
Measure ¹	Mean	SE	SD	C	Mean	SE	SD	CV	Mean	SE	SD	cv	Mean	SE	SD	СV
								88								
UE / DE	3.6	Ι.	9.	7.2	3.3	ι.	9.	17.6	3.7	ι.	9.	16.5	3.8	.1	9.	15.7
CH4 / DE	6.7		1.3	18.8	5.8	.2	1.4	24.0	6.8	ι.	۲.	10.6	7.6	.1	œ.	1.0
HP / ME	49.0	s.	4.9	9.9	47.7	ø.	4.7	9.8	49.0	6.	5.0	10.1	50.4	ø.	4.7	9.4
MNT / ME	26.9	4	3.6	13.4	26.4	ι.	4.2	15.8	26.7	9.	3.5	13.0	27.6	s.	3.1	1.3
MNT / NE	34.3	s.	4.8	14.0	33.3	6.	5.3	15.9	34.2	æ.	4.9	14.2	35.4	L.	4.1	111.5
MKE / ME	48.2	ø.	8.1	16.8	51.9	1.5	8.5	16.3	48.2	1.2	6.9	14.4	44.5	1.2	7.2	16.3
MKE / NE	61.4	1.0	10.4	16.9	65.5	1.8	10.7	16.3	61.6	1.6	9.1	14.7	57.3	1.7	10.0	17.5
EB / ME	3.5	6.	8.8	253.8	1.0	6.	1.7	962.0	3.5	1.3	7.4	213.6	5.9	1.5	8.7	145.0
¹ UE = urinary energy, EB =	energy, energy b	DE = alance,	digestil and N	ble energy, E = net en	HP = h ergy.	cat pro	duction	, MNT	= maintens	unce, N	E E	metabolizi	able energ	y, MK	1 	nilk

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У _Ш ¹	Wk. postpartu m	Treatment	Parity	Season	Estime of b	te SE	P - value	Estima of b	ute SE	P - value	\bar{R}^2
HP	6	.27	.84	.55	.79	.52	.15	.17	.09	.08	.15
	10	.19	.97	.48	1.20	.66	.003	.19	.14	.01	.41
	14	.13	.42	.26	1.77	.41	.01	.20	.07	.17	.34
ME	6	.18	.87	.36	-1.09	1.24	.39	.84	.22	.001	.30
	10	.89	.65	.23	1.75	.90	.06	.82	.16	.0001	.52
	14	.03	.55	.18	2.71	.98	.01	.68	.21	.003	.54
NE	6	.28	.82	.26	98	.98	.33	.68	.18	.001	.30
	10	.65	.69	.39	1.50	.82	.08	.61	.15	.0003	.42
	14	.31	.78	.63	1.91	.10	.07	.47	.21	.03	.25
мке	6	.48	.70	.08	1.50	1.03	.17	Dropp	ed		.10
	10	.82	.68	.21	.55	1.12	.63				06
	14	.69	.18	.03	.09	.96	.93				.12
MNT	6	.51	.24	.70	Dropp	ed		.04	.03	.17	01
	10	.36	.20	.83				.02	.04	.63	05
	14	.27	.09	.60				.004	.04	.93	
EB	6	.28	.82	.26	-1.98	.98	.05	32	.18	.08	.24
	10	.65	.69	.39	39	.82	.55	39	.15	.01	.02
	14	.31	.78	.63	53	1	.37	53	.21	.02	.17

TABLE 4. Critical levels (P - value) for main effects and partial regression coefficients for covariates from within period model: energy partition measures.

 ^{1}EB = energy balance, HP = heat production, ME = metabolizable energy, MKE = milk energy, MNT = maintenance, NE = net energy.

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۷۱	Wk.				Estime	9	م	Estimat	0	P.	
	postpartum	Treatm	ent Pau	nity Season	of b	SE	value	of b	SE	value	-
HP / ME	6	.82	69.	.19	.003	100.	1 00.	00	.0002	.003	ю.
	10	.42	.75	.73	100.	10 0.	.52	0004	.000	10.	.19
	14	61.	.63	.89	100 .	100.	.56	0003	.0003	.26	11
MKE / ME	Q	.23	8	.05	.003	.002	.14	Droppe	ק		.13
	10	8.	61.	.18	001	.00	.55				- 10
	14	.50	.68	.07	002	.002	.20				.13
MKE / NE	Q	.32	.93	Ş.	.003	.002	.13	Droppe	q		.11
	10	1.00	67.	.27	001	.002	.51	•			16
	14	.81	.63	.07	002	.002	.32				.05
MNT / ME	6	.52	.76	.81	Dropp	ह		0004	.0002	.03	<i>L</i> 0.
	10	.85	.26	.30	1			0005	.000	.000	.42
	14	Ş.	.62	.11				-0004	.000	.002	.48
MNT / NE	Q	<u>9</u> .	.85	.75	Dropp	g		000	.0002	.03	8
	10	.56	.36	.48				001	.0002	.0005	.37
	14	.31	16.	.49				0004	.0002	.03	.19
EB / ME	6	.34	.75	.30	004	.002	8	001	.000	80.	.22
	10	69.	.70	.42	001	.002	.58	001	.0003	.01	2
	14	34	.65	.62	001	002	4 .	001	.0004	90 .	પ્ર

TABLE 5. Critical levels (P - value) for main effects and partial regression coefficients for covariates from within period

Not shown are comparable results for water intake and body tissue balance (Appendix III).

Energy for maintenance accounted for a significant proportion of the variation in HP, ME and NE at wk 10 and 14 postpartum. As expected, the partial coefficients for maintenance generally were higher than those for milk production. Replacing MKE and MNT in the model by SCM and BW^{.75}, respectively, yielded almost identical results.

4.5 CONCLUSIONS

Dietary energy consumed in the postpartum period by lactating Holstein cows was partitioned by indirect calorimetry. Average values in partitioning of energy intake agreed with textbook estimates. Variation in energy utilization traits was found to be high while variation among cows, for most of the traits except energy balance, was low. It was observed that the utilization of ME for milk decreased as lactation progressed. For these data, dietary source of energy, season, and parity were not very important factors in explaining variation in the partitioning of DE or ME for HP, MKE, or MNT. Clearly, much of the variation in energy traits can be attributed to energy in the milk.

Variation exists in the efficiency with which energy is utilized; if genetics is a major factor in that variation, then evaluation of individual genetic merit for energetic efficiency traits should provide useful management information. This could be made possible from dietary attributes observed on the animal in the field or barn. However,

the validity of this approach is still questionable because previous studies have not examined energy chamber and field data on the same cows. Therefore, comparisons of energy partition measures determined from calorimetry with those from field or barn data, on the same cows, are necessary in order to provide pertinence for field data.

5 Energy intake and Gross Efficiency Comparisons from Calorimetric and Field data on the Same Lactating Cows

5.1 ABSTRACT

Estimates on gross efficiency were obtained from feed intake and production data on 30 pluriparous Holsteins cows during wk 5, 7, 9, 11, 13 and 15 postpartum. Energy intake and efficiency measures from energy chamber on the same cows were taken during wk 6, 10, and 14 postpartum. Measures of gross efficiency were expressed in terms of utilization of metabolizable energy or net energy for production and maintenance. For corresponding postpartum periods, comparisons were made between chamber measures and field estimates by canonical correlation analysis. All energy and gross efficiency estimates from field data closely approximated measures of the same traits from energy chamber data. Variation among cows in gross efficiency for field estimates was one half that for chamber measures. On the other hand, variation among cows in energy partition traits was consistent for both field estimates and energy chamber measures. Correlations greater than .87 were observed between field estimates and chamber measures on maintenance energy and milk energy. Field estimates and chamber measurements of metabolizable energy and net energy had correlations of .58 and .37, respectively.

5.2 INTRODUCTION

Allocating energy intake to energy for milk yield in a lactating cow is an important aspect in energy metabolism. Exact measures of energy intake from dietary sources can be determined by direct (Knott, 1943) or indirect calorimetry (Moe et al., 1972) but this can be costly. So, several methods have been developed to predict feed (Brown et al., 1977; NRC, 1989; Moore and Mao, 1990; Van Soest, 1967) and energy (Moe and Tyrrell, 1972; Moore and Mao, 1992; NRC, 1989; Tyrrell and Reid, 1965; Walter and Mao, 1989) intake using variables such as BW, milk production, forage type, fiber content, age, parity, and season. Genetic selection for energetic efficiency is of increasing importance.

Numerous studies have shown that selection for milk yield brings linear increments of feed efficiency (Blake 1979; Freeman, 1975). Nonetheless, Blake and Custodio (1984) concluded that efficiencies of nutrient utilization have not been influenced by selection for milk production.

Despite the rising costs of feeding cattle, current dairy cattle evaluations do not consider information on individual feed intake nor on efficiency of energy partitioning. This is, in part, because the establishment of such a data base, by installing calorimetric apparutus on farms, would be both expensive and impractical. Therefore, accurate approximation of energy efficiency using data obtainable under normal conditions would be highly desirable. Walter and Mao (1989) compared estimates of energy intake from field collected data with literature chamber results and found that accurate approximation was plausible. However, in order to determine the validity of efficiency estimates from field data, it would be necessary to compare estimates from field data with exact measures from energy chambers on the same cows which was the objective of this study.

5.3 MATERIALS AND METHODS

5.3.1 Experimental Design and Data

Data used in this study came from a study which examined the effects of percentages of crude protein and nitrogen solubility in the diet and their interactions on digestibility, energy and protein balances (Janicki, 1985). In that study measurements were taken on 30 pluriparous cows, in energy chamber, during wk 6, 10, and 14 postpartum. Diets were as described by Holter et al. (1982) and Janicki (1985) and energy balance was determined by methods described by Saama et al (1992[•]). Energy intake variables were metabolizable energy (ME), net energy (NE), milk energy (MKE), and maintenance energy (MNT). Gross efficiency (GREF) measures from energy chamber were thus expressed as ratios of MNT/ME, MNT/NE, MKE/ME and MKE/NE.

Recorded for each cow in wk 5, 7, 9, 11, 13 and 15 postpartum were DMI, milk yield, milk fat, and body weight. Estimated ME (eME) and estimated NE (eNE), and estimated GREF (eGREF) were obtained from DMI:

 $eME (Mcal/d) = [(1.57 \times Grain) + (1.29 \times CS) + (1.07 \times HCS) - (1.31 \times Orts)],$

eNE (Mcal/d) = [(.93 x Grain) + (.77 x CS) + (.65 x HCS) - (.78 x Orts)],where Grain, CS and HCS are daily consumption, in kilogram per day, of grain concentrate, corn silage and haycrop silage, respectively, and orts in kilogram per day. Coefficients for energy value of feeds are those reported by NRC (1989). Estimated energy in milk (eMIKE) was,

eMKE (Mcal/kg of milk) = [(.3512 + (.0962 x % fat)].

Estimated MNT (eMNT) was (NRC, 1989),

eMNT (Mcal/kg of BW^{.75}) = $.086 \times BW^{.75}$ (kg).

5.3.2 Analysis Procedures

The variables for comparison were: 1) chamber measures of ME, NE, MKE, and MNT in wk 6, 10, and 14 postpartum; 2) estimates from field data on eME, eNE, eMKE, and eMNT from averages of wk 5 and 7, 9 and 11, 13 and 15 postpartum; 3) chamber measures of GREF in MKE/ME, MNT/ME, MKE/NE, and MNT/NE; and 4) eGREF from field data as eMKE/eME, eMNT/eME, eMKE/eNE and eMNT/eNE.

Paired comparisons of means, SD and CV's, and computations of productmoment and rank correlations were done: 1) between GREF and eGREF in ME; 2) between GREF and eGREF in NE.

Canonical correlation analysis (CCA) was performed to compare estimates from field data to chamber measures. Canonical correlations refer to correlations that are independent of each other (Hotelling, 1936). Its use is most suited to examining correlations between a group of p X-variables and a group of q Y-variables, when one wishes to test the null hypothesis that X_p and Y_q variables are independent. Various linear combinations in X_p and Y_q are established in CCA. Then correlations between the linear combinations from the sets of variables are computed. The highest correlation would correlation between X_p and Y_q . Thus, the CCA model reduces the dimensionality to a few linear functions of the measures under study.

The null hypothesis that a canonical correlation is 0 in the population was tested by a likelihood ratio (Lawley, 1959). Redundancy analysis (Cooley and Lohnes, 1971), which measures the standardized proportion of total variation in a variable, X_p or Y_q , that is predictable from linear functions of X_p or Y_q also was performed. All analyses were accomplished using SAS[®] (1985).

5.4 RESULTS AND DISCUSSION

Means of energy estimates from field data were within the normal range and approximated closely energy chamber measures (Table 6). Corresponding standard errors also were similar. Variation among cows in energy use for MKE and MNT was slightly lower for estimates from field data. Averages for ME and MKE as estimated from field data were slightly higher than those for chamber measures while NE and MNT means were slightly lower. Similar trends were observed for means computed within periods (Table 7). Differences between ME and eME and between MKE and eMKE decreased as lactation progressed while differences between MNT and eMNT and between NE and eNE remained fairly constant. The large differences in wk 6 postpartum may be due peak lactation as shown in Figure 4, and the state of negative energy balance, during that period. Therefore, field estimates at wk 14 postpartum perhaps were most representative of actual energetic efficiency of cows.

Energy measure		Energy c	hamber			Fie	eld	
	Mean	SE	SD	CV	Mean	SE	SD	CV
]	Mcal/d -		%		Mcal/d		%
Metabolizable energy	50.68	.64	6.03	11.9	61.19	.92	8.76	14.31
Net energy	39.78	.52	4.98	12.51	36.44	.55	5.21	14.29
Milk energy	24.74	.52	4.91	19.83	26.33	.48	4.58	17.39
Maintenance energy	13.29	.08	.79	5.98	10.11	.07	.63	6.20

TABLE 6. Overall mean, SE, SD and CV for energy measures from energy chamber and from field data on the same 30 pluriparous Holstein cows in early lactation.

TABLE 7. Mean, SE, SD and CV of energy measures from energy chamber and estimates from field data on the same 30 pluriparous Holstein cows in early lactation.

Energy measure		Energy of	chamber			Fie	bld	
	Mean	SE	SD	CV	Mean	SE	SD	CV
		Mcal/d -		%		Mcal/d -		%
Wk 6 postpartum								
Metabolizable energy	51.84	1.17	6.39	12.32	64.57	1.56	8.56	13.26
Net energy	41.13	.94	5.13	12.47	38.39	.93	5.10	13.29
Milk energy	27.21	.90	4.91	18.05	28.91	.80	4.39	15.20
Maintenance energy	13.32	.16	.86	6.45	10.18	.13	.70	6.82
Wk 10 postpartum								
Metabolizable energy	50.58	1.07	5.85	11.56	61.06	1.68	9.20	15.06
Net energy	39.65	.91	4.96	12.51	36.36	1.00	5.48	15.08
Milk energy	24.72	.86	4.74	19.15	26.46	.78	4.26	16.10
Maintenance energy	13.26	.15	.80	6.06	10.04	.12	.64	6.40
Wk 14 postpartum								
Metabolizable energy	49.61	1.06	5.83	11.75	57.93	1.35	7.39	12.75
Net energy	38.57	.85	4.66	12.08	34.56	.81	4.41	12.77
Milk energy	22.27	.70	3.83	17.20	23.61	.64	3.52	14.89
Maintenance energy	13.29	.14	.74	5.59	10.09	.10	.54	5.40

However, results from paired t-tests indicated that means were significantly different (P < .0001) in all postpartum periods. Notwithstanding, CV for mean absolute value of differences between field estimates and chamber measures were as high as 70%. This suggested differences between estimates and measures for energy traits were quite erratic and misleading as evidence for correspondence between chamber measures and field estimates.



Figure 4. Lactation curve for 30 pluriparous Holstein cows

The field estimates of efficiency in eMKE and eMNT from eME were significantly lower than measures from energy chamber (P < .0001) as shown in Table 8. Approximation of NE utilization for MKE by eMKE / eNE were higher, while that for eMNT was lower (P < .0001). This implies that the formulae for estimating MKE was more precise than that for MNT.

		Energy	chamb	er		Fi	ield	
Efficiency measure ¹	Mean	SE	SD	CV	Mean	SE	SD	CV
				%				%
MKE/ME	.48	.01	.08	16.21	.43	.01	.07	6.97
MKE/NE	.62	.01	.10	16.51	.73	.01	.12	7.03
MNT/ME	.27	.004	.04	13.62	.17	.002	.03	6.91
MNT/NE	.34	.01	.05	14.08	.28	.004	.05	6.91

TABLE 8. Overall mean, SE, SD and CV for efficiency measures from energy chamber and estimates from field data on the same 30 pluriparous Holstein cows in early lactation.

 ${}^{1}ME$ = metabolizable energy, MKE = milk energy, MNT = maintenance energy, and NE = net energy.

The within period means for GREF and eGREF are given in Table 9. In constrast to results in Table 8, among cow variation in energy utilization from field data was not always lower than that for corresponding chamber measures; variation in GREF in ME and NE for maintenance was higher at wk 10 and 14. From wk 6 to wk 10 postpartum, mean differences between GREF and eGREF remained consistent.

The product-moment and rank correlations between field estimates and chamber measures in energy are presented in Table 10. Correlations among MNT and eMNT were the highest. Correlations between MKE and eMKE, between MNT and eMNT were higher than correlations between either NE and eNE or ME and eME. The rank correlations were moderate to high and consistent with the product-moment correlations.

name 30 plumparous Holstein cows in ea	ariy lactatio	u.						
		Energy o	hamber			Fi	ekd	
Efficiency measure ¹	Mcan	SE	SD	cv	Mcan	SE	SD	cv
				×				æ
WK 6 postpartum								
MKE/ME	.45	10 [.]	. 07	16.10	.52	8	8 .	16.60
MKE/NE	92.	ġ	.12	16.13	%	8	11.	16.74
MNT/ME	.26	10	2	16.16	.16	.003	8	14.21
MNT/NE	.33	10 [.]	<u>.</u> 05	16.10	.27	. 01	ą	14.25
WK 10 postpartum								
MKE/ME	4	10	6.	15.96	84 .	10 [.]	<u>.</u>	13.72
MKE/NE	.74	8	.12	15.97	.61	8	8	14.53
MNT/ME	.27	.01	2	13.44	.17	90 .	8.	19.10
MNT/NE	34	10	3 2	14.72	.28	.01	8.	19.11
Wk 14 postpartum								
MKE/ME	.41	.01	6	18.02	.45	.01	8	14.21
MKE/NE	9 9.	2 9.	.13	18.06	.57	8 .	8 .	15.55
MNT/ME	.27	10.	8	11.22	.18	10 0.	8	15.54
MNT/NE	.35	.01	8	11.17	.30	.01	5 0.	15.59

TABLE 9. Mean, SE, SD and CV for efficiency measures from energy chamber and estimates from field data on the same 30 pluriparous Holstein cows in early lactation.

¹ME = metabolizable energy, MKE = milk energy, MNT = maintenance energy, and NE = net energy.

		Field	l estimate ²	
Chamber meas	sure ¹ eME	eNE	eMKE	eMNT
ME	.71	.71	.58	.37
	(.73)	(.66)	(.63)	(.18)
NE	.65	. 65	.57	.32
	(.73)	(. 66)	(.62)	(.18)
MKE	.58	.58	.87	.21
	(.56)	(.53)	(.86)	(.22)
MNT	.23	.23	.24	.91
	(.32)	(.29)	(.16)	(.92)

TABLE 10. Product-moment correlations between field and energy chamber measures of energy intake from data on the same 30 pluriparous Holstein cows in early lactation; values in parentheses are rank correlations.

¹ME = metabolizable energy, NE = net energy, MKE = milk energy, MNT = maintenance energy. ²eME = estimated ME, eNE = estimated NE, eMKE = estimated MKE, and eMNT = estimated MNT.

Correlations between GREF and eGREF, in Table 11, were relatively high but lower than those in energy traits. The rank correlations between GREF and eGREF were, in most instances, higher than the product-moment correlations. Negative correlations between utilization of either NE or ME for MKE and use of ME or NE for MNT reflect that the lactating cow must sacrifice efficiency for production in order to partition more energy for maintenance.

		Field	l estimate ²	
Efficiency	eMKE/	eMKE/	eMNT/	eMNT/
measure ¹	eME	eNE	eME	eNE
MKE/ME	.59	.59	25	24
	(.59)	(.56)	(.04)	(.03)
MKE/NE	.55	.56	.24	24
	(.59)	(.56)	(.04)	(.03)
MNT/ME	04	04	. 59	.60
	(26)	(25)	(.71)	(.64)
MNT/NE	06	06	. 5 7	.57
	(26)	(25)	(.71)	(.64)

TABLE 11. Product-moment correlations between field and energy chamber measures of energy efficiency from data on the same 30 pluriparous Holstein cows in early lactation; values in parentheses are rank correlations.

¹ME = metabolizable energy, NE = net energy, MKE = milk energy, MNT = maintenance energy. ²eME = estimated ME, eNE = estimated NE, eMKE =

estimated MKE, and eMNT = estimated MNT.

Linear combinations of the field estimates and chamber energy measures were examined by CCA. Tables 12 and 13 show CCA results for comparisons between chamber measures and field estimates of energy partitioning and efficiency, respectively. Because the comparisons involved four energy partitioning or efficiency variables at a time, we could have, at most, four orders or dimensions. As expected, the canonical root for first order was the largest. The first dimension also gave the largest correlation among the linear combinations of the chamber and field variables. Within each period, summing all four canonical roots yielded the total variance. At wk 6, 10, and 14 postpartum the first squared canonical correlation was significant (P< .0001) and the first two dimensions accounted for over 90% of the total variation with the highest cumulative proportions occuring in wk 14. These dimensions depicted convincing evidence for strong linear associations between the factors.

Results of the redundancy analysis showed slightly reduced cumulative proportions of variation in GREF, at wk 6 and 14 postpartum, which was indicative of lower precision in those estimates. This might also imply that some of the negatively correlated variables could have been acting as suppressors. Notwithstanding, for energy intake and GREF measures in the energy chamber, the highest proportion explained by the field variates was at wk 10.

A factor loading is a correlation between the underlying canonical variable and the observed trait in question. The factor loadings for the energy intake variables showed that all the measures from field data contributed significantly in the relationships between the canonical variables and energy traits (Appendix V). The chamber canonical variables had the highest loadings for field MKE and MNT. On the other hand, the mixture of signs on the factor loadings for the GREF measures confirmed the existence of suppression. The GREF in ME and NE for MKE acted to suppress the relationships between the canonical variables and the GREF in ME and NE for maintenance. This could be so because, in the first vector, the contrast was between efficiencies for milk energy and those for maintenance. It is worth noting that the second canonical variable for the field variables, at wk 10, had very strong positive correlations with all the field GREF variables. These data are in agreement with the initial observations that the post-peak GREF estimates were more precise.

TABLE postpart	um.	nonical roots a	und correlations (R ² ,) between	field and	calorimetric e	nergy intake me	asures on the	e same 30	lactating cov	vs at wk 6, 10 a	nd 14
			Wk 6	1			Wk 10				Mk 14	
Order	Root	% of total variation	Cumulative percentage	(R²)	Root	% of total variation	Cumulative percentage	(R²)	Root	% of total variation	Cumulative percentage	(R²)
-	9.98	- <u>5</u> 9	- 65.	.95***	10.93	8	3 8.	***96.	6.11	છ .	8	***C6.
6	5.63	.37	%	** *£6'	4.58	.28	96 .	***16.	3.34	34	76.	***16.
ũ	.62	8	8 ;	.62*	%	8	8 .	.71**	2	8 .	8	.76 **
4	:	:	1.00	80.	:	1.00	.15		:	:	1.00	.43
> d***	.0001,	**P < .01, *	20 . > 4									

TABLE 13. Canonical roots and correlations (R²) between field and calorimetric gross efficiency measures on the same 30 lactating cows at wk 6, 10 and 14 postpartum.

			Wk 6				WK 10			×	1 k 14	
		% of total	Cumulative			% of total	Cumulative			% of total	Cumulative	
Order	Root	variation	percentage	(R ²)	Root	variation	percentage	(R²,)	Root	variation	percentage	(R ²)
1	7.81	8 .	%	.94***	5.00	.78	8 2.	***16.	2.84	68.	8.	.86**
6	.57	60.	.97	* 09.	<u>.</u>	.15	. 93	**6 9'	52	8 0.	7 6.	.45
ŝ	.28	8	8 ;	L4.	Ź,	60.	8 .	.55*	8	8 9.	8 ;	.27
4	8	÷	1.00	.16	8	:	1.00	.14	.01	:	1.00	.10

****P* < .0001, ***P* < .01, **P* < .05

5.5 CONCLUSIONS

Estimates of energy intake and gross efficiency estimates from data obtainable from field data closely approximate measures from energy chamber. Therefore, establishing a database on energy partitioning and energetic efficiency of individual cows from field data may be worthwhile if such measures are desirable for management and if genetic evaluation of animal's energetic is desired. The use of post-peak field data to estimate energetic efficiency provided more reliable estimates of energy partitioning than those obtained during peak lactation. This study examined measures versus estimates, a closer examination would necessarily involve the partitioning of phenotypic means and variation into genotypic and environmental means and variation.

6 Comparisons of Genetic Parameters for Energy Intake Estimated from Energy Chamber and from Field Collected data on the Same Lactating Cows

6.1 ABSTRACT

Measures of energy intake from energy chamber can be approximated closely by estimates from field collected data according to a study using the same data as in this one. This study estimated genetic parameters of these measures and of partial energy requirements from energy chamber and field collected data. Data from 67 primiparous Holstein cows collected at peak and post peak lactation consisted of measures of DMI, milk yield, BW, metabolizable energy, net energy, and maintenance energy. From DMI and milk yield, energy partitioning was estimated. Univariate and multivariate animal models were used to estimate genetic parameters for these energy traits. Partial energy requirements were estimated using an animal model which included covariates of age at calving, milk energy, maintenance energy, and weight change. (Co)variance components were estimated by a derivative-free REML algorithm. Genetic and phenotypic variations and heritability estimates in energy intake variables, at postpeak lactation, were similar from chamber and from field data. This was not always the case at peak lactation. There was little difference in solutions for covariates with and without animal effects. However only solutions for maintenance energy from animal models matched literature values.

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6.2 INTRODUCTION

The potential for increasing milk production through feeding is well appreciated. Efficiency is usually defined as the ratio of output over input or its inverse. Selection for improved efficiency may replace selection for total outputs such as milk yield in dairy enterprize today and future. Feed consumption data is required in order to measure efficiency. Good knowledge about partial energetic requirements is fundamental to establishing energy efficiency criteria.

Freeman (1967) showed that the direct measure of efficiency under commercial conditions does not seem to be economically feasible. He concluded that, "Selection for higher milk yield automatically improves feed efficiency". Notwithstanding, Grieve et al. (1976) and Custodio et al. (1983) examined the relationship between estimated transmitting ability for milk production and digestibility of dietary components in Holstein cows. Both studies concluded that digestive ability of a cow was independent of predicted transmitting ability. Buttazoni and Mao (1989) found that the genetic correlation between net efficiency and production was only 60%. We can attribute this lack of association to the low variability among cows in digestive ability.

Van Es (1961), Wagner (1965) and others (Andersen et al., 1959; Saama et al., 1992^a, Taylor et al., 1986) demonstrated that little variability exists among cows in their ability to digest a given diet, particularly when intakes are standardized. However, considerable variation exists in maintenance energy requirement (Bauman, 1985; Taylor et al., 1986) and energy requirement for producing milk (Saama et al.,

1992[•]) in cattle. Korver (1988) reviewed the importance of different components of efficiency in selection programs.

Genetic aspects of feed and energy intake have been studied (Blake and Custodio, 1984; Freeman, 1967; Korver, 1988). Genetic parameters for feed intake (Korver, 1988; Stone et al., 1960) and feed efficiency (Blake and Custodio, 1984; Buttazoni and Mao, 1989; Hooven et al., 1968), energy intake (Taylor et al., 1981) and energy efficiency (Buttazoni and Mao, 1989) traits of lactating cows also are documented. These studies indicated that feed and energy efficiency are moderately heritable traits. But genetic estimates can be valid only in data collected from a large number of animals.

In view of the high cost of calorimetric determinations of energy partitioning, generating similar information from field collected data is highly desirable. Walter and Mao (1989) estimated net efficiency of energy conversion from on-farm data and found them to be in close agreement with published chamber results. They indicated that in order to verify these results, similar comparisons involving field and chamber data on the same cows would be desirable. Saama et al. (1992^b), using field estimates and chamber measures of energy utilization on the same cows at peak and postpeak lactation, showing that field estimates approximated energy chamber measures closely, hence supported the validity of using field data to approximate chamber energy measures. However, the efficacy of using field data to estimate genetic parameters for energy efficiency needs to be examined. At peak and postpeak lactation, using energy chamber measures and field estimates of energy partitioning on

the same cows, the objectives of this study were to make comparisons between chamber and field: 1) genetic parameter estimates for energy utilization traits; 2) partial energetic efficiency and weight change requirements; 3) partial energetic efficiency and weight change requirements with and without animal effects in the model.

6.3 MATERIALS AND METHODS

6.3.1 Experimental Procedure and Data

Field collected and energy chamber data on 28 pluriparous Holstein cows were available from a study which examined the effects of percentages of crude protein and nitrogen solubility on digestibility, energy and protein balances (Janicki, 1985); herein referred to as study A. Chamber measures were collected at wk 6, 10, and 14 postpartum. Barn DMI, BW, and milk yield were recorded at wk 5, 7, 9, 11, 13, and 15. From separate energy balance trials (Holter et al., 1992), study B, field and energy chamber data on 39 primiparous Holstein cows were available. In study B cows were in the energy chamber at wk 7 and 16 postpartum. Barn DMI, BW, and production data was recorded at wk 6, 8, 15, and 17 after calving. Diets were as specified in (Janicki, 1985; Holter, 1992), energy balance was determined by methods described in (Saama et al., 1992^a), and field estimates of energy partitioning were obtained using formula outlined in (Saama, 1992^b).

The variables for analysis were metabolizable energy (ME), net energy (NE), milk energy (MKE) and maintenance energy (MNT). Estimated from the field collected data were estimated ME (eME), estimated NE (eNE), estimated MKE (eMKE) and estimated MNT (eMNT). Two periods of measurement, peak (PL) and postpeak (PPL) lactation, were established. From study A, PL data were wk 6 chamber data and averages of wk 5 and 7 field data; PPL were wk 14 and averages of wk 13 and 15 postpartum field data. From study B, PL data were wk 7 chamber measurements and averages of wk 6 and 8 field estimates; PPL were wk 16 chamber data and averages of wk 15 and 17 postpartum field data. At PL and PPL, weight change (WC) was computed as the difference between BW (kg) at wk 5 and 7, and between wk 13 and 15 from study A. Similarly WC was calculated as the difference between BW (kg) at wk 6 and 8, and between wk 13 and 15 postpartum from study B measurements.

6.3.2 Estimation of Genetic Parameters

Using estimates from field or measures from energy chamber, within PL and PPL periods, the *i*th trait, i = ME, NE, MKE, or MNT was entered one at a time in an animal model (AM) [1]:

$$y_i = a_i + e_i$$
 [1]

where y_i is a vector of 67 observations for the *i*th trait; a_i is a vector of unknown random effects of 40 sires, 10 dams with records, 49 dams without records and 57 animals without offspring on the *i*th trait which was assumed to be distributed as $N(0,A\sigma_a^2)$ where σ_a^2 is the additive genetic variance of the *i*th trait and A is the additive genetic relationship matrix between the total of 156 animals; e_i is a vector of 67 random residuals for the *i*th trait corresponding to y and was assumed to be distributed as, N(0, $I\sigma_e^2$) where σ_e^2 is the residual variance with

E(y) = E(a) = E(e) = 0.

Using field estimates or chamber measures, ME, NE, MKE and MNT were entered two at a time, within PL and PPL, in a multivariate AM [2]:

$$y = Z_a a + e$$
 [2]

where y, a, and e are as defined in [1]. For a pair of energy intake traits, the

random elements in [2] had distribution:
$$\begin{bmatrix} y \\ e \\ a \end{bmatrix} \sim N \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} V & R & Z_a G_A \\ R & R & 0 \\ G_A Z_a' & 0 & G_A \end{bmatrix}$$

where, $\mathbf{V} = \mathbf{R} + \mathbf{Z}_{\mathbf{s}} \mathbf{G}_{\mathbf{A}} \mathbf{Z}_{\mathbf{s}}' \mathbf{R} = \mathbf{I}_{\mathbf{s}} \otimes \mathbf{R}_{0}$, $\mathbf{G}_{\mathbf{A}} = \mathbf{A} \otimes \mathbf{G}_{0}$ with $\mathbf{Z}_{\mathbf{s}}$ being an incidence matrix for the animal effects, \mathbf{A} is the numerator relationship matrix of order 156, \mathbf{R}_{0} is residual covariance matrix among measurements or estimates on the same animal, \mathbf{G}_{0} is covariance matrix for additive genetic effect among measurements or estimates on the same animal, and \otimes denotes Kronecker (direct) product.

Within PL and PPL, the estimated genetic and phenotypic covariance matrices

from field data were compared with those from chamber data using a generalization of Bartlett's likelihood ratio test by Box (1949). The variance ratio test was used to make specific comparisons between individual variances.

6.3.3 Estimation of Partial Energetic Efficiency

Within PL or PPL, partial requirements for MKE, MNT, WC were computed from an AM [3], analogous to that fitted by Ngwerume and Mao (1992),

$$y_i = b_1(Age) + b_2(MKE) + b_3(MNT) + b_4(WC) + a_i + e_i$$
 [3]

where y_i is NE; b_1 , b_2 , b_3 and b_4 are partial regression coefficients for age at calving (months), MKE (Mcal), MNT (Mcal), and WC (kg), respectively, with a_i and e_i are as defined in [1]. Age at calving is included in [3] because of its effect on nutrient partitioning (Bauman and Currie, 1980; Bauman et al., 1985). (Co)variance component estimation in [1] and [2] and solutions for b_i in [3] were obtained using a derivative-free REML algorithm described by Meyer (1991). For each run, convergence was declared when the variance of the log-likelihood function was less than 10⁻⁴. Sampling errors for individual parameters were estimated using univariate approximation techniques outlined by Meyer and Hill (1991).

Omitting a_i from [3] gave a multiple regression model (MRM), [4], which was used to estimate partial energy efficiencies ignoring animal effects. Analyses for the MRM were performed using SAS[•] (1985).
6.4 RESULTS AND DISCUSSION

Genetic parameter estimates from [1] and [2] and solutions from [3] and [4] were used for the purpose of making comparisons between chamber measures and field estimates of ME, NE, MNT, and MKE. The direct use of these etimates may not be appropriate due to the very small sample size.

6.4.1 Genetic and Phenotypic Variation

In general, convergence was reached after approximately 30 evaluations of a mixed model equations. The genetic and phenotypic standard deviations, heritability estimates and associated standard errors for energy intake traits, at PL and PPL are shown in Table 14. At PL, genetic variation in ME, MKE, and MNT were not different from that in eME, eMKE, and eMNT. However, genetic variation in NE and in eNE was significantly different (P < .05). During PPL, genetic variation in all intake traits estimated from chamber and those estimated from field data was very similar. With the exception of phenotypic variation in MNT and eMNT, all chamber and field energy intake characteristics were comparable (P < .05), at PL.

Notwithstanding, at PPL, phenotypic variation in chamber energy utilization traits and corresponding field traits was not different. Although the heritability estimates for ME and eME, MNT and eMNT were alike at PL, the heritability estimate for eMKE was higher than the heritability estimate for MKE. Furthermore, the heritability estimate for eNE was twice as high as that for NE, at PL. Also, standard errors for heritability estimates, at PL, tended to be high. Yet at PPL, heritability estimates for all

		Chambe	স			· · ··	Field	1		
Trait ¹	Additive genetic SD (Mcal)	Phenotypic SD (Mcal)	Herital estima	bility te	SE	Additive genetic S (Mcal)	SD Phenotypic SD (Mcal)	Heritab estimat	oility e	SE
					peak -					
ME	1.08	8.50	.02	.03		1.05	10.98	.01	.02	
NE	5.88	7.25	.66	.34		3.85	6.42	.36	.41	
MKE	4.10	5.38	.58	.50		4.84	5.41	.80	.38	
MNT	.70	1.07*	.43	.25		.59	.80	.54	.25	
		<u></u>		I	postpeal	k				_
ME	1.02	7.80	.02	.03		.98	9.64	.01	.01	
NE	1.09	6.49	.03	.02		.95	5.79	.03	.04	
MKE	.95	4.33	.05	.06		.92	4.44	.04	.06	
MNT	.73	1.02	.51	.29		.59	.77	.58	.27	

TABLE 14. Additive genetic and phenotypic SD and heritability for energy measure traits at peak and postpeak lactation.

 ${}^{1}ME$ = metabolizable energy, MKE = milk energy, MNT = maintenance energy, and NE = net energy.

Corresponding variance components significantly different (P < .05).

chamber traits considered were, in some instances, identical to heritability estimates for corresponding field traits. Buttazoni and Mao (1989) found comparable heritability estimates of $.05\pm.37$ and $.13\pm.34$ for NE and NE for maintenance from single trait sire models, respectively. No prior heritability estimates for ME and MKE could be found in the literature.

6.4.2 Genetic and Phenotypic Correlations

An average of around 240 evaluations of the mixed model equations was required before reaching convergence. Estimates of genetic and phenotypic correlations for energy usage traits are given in Table 15. The estimates were generally consistent within data source but disparagingly divergent when compared between data sources.

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				Pe	놀							Post	tpeak			
		Char	nber				Field			10	amber			Ľ,	ield	
Trait ¹	ME	NE	MKE	MNT	ME	NE	MKE	TNM	ME	NE	MKE	TNM	ME	NE	MKE	MNT
ME		0 9.	11.	.61		.23	10	.83		.82	.53	.58		.26	12	.85
NE	79		.17	<u>8</u> .	.14		.70	62.	84		.27	.78	.14		.65	.62
MKE	.41	46		.75	6	.03		.85	66	.14		.43	8	1.00		.89
MNT	.83	.56	.76		.81	%	<i>TT</i> .		.65	.72	98		.86	4 .	8	
¹ ME = met	abolizabl	le energ	y, MK	E = milk e	nergy,	MNT	= mainte	nance energy	', and h	HE = D	let energ	2				

This may be attributable to the small sample size and its effect on the log-likelihood surface. This could have led to the possibility of local maxima at the point of convergence. Groeneveld and Kovac (1990) observed that, for small datasets, multiple solutions can exist from multivariate derivative-free REML algorithms. The space around the converged solutions was not investigated.

The genetic and phenotypic (co)variance matrices for the chamber and field traits, at PL and PPL, were significantly different (P < .05). Regardless, at PL and PPL, estimates of genetic and phenotypic correlations between MNT and ME, and MNT and NE from field estimates were in reasonable agreement with those estimated from chamber measures. The estimate of genetic correlation between NE and MNT at PPL was much higher than the value of -.3 reported by (Buttazoni, 1989) but gave the most accurate portrayal of the biological relationship between those two traits.

6.4.3 Partial Energy Requirements

The partial regression coefficients for covariates in AM at PL and PPL are shown in Table 16 for chamber and field data. Although the coefficients for age at calving from chamber and field data were generally in close proximity, they were much closer at PPL than at PL. While maintenance requirements would consist of the energy required to maintain and conduct activities related to homeostasis, milk energy and weight change requirements are usually associated with homeorhesis (Bauman and Currie, 1980). The requirements for MKE and eMKE, at PL and PPL, and MNT and eMNT, at PL were proximate and within the range of values reported by Walter and Mao (1989) and others (NRC, 1989; Ngwerume and Mao, 1992). At PPL, the requirements for MNT were higher than requirements for eMNT (P < .05). A similar trend was observed for WC. In addition, the R² values were remarkably higher for PPL analyses. In general, these trends for MKE and age at calving were not altered by exclusion of animal effects from the underlying statistical model (Appendix VI).

The partial regression coefficients in Table 17 are from MRM of [4] which ommitted the animal effects. Visual appraisal of results at PL, reveals only trivial differences between MRM and AM. The closeness between coefficients for age at calving and MKE was greater with MRM. Nevertheless, trends for MNT and WC were reversed by using MRM but magnitude of differences between coefficients from field estimates and chamber measures was consistent, at PL and PPL. Whereas estimated requirements for MKE from chamber measures using MRM, at PL, and those from field data, at PL, coincided with values published by NRC (1989), it is worth noting that the estimate for maintenance requirements, at PL, from chamber measures using AM was the only one that agreed with values reported in the literature (Walter and Mao, 1989). The theoretical expectation of y under [3] and [4] is the same but inferences from parameter estimates were not the same.

		ď	eak			Por	tpeak	
	Chamber	$(R^2 = 62)$	Field (R	² = .69)	Chamber	(R ² = .73)	Field (R ² -	(67. =
Effect	Coeff.	SE	Coeff.	SE	Coeff.	SE	Coeff.	SE
Age at calving (months)	900.	.035	.029	.031	.00	.031	.007	.025
Milk energy (Mcal)	.835**	** .152	.631***	* .129	.811**	** .142	.729****	.106
Maintenance (Mcal)	.078	.743	1.939**	.872	1.140**	£09 [.] **	3.088**	.669
Weight change (kg)	.344	.314	.469	.265	.020	.272	.652	.229

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Partial regression coefficients (Coeff.) for c	
16. Partial regression coefficients (Coeff.) for c	
LE 16. Partial regression coefficients (Coeff.) for α	
TABLE 16. Partial regression coefficients (Coeff.) for α	

****P < .001, ***P < .01, **P < .05, and *P < .1

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	Chamber	$(R^2 = .63)$	Field (R ²	: = .73)	Chamber ([R ² = .63)	Field (R ²	= .73)
Effect	Coeff.	SE	Coeff.	SE	Coeff.	SE	Coeff.	SE
Age at calving (months)	.022	.039	.027	.032	001	.031	001	.025
Milk energy (Mcal)	.743**	** .149	.61***	.126	.810***	+ .143	.706***	• .109
Maintenance (Mcal)	.267	.743	1.929**	.884	1.213**	604	3.164***	• .678
Weight change (kg)	.299	.329	.455*	.272	027	.276	**665"	.235
/ Q *** 100 / Q ****	0 / 0 ** 0 / 0	A the A	-					

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6.5 CONCLUSIONS

Genetic parameter estimates and partial requirements for energy intake traits from field collected and energy chamber data were quite similar. This similarity was greater with data collected during postpeak lactation. Accurate measurement of individual intake and production data is not limited to experimental herds.

Milk recording and management programs can provide individual concentrateintake data, especially those systems with automated individual feeders. Forage intake and testing data can be obtained on a herd basis. In practice, cows are fed according to milk yield. This may cause a high correlation between feed intake and feed efficiency. Korver (1988) suggested that considering only the first 60 days of lactation, during which cows have a negative energy balance and are fed less adequately according to production requirements might alleviate this problem. But direct selection on gross efficiency has little advantage (Buttazoni and Mao, 1989; Korver, 1988). So, for purposes of estimating genetic parameters for net efficiency, the authors suggest using intake and production during 60 to 150 days as these data provided a closer approximation.

Several formula for estimating energy intake from field collected data are available from the literature. Standards needs to be established with regard to which formula to use for prediction. Wide acceptance of such formula can be anticipated if the statistical properties of these formula are well elucidated. This is a matter that has received little attention in the literature.

There was trivial evidence to suggest estimates of partial energy requirements from animal models and multiple regression models differed. Including animal effects in the model reduced the error sums of squares but did not necessary increase accuracy of estimates. Omitting animal effects led to discrepant estimates of energy requirements for maintenance. Research is needed to examine the biological and statistical merits and demerits of using animal models versus multiple regression models to estimate energy requirements for maintenance.

7 SUMMARY

Energy balance trials involving 34 pluriparous Holstein cows were conducted at the University of New Hampshire, Durham, during wk 6, 10, and 14 postpartum. Dietary energy was partitioned by indirect calorimetry. Average percentages in partitioning of energy intake were in agreement with classical values. With the exception of energy balance, within cow variation in energy intake traits was low. The utilization of metabolizable energy for milk energy decreased as lactation progressed. Evidence from a within period model indicated that milk energy accounted for a highly significant proportion of the variation in energy intake and efficiency traits.

Field estimates of energy utilization measures were computed from dry matter intake, consumed by the 34 Holstein cows, at peak and post peak lactation. Both energy intake and gross efficiency estimates from field collected data approximately closely corresponding measures from the energy chamber. The precision of field estimates was higher at postpeak lactation.

From a separate energy study, energy chamber measures and field estimates of energy intake on 37 primiparous Holstein cows were obtained. Data from the two studies were merged and genetic parameters for metabolizable energy, net energy, milk energy, and maintenance energy were computed. Partial energetic requirements were then estimated from animal models and multiple regression models. Excluding animal effects from the underlying statistical model did not lead to a change in estimates for energy requirements. It was verified that genetic parameter estimates for

energy intake traits estimated from data obtainable from barns were in close agreement with those estimated from energy chambers.

APPENDICES

Appendix I: Frequency distributions for study A

		Wk po	stpartum	
Treatment ¹	Wk 6	Wk 10	Wk 14	Total
High CP - high N	9	9	9	27
Low CP - low N	9	9	9	27
High CP - low N	8	8	8	24
Low CP - high N	8	8	8	24
Total	34	34	34	102

TABLE I.1. Frequency distribution of 34 pluriparous Holstein cows by treatment and Wk of measurement in early lactation.

¹ CP = crude protein, N = nitrogen.

TABLE I.2. Frequency distribution of 34 pluriparous Holstein cows by parity group and Wk of measurement in early lactation.

		Wk p	ostpartum	
Parity	Wk 6	Wk 10	Wk 14	Total
Lactation $= 2$	14	41	14	42
Lactation $= 3$	10	10	10	30
Lactation $= 4$	5	5	5	15
Lactation $= 5$	4	4	4	12
Lactation $= 7$	1	1	1	3
Total	34	34	34	102

		Wk p	ostpartum	
Month	Wk 6	Wk 10	Wk 14	Total
January	4	3	2	9
February	1	3	3	7
March	5	1	3	9
April	2	5	1	8
May	3	2	5	10
June	3	3	4	10
July	5	4	3	12
August	2	3	2	7
September	2	2	2	6
October	2	3	3	8
November	3	3	3	9
December	2	2	3	7
Total	34	34	34	102

TABLE I.3. Frequency distribution of 34 pluriparous Holstein cows by month and Wk of measurement in early lactation.

		Wk po	ostpartum	
Season ¹	Wk 6	Wk 10	Wk 14	Total
Cold	15	12	14	41
Mild	9	12	11	32
Warm	10	10	9	29
Total	34	34	34	102

TABLE I.4. Frequency distribution of 34 pluriparous Holstein cows by season and Wk of measurement in early lactation.

 1 Cold = November to March, Mild = April, May, September, and October, and Warm = June, July, and August.

TABLE I.5. Frequency distribution of 34 pluriparous Holstein cows by energy balance status and Wk of measurement in early lactation.

		Wk pos	stpartum	
EB ¹ status	Wk 6	Wk 10	Wk 14	Total
Negative balance	13	11	8	32
Positive balance	21	23	26	70
Total	34	34	34	102

 $^{1}EB = energy balance$

Appendix II: Frequency distributions for study B.

		Wk postpartun	n
Treatment ¹	Wk 7	Wk 16	Total
WCS + Ca-LCFA	19	19	38
WCS	18	18	36
Control	14	14	28
Total	51	51	102

TABLE II.1. Frequency distribution of 51 primiparous Holstein cows by treatment and Wk of measurement in early lactation.

 $^{1}Ca-LCFA$ = calcium salts of long-chain fatty acids and WCS = whole cotton seed

		Wk postpartum	
Parity	Wk 7	Wk 16	Total
Lactation $= 1$	18	18	36
Lactation $= 2$	11	11	22
Lactation $= 3$	10	10	20
Lactation $= 4$	6	6	12
Lactation $= 5$	2	2	4
Lactation $= 6$	3	3	6
Lactation $= 8$	1	1	2
Total	59	27	102

TABLE II.2. Frequency distribution of 51 pluriparous Holstein cows by parity group and Wk of measurement in early lactation.

		Wk postpartum	
Month	Wk 7	Wk 16	Total
January	8	8	16
February	3	6	9
March	5	8	13
April	2	2	4
Мау	1	6	7
June	3	2	5
July	1	3	4
August	6	1	7
September	3	1	4
October	6	6	12
November	7	2	9
December	6	6	12
Total	51	51	102

TABLE II.3. Frequency distribution of 51 primiparous Holstein cows by month and Wk of measurement in early lactation.

		Wk postpartum	
Season ¹	Wk 7	Wk 16	Total
Cold	29	30	59
Mild	12	15	27
Warm	10	6	16
Total	51	51	102

TABLE II.4. Frequency distribution of 51 primiparous Holstein cows by season and Wk of measurement in early lactation.

 1 Cold = November to Match, Mild = April, May, September, and October, and Warm = June, July, and August.

TABLE II.5. Frequency distribution of 51 primiparous Holstein cows by energy balance status and Wk of measurement in early lactation.

_		Wk postpartum	
EB ¹ status	Wk 7	Wk 16	Total
Negative balance	39	37	76
Positive balance	12	14	26
Total	51	51	102

 $^{1}EB = energy balance$

Appendix III: Critical levels and regression coefficients for effects in within period model to partition variation in dietary and energy intake traits

			P -	value		Ŀ	(MN	T)		b(MK	E)	
Trait ¹	Wk.				Est	imate		P -	Estim	utc	P -	
	postpartum	Treatm	ent	Parity Scason	of	<u>b</u>	SE	value	of b	SE	value	;
GE	6	.61	.64	.71	-1.30	2.21	.56		1.27	.40	.004	.18
	10	.88	.57	.11	2.92	1.69	.10		1.41	.30	.0001	.48
	14	.13	.63	.22	3.52	1.58	.04		1.26	.33	.0008	.50
wī	6	.74	.29	.003	.00	2.00:	3.57		.001	. 00 1	.14	.26
	10	.41	.14	.21	.00	3.00.	3.43			.001	.96	.11
	14	.33	.78	.01	.00	1.002	2 .59		.001	.0004	.03	.23
FE	6	.87	.40	.92	19	1.05	.86		.39	.19	.05	01
	10	.37	.37	.11	.94	.93	.32		.46	.16	.01	.26
	14	.85	.48	.48	.71	.85	.41		.52	.18	.01	.16
UE	6	.12	.93	.47	03	.08	.66		.04	.01	.02	.20
	10	.003	.37	.07	.16	.06	.01		.05	.01	.0001	.68
	14	.05	.07	.84	.09	.08	.26		.03	.02	. 09	.38
СН₄	6	.75	.53	.04	.11	.17	.54		.96	.03	.96	.14
•	10	.93	.79	.64	.11	.12	.37		.001	.02	.001	.23
	14	.61	.64	.68	.03	.10	.71		.04	.02	.04	.03
DE	6	.16	.85	.65	-1.12	1.38	.43		.88	.25	.002	.28
	10	.94	.77	.24	1.97	1.00	.06		.95	.18	.0001	.54
	14	.02	.55	.21	2.81	1.05	.01		.74	.22	.002	.55

TABLE III.1. Critical levels (P - value) for main effects and partial regression coefficients for covariates from within period model: selected energy partition measures.

 ${}^{1}CH_{4}$ = methane energy, DE = digestible energy, GE = gross energy, FE = fecal energy, MKE = milk energy, MNT = maintenance energy, UE = urinary energy, WI = water intake.

			- d	lue		104	CLNW		bCMK	(E)	
Trait	WŁ.				Estim	Ee	. d.	Estima		P	
	postpartum	Treatm	ent Pa	rity Season	of b	SE	value	of b	SE	value	
HI	6	.36	28.	.49	-11	50	.82	.17	8	-07	ß
	10	.21	8.	.47	52.	.39	.53	.20	6.	.01	.21
	14	.19	.43	.29	8.	%	.24	.21	.14	.14	.21
BF	6	.55	16.	.13	16	8	8	8	.02	ş	.29
	10	.51	.54	.35	.08	.08	.35	9	.01	.01	.08
	14	.37	.82	-59	11.	8	.24	05	8		.18
BP	Q	.03	.56	6.	08	8	.07	.002	.01	.78	.18
	10	.51	.	6 .	8	.03	.20	•	10.	.95	14
	14	.03	.68	.33		.03	.53	01	10.	8	.18
Milk (kg)	Q	.41	.62	.67	.13	.14	.38	Droppe	ß		
	10	.36	.58	16.	.01	.12	16.				08
	14	.61	.33	.83	03	.11	62.				10
Fat (kg)	6	.38	.62	.01	10.	10.	.17	Droppe	R		.20
	10	<i>1</i> 6.	.81	. 9	.01	.01	.54				.03
	14	.48	8.	.002	.0004	.01	<u> 95</u>				.32
SNF (kg)	6	.28	.47	.98	.014	10.	.24	Droppe	R		8
	10	4 .	.65	.62	60 0.	10	50				10
	14	11.	6	.46	.002	.01	.82				12

TABLE III.2. Critical levels (P - value) for main effects and partial regression coefficients for covariates from within

			2 - A	alue		N N	(TNI)		b (MK	Ê	
Trait ¹	WŁ.				Estimat	9	P	Estime	đ	Ъ.	
	postpartum	Treatn	nent Pau	ity Season	of b	SE	value	of b	SE	value	
FE/GE	6	.16	90	.91	.0002	100.	.68		.000	69.	08
	10	8	.20	.29	0001	100.	.87		.000	.75	8
	14	.19	68.	.17	001	.00	.39	.000	.000	.49	03
DMI/MBW	Ŷ	.85	.39	8	Droppe	ק		.002	100.	E 0.	.0
	10	.36	.32	.19	1			.002	.0005	.000	4 .
	14	.48	.65	.20				.002	.00	.003	.35
ME/MBW	Q	.39	.58	<u>8</u> .	Droppe	ę		4.34	1.69	20.	.11
	10	.63	.29	.36	1			5.11	1.10	.000	4
	14	6	۲.	.10				5.27	1.27	.0003	.54
JE/DE	Q	.47	62.	.32	•	1000.	96.		•	.56	8.
	10	20 2	.13	.10	.000	.000	.12	•	•	<i>L</i> 0.	.48
	14	36	.17	.92	•	1000.	.95		•	.98	<u>.</u>
CH_/DE	6	.72	46	.01	.0003	.0003	23	000	.000	ર્ષ્ટ	.20
	10	88.	.73	8.	•	.0002	8.	•	•	.43	27
	14	.23	. 3	.11	0003	.000	.17	•	•	.62	.14

coefficients for covariates from within eci.oo TABLE III.3. Critical levels (P - value) for main effects and narrial mo

UE = urinary energy

Appendix IV: Product moment and rank correlations between energy and efficiency measures during early lactation

			ซื	amber				^c ield			Cha	mber			ά,	ield	
		ME	NE	MKE	MNT	cME	cNE	cMKE	eMNT	MKE/ ME	MKE/ NE	MNT/ ME	MNT/ NE	eMKE/ eME	cMKE cNE	/cMNT/ cME	eMNT/ eNE
Chamber	ME		<u>Š</u>	છ	52	17.	11.	.58	.37	.	ι.	87	80 . '	S 9.	S i	54	54
	NE	16.		, v	53	3	S.	.57	.32	8 .	. 0	80 '	88	80 .	80 .	51	51
	MKE	.61	.58		.16	.58	.58	.87	.21	.82	ø.	56	54	.49	49	ŗ.	49
	MNT	2	2	.12		.23	.23	.24	.91	8	8	53	.22	.1	ι.	.18	.18
Field	eME	3	8	છ	.18		8 .	.61	.31	53	.24	56	52	23	23	87	87
	eNE	5	8.	.62	.18	8		.61	.31	.22	.24	56	52	23	23	87	87
	eMKE	.56	.53	8.	.22	<u>8</u> .	2		.31	S .	8	.46	4 .	.62	.62	48	48
	eMNT	.32	. 29	.16	.92	2	2	.27		. 01	8	6.	8 .	.12	.12	15	.15
Chamber	MKE/ME	8		.81	01	.28	.27	%	02		\$	8	11	<u>59</u>	6 5.	25	24
	MKE/NE	.13	8	ઌ		.28	.28	<u>8</u>	01	<u>95</u>		11	03	.55	.56	.24	24
	MNT/ME	8	و7؟	51	S	. .	2.	43	.14	07	8 .		.93	8	8.	5 9	9.
	MNT/NE	Ŀ.	786	48	12	57	57	39	.13	8 0'-		.93		9 0	06	.57	.57
Field	eMKE/cME	8	8	. 4	8 .	14	15	.61	.13	6 5:	\$	2	8		8.	.31	.31
	eMKE/eNE	8	8	8 4.	8	14	15	.61	.12	.59	\$	Ş	8	8 .		.31	.31
	cMNT/cME	:5	754	53	.21	89	89	51	ij	26	25	.71	2	נ ז	53		8 .
	eMNT/eNE	5	754	53	.21	89	89	ŗ.	ų	26	25	.71	1 9.	ង	หฺ	8 .	
9																	

TABLE IV.1. Overall Product-moment (upper-half) and rank (lower-half) correlations between field and energy chamber measures of

ME = metabolizable energy, NE = net energy, MKE = milk energy, MNT = maintenance energy, eME = estimated metabolizable energy, eNE = estimated net energy, eMKE = estimated milk energy, and eMNT = estimated maintenance energy.

			hamt	čr			⁻ ield			Cha	mber				ield	
		ME NI	B MK	E MNT	eME	eNE	eMKE	eMNT	MKE/ ME	MKE/ NE	MNT/ ME	MNT/ NE	eMKE/ eME	cMKE eNE	/cMNT/ cME	eMNT/ eNE
Chamber	ME	oi	N N	4 80.	\$ 9	\$;	.52	23	13	7	87	85	01	01	53	53
	NE	95	Ň	S. 08	.59	6 5:	.51	.19	6 9.''	14	84	88	S .	8	48	48
	MKE	4. 64.	Ŷ	.22	.52	.52	.87	.28	.76	.75	44.	44.	i.	i.	36	36
	MNT	0 [.] 60 [.]	1 12	e	i	?	.22	.92	.17	.16	.37	.36	1.	Ŀ	.35	.35
Field	eME	. 1 2. 6	e e	4 .07		8 .	i.	.27	8	.15	48	- 43	31	31	81	81
	eNE	. 2 7.	e. e	• .07	<u>8</u> .		.49	.27	8 .	.15	42	43	31	31	81	82
	eMKE	4. 64.	60	9 .21	5 9	5 9		.31	.62	.62	4	.41	8	8	31	31
	eMNT	.12 .1	2	6.91	8	8	.26		.15	.16	.21	.21	.15	.15	.33	.33
Chamber	MKE/ME	141	14 .7	5.12	.21	.21	S 9.	1 .		76.	1 4	.12	58	.58	03	03
	MKE/NE	60	15 .7	7 .11	22	ห	.67	11.	76.		.12	.15	55	55	06	06
	MNT/ME	398	332	5 .38	2	63	24	Ŀ.	.28	.24		76.	05	. 8	.58	.58
	MNT/NE	828	882	4 .38	57	56	22	e.	.27	.27	<u>95</u>		07	07	.55	.55
Field	cMKE/cME	13 .0	e S	2.03	12	12	%	1 :	.61	5 9	i	.16		8 ;	3 9	.39
	eMKE/eNE	13 .0	e S	2.02	12	13	%	8	.61	. 59	i	.16	8 .		.39	39
	eMNT/eME	564	6- 6t	3.38	81	82	29	.38		05	2	2	¥.	¥.		6 .
	eMNT/eNE	574	6- et	2 .38	81	81	29	.38	.01	04	и.	.64	.34	.34	6.	
ME = m energy, cl	ctabolizable c NE = estima	ted net	NE = energ	not ene y, cMKI	argy, MK 3 = estii	Te =	milk en milk en	argy, an	NT = a	nainten = esti	ance en mated	ergy, cM maintenau	E = estim nee energ	lated me cy.	tabolizal	ą

TABLE IV.2. Product-moment (upper-half) and rank (lower-half) correlations between field and energy chamber measures of energy and efficiency from data on the same cover at wk 6 matractium (n = 30).

efficiency	from data o	ŝ	Ĕ	800		10 post	pertu	= 9 2	<u>,</u>								
			ч С	umber			-	ickd			ç	umber			с ,	ield	
		ME	NE	MKE	MNT	cME	eNE	cMKE	eMNT	MKE/ ME	MKE NE	/MNT/ ME	MNT/ NE	eMKE/ eME	eMKB eNE	u/cMNT/c cME c	MNT/ NE
Chamber	ME		26 .	.78	.31	.75	.75	۲.	.32	.32	.28	87	. 8.	8	8	- 79.	2
	NE	8.		.71	.29	2	2	2	Ŀ.	.27	.15	83	89	.05	.05	56	56
	MKE	5	.		1	59	59	2 8.	.12	2.	ø.		67	.38	.38	55	55
	MNT	.27	5	6.		.21	.21	.32	. 95	9 8	05	.16	.14	.22	.22	4	.19
Field	eME	.78	ف	.58	.21		<u>8</u>	.71	.24	2 7	.28	65	56	28	28	6	6 [.] -
	eNE	.78	Ŕ	59	.21	8 .		11.	.24	2	.28	65	56	28	28	6	6
	eMKE	S .	.53	۴.	¥.	Ę.	8		.32	.67	2	55	52	4	.	58	58
	eMNT	52	5	ġ	8	.15	.15	.31		60	6 0	.13	.11	ij	ij	.19	.18
Chamber	MKE/ME	.27	.16	.82	80	.28	8	.61	12		76.	37	33	.57	.57	29	29
	MKE/NE	หฺ	8	.78	80	.29	.31	İ	14	<i>1</i> 6.		32	21	.51	.51	с.	<u>د</u> .
	MNT/ME	¢	5.	.65	ei	9	61	.46	.31	32	27		8.	8	80 .	.75	.75
	MNT/NE	7	F.	53	67	48	48	35	.28	2	60	.93		<u>8</u>	8	.67	.67
Field	eMKE/eME	8	ġ	.37	.33	15	14	64 .	34	.52	Ņ	.1	.11		8 .	.37	.37
	eMKE/eNE	8	\$	38	.32	16	16	84 .	.33	.52	s.	.12	.13	8 .		.37	.37
	eMNT/eME	61	43	52	.21	88	88	51	.29	31	35	£.	.58	ų	.31		8 ;
	cMNT/cNE	61	43	52	.21	88	88	51	.29	31	35	٤.	.58	e.	.31	66.	
ME = m energy, el	ctabolizable c NE = estima	merg.	N S	E = n cryy,	et ener cMKE	zy, MK = estin	La =	mik en mik en	ergy, an	INT = n d cMNT	nainten = est	ance en imated	ergy, cN maintena	fE = extim noe energ	ated m	ctabolizab	9

TABLE IV.3. Product-moment (upper-half) and mark (lower-half) correlations between field and energy chamber measures of energy and

			Cha	umber				Field			Cha	mber			F	Icid	
		ME	NE	MKE	MNT	eME	ene	cMKE	eMNT	MKE/ ME	MKE/ Ne	MNT/ ME	MNT/ NE	cMKE cME	cMKE cNE	/cMNT/ cME	cMNT) cNE
Chamber	ME		.85	58	.39	۲.	י	.57	.62	90 [.] -	8	87	89	8 .	8	4.	4.
	NE	.81		49	.35	8 9.	8 9.	,	.53	07	18	73	87	 20		4	4
	MKE	56	.48		.14	.45	.45	83.	1	F.	Ľ.	58	47	4	4	36	536
	MNT	4 6.	36	8		.35	.35	.29	84	13	60	.11	.15	01	01		
Field	eME	S .	.58	49	22		8	₹.	.48		.01	56	52	- 43	43	- 8	S86
	eNE	%	.58	84 .	53	8 .		₹.	.48		.01	56	52	43	43	87	786
	eMKE	.58	.52	.74	<u>.</u> 26	84 .	8 4.		36	56	.56	48	4	2	2	26	526
	eMNT	s.	Ň	.19	88.	.37	36	.37		23	15	21	11		02	, S	- 9
Chamber	MKE/ME	8	10 .	F.	22	8	8	Į.	19		.91	8	.03	.51	.51	13	.13
	MKE/NE	ι.	13	۶.	13	11.	11.	.49	6 8.	.87		15	.11	.	.49	<u>ci</u> .	212
	MNT/ME	88	Ľ-	52	8 .	59	58	4	16	01	60		.81	07	07	4.	.42
	MNT/NE	71	86	4	11.	48	- 48	35	6 8.	 20.	.11	.85		8 .	02	4	1
Field	eMKE/eME	8	8	.43	.01	33	33	9.	8	.53	.52	01			<u>8</u> ;	.	l .51
	eMKE/eNE	Ş	ß	14.		33	33	6 5:	8	.52	.52	01	10.	8 .		. 5	l .51
	eMNT/cME	- 49	.46	45	11.	89	89	35	8	18	13	.55	'n	38.	.39		8 .
	eMNT/eNE	s.	.	46	.1	68	6	35	.01	18	14	SS	.51	38.	.38	Ϋ́.	~

TABLE IV.5. Product-moment (upper-half) and rank (lower-half) correlations between field and energy chamber measures of energy and

Appendix V: Canonical Correlation Analysis

Canonical correlation analysis was used to relate energy chamber values to field estimates on the same lactating cows. The objectives of CCA, in this project were to find linear combinations that produce maximum correlation between linear combinations of the energy chamber and field variables; and to look at the pattern of association between the two sets of variables.

Procedures for Canonical Correlation Analysis

Assuming that X_1 , ..., X_p and Y_1 , ..., Y_q are two sets of random variables. Let X be a set of field estimates. Define X as $[X_1, ..., X_p]$, the predictor variables and X ~ MVN(U_x, Σ_y). Let Y be a set of energy chamber measures. Define Y as $[Y_1, ..., Y_q]$, the outcome variables and Y ~ MVN(U_y, Σ_y). After X and Y are partitioned into the energy intake and gross efficiency variables, let the Pearson correlation matrix, R_{xy} of all these intake or gross efficiency variables be

$$R_{xy} = R \begin{bmatrix} X \\ -Y \end{bmatrix} = \begin{bmatrix} R_{11} & | & R_{12} \\ - & - & - \\ R_{21} & | & R_{22} \end{bmatrix} \begin{pmatrix} p \\ - & - \\ R_{21} & | & R_{22} \\ p & q \end{pmatrix}$$

where R_{11} contains intercorrelations among the field variables, R_{22} is the intercorrelations among the calorimetric variables, and $R_{21} = R_{12}$ cross-correlations between the chamber and field variables. If X and Y are of full rank, then define the $p \times p$ matrix, G of rank, k and a $q \times q$ matrix D as,

$$G = R_{11}^{-1} R_{12} R_{22}^{-1} R_{12}' \text{ and}$$
$$D = R_{22}^{-1} R_{21} R_{11}^{-1} R_{21}'$$

Because both G and D are non-symmetric matrices of the form, $E^{-1}H$ to decompose either G or, D define F as the upper triangular Cholesky decomposition of E^{-1} . Let, P = FHF' then obtain the Λ eigenvalues and W eigenvectors of P. Let V = F'W. The diagonal elements of, $\Lambda \lambda_1, ..., \lambda_k$, are the nonzero latent roots of $E^{-1}H$ and the columns of V are the orthonomal latent vectors of $E^{-1}H$. Note that the eigenvalues of G and D are equal.

Let A contain the latent vectors of G. Similarly, let B contain the latent vectors of D. Hence, A are canonical coefficients or weights for the chamber variables, B are the canonical coefficients for the field variables, and the diagonals of Λ are the squared canonical correlations (R_c^2) between the two sets of variables.

Observe that, $tr(\Lambda) = \sum_{i=1}^{k} \lambda_i$; $\lambda_1 > \lambda_2 > ... > \lambda_k$, gives the total variance.

Form, $U_i = XA_i$ a linear combination of the field, and, $V_j = YB_j$ a linear combination of the calorimetric variables, such that the correlation between U_i and V_j is maximized. These linear combinations are the canonical variates. We are interested in the correlations between these canonical variates. It follows immediately that because A and B are orthornomal, the correlation matrix of U_i and V_j is,

$$R\begin{bmatrix} U\\ -\\ V \end{bmatrix} = \begin{bmatrix} I_p & | & \Lambda \\ -\\ - & -\\ \Lambda' & | & I_q \end{bmatrix}$$

Therefore, U are the canonical variates of the field variables and V are the canonical variates of the energy chamber variables. Thus, U_1 is the first canonical variate of the field estimates, and V_1 is the first canonical variable of the chamber measures; U_2 will be the second, and so on.

If U_1 and V_1 have the maximum canonical correlation of all linear combinations, then (U_1, V_1) are the first pair of canonical variates, which are independent, i.e., the correlation between (U_p, V_1) and (U_p, V_j) is zero. The correlation between (U_1, V_1) would be the first canonical correlation and is given by λ_1 . The variable-variate correlations between $[U_1; (X_1, ..., X_p)]$ and $[V_1; (Y_1, ..., Y_q)]$ are the canonical factors or factor loadings. Thus, the entire relationship between p field variables and q calorimetric variables is expressed only

in terms of k parameters $\lambda_1, \lambda_2, ..., \lambda_k$. Hence the name canonical correlations.

	W	7 k 6	W	k 10	W	% 14
	Proportio	n explained by	Proportio	n explained by	Proportio	n explained by
Order	Chamber	Field	Chamber	Field	Chamber	Field
1	.46	.42	.26	.24	.52	.44
2	.67	.57	.78	.66	.79	.65
3	.84	.67	.89	.72	.96	.69
4	1	.67	1	.72	1	.69

TABLE V.1. Cumulative proportions of standardized variance of the chamber energy intake measures explained by the chamber and field canonical variables at wk 6, 10 and 14 postpartum.

TABLE V.2. Cumulative proportions of standardized variance of the chamber gross efficiency measures explained by the chamber and field canonical variables at wk 6, 10 and 14 postpartum.

	W	7 k 6	W	k 10	W	k 14
	Proportio	n explained by	Proportio	n explained by	Proportio	n explained by
Order	Chamber	Field	Chamber	Field	Chamber	Field
1	.37	.33	.59	.5	.45	.33
2	.59	.41	.19	.58	.82	.41
3	.8	.46	.2	.65	.92	.41
4	1	.46	1	.65	1	.41

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	-			Loadi	1 Su			ļ		13	adings					3	l ibi			
		Ü	hamber			Field			Chan	nber		Field			Chamb	đ		ш,	ickd	
Order / T	'rait'	-	7	9	-	7	e	-	6	3	-	5	æ	-	3	3)	-	6	9
ME	.58	<u>ร</u>	.65	۹	21	75	ų	2 .7	5 - 5	5 .1	2 .63	μ	r.	ω.	546		3	ų.	8.	
NE	.54	28	4	.61	21	75	i	3	.4.	1.1	2 .63	F	3 9.	e.	356		3	ų	89.	
MKE	S :	3	ų	F.	55	8	о.	2	ġ	4 .1:	76. E	12	₫.	•;	.16	41	5	8	52	
MNT	7 .	2	.21	۴.	.61	8 0.	e.	5	č.	6. 6	8 2		•:	'	2 .37	-, -,	2	ų	11.	
^{II} = = ^{II}	icta boliz	able	cnergy	, MKE		nilk en	crgy	WW	*	mainten	lance e	nergy,	IN pure	₩ 	at ene	rgy.				

TABLE V.4. Chamber and field loadings for the significant roots of the gross efficiency measures at wk 6, 10 and 14 postpartum.

	l		Wk 6					Wk	10		Wk	14
	I		Loadin	Sð				Load	lings		Load	ings
		Chambei		Field	_		Chamb	٦		Field	Chamber	Field
Order / Trait		1 2		1	8		_	5	1	3	1	1
MKE / ME	٩	-51	3.	21	•	8	.52	ì	4	Ŗ	78	.S1
MKE / NE	67	34	3	21	•	÷	4	7	43	ક્ષ	76	2:
MNT / ME	ß	59	.41	58		.76	8 .	-	3	11.	۹	89 .
MNT / NE	.55	39	.41	58		.71	е.	-	99	.71	.51	.65
¹ ME = metal	Solizat	ole energ.	y, MKE		lk en	ergy, l	MNT	= mai	ntenan	ce energy,	and NE = n	et energy.

Appendix VI: Mean Regression Coefficients in multiple regression models to estimate partial energetic coefficients.

Multiple regression models for metabolizable and net energy intake were similar to those analyzed by Walter and Mao (1989).

$$NEI_i = b_0 + b_1 SCM_i + e_i$$
[1]

$$MEI_i = b_0 + b_1 SCM_i + e_i$$
^[2]

$$NEI_i = b_0 + b_1 SCM_i + b_2 WgtChng_i + e_i$$
[3]

$$NEI_{i}/MBW_{i} = b_{0} + b_{1}(SCM_{i}/MBW_{i}) + e_{i}$$
[4]

$$NEI/MBW_i = b_0 + b_1(SCM_i/MBW_i) + b_2(WgtChng/MBW_i) + e_i$$
[5]

$$NEI_i = b_0 + b_1 NE_{SCM,i} + e_i$$
[6]

$$NEI_i = b_0 + b_1 NE_{SCM,i} + b_2 NE_{WgsChag,i} + e_i$$
[7]

$$MEI/MBW_i = b_0 + b_1(NE_{SCM}/MBW_i) + e_i$$
[8]

$$MEI/MBW_i = b_0 + b_1(NE_{SCM}/MBW_i) + b_2(NE_{WgsChag}/MBW_i) + e_i$$
[9]

Two-stage multiple regression for net energy intake were:

Stage 1:
$$NEI/MBW_i = b_0 + b(NE_{SCM,i} + NE_{WgeChng,i})/MBW_i + e_i$$

Stage 2: $(NEI_i - b_0MBW_i)/SCM_i = b_1 + b_2(WgtChng/SCM_i) + e_i'$ [10]

Stage 1:
$$NEI/SCM_i = b_1 + b(NE_{MBW,i} + NE_{WgtChag}/SCM_i) + e_i$$

Stage 2:
$$(NEI_i - b_1 SCM_i) MBW_i = b_0 + b_2 (WgtChng/MBW_i) + e_i'$$
 [11]

.

TABLE VI.1.	Mean regre	ssion coeffici	ients in models	with depend	ent variable	measured as I	let energy or	metabolizab	le energy
over periods o	of negative(-) and positive	e (+) energy au	nd accross the	e entire meas	surement peri	od (P). SE ar	e shown in	parentheses.
		ዋ			b _i [SCM] ¹	_		b ₂ [WgtCh	ıg]²
Model	4	+	•	Ъ.	+	•	а.	+	•
[1]: Chamber	22.664	17.808	13.289	.494	689.	.636			
	(1:631)	(2.730)	(2.612)	(.053)	(610.)	(020)			
[1]: Field	20.922	16.993	17.189	.448	.586	.512			
	(3.448)	(3.948)	(4.521)	(760.)	(.127)	(.113)			
Walter and	21.116	21.091	20.244	.332	.350	.337			
Mac (1989)	(.365)	(392)	(026)	(.018)	(.018)	(040)			
[2]: Chamber	29.174	23.994	20.648	.623	.831	.734			
1	(2.125)	(2.574)	(2.506)	(.067)	(.074)	(.124)			
[2]: Field	35.179	28.591	28.892	.752	.982	.858			
1	(5.770)	(6.580)	(7.553)	(.162)	(.213)	(.187)			
[3]: Chamber	21.496	17.352	12.226	.522	.693	.661	303	226	185
	(2.619)	(2.984)	(3.143)	(690.)	(.081)	(.071)	(.173)	(.130)	(.104)
[3]: Field	21.291	16.143	23.893	.443	599	.323	.104	271	.760
	(4.117)	(4.543)	(5.311)	(.110)	(.134)	(.128)	(.173)	(.283)	(.141)
Walter and	19.647	20.949	21.305	.374	.348	.350	1.920	.581	4.461
Mao (1989)	(.400)	(.471)	(.817)	(.018)	(.018)	(.033)	(.293)	(:353)	(1.202)
NRC (1989) Mcal/kg/d					.748			5.12	4.92
1 SCM = solid	ls-corrected	milk.							

²WgtChng = average BW loss or gain at every 2 wk during the postpartum period.

		b ₆ [MBW]			b _i [SCM] ¹			b ₂ [WgtChng	J ²
Model	4	+		d	+		ď	+	•
[4]: Chamber	.209 (019)	.171 (910.)	.125 (.018)	.454 (.059)	.618 (.067)	.606 (.052)			
[4]: Field	.188 (.034)	.170 (.030)	.147 (.049)	. 4 11 (.118)	.500 (.119)	.489 (.159)			
Walter and Mao (1989)	.154 (.003)	.152 (.003)	.160 (.005)	.438 (.018)	.464 (.018)	.370 (.037)			
[5]: Chamber	.203 (.024)	.180 (.024)	.116 (.019)	.475 (.074)	.008 (.078)	.63 4 (.054)	227 (.169)	:	276 (.070)
[5]: Field	.196 (.037)	.170 (.033)	.179 (.056)	.39 4 (.125)	.501 (.124)	.386 (.190)	.225 (.135)	.060 (.160)	.554 (.091)
Walter and Mao (1989)	.147 (.004)	.1 <i>51</i> (.004)	.170 (.007)	.466 (.018)	.442 (.018)	.376 (.033)	1.468 (.466)	001 (.508)	4.466 (1.209)
NRC (1989) Mcal/kg/d		.086			.748			5.120	4.920

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		.			b,[NEscul]			b ₂ [NEwenner]	7
Model	Ь	+		ፈ	+		۵.	+	
[6]: Chamber	22.664	17.808	13.289	1.516	1.086	1.176			
	(1:031)	(2.730)	(2.612)	(010)	(0110)	(.076)			
[6]: Field	20.922	16.993	17.189	1.668	1.277	1.461			
	(3.448)	(3.948)	(4.520)	(.129)	(.170)	(121)			
Walter and	30.631	30.619	29.509	.706	.741	.706			
Mao (1989)	(.547)	(.586)	(1.426)	(+034)	(.036)	(.078)			
[7]: Chamber	28.466	23.429	20.995	1.164	.894	1.037	034	047	.00
1	(2.899)	(3.061)	(6.218)	(111)	(101)	(.198)	(.034)	(.058)	(.027)
[7]: Field	35.812	27.174	40.190	1.007	.745	1.391	.037	093	.255
1	(6.881)	(7.563)	(8.888)	(.247)	(10£.)	(.287)	(.058)	(960)	(.048)
Walter and	28.484	30.421	31.073	.789	.735	.718	.579	.174	1.380
Mao (1989)	(209.)	(.706)	(1.234)	(036)	(.038)	(.067)	(680)	(.107)	(.367)
NRC (1989)									
Mcal/kg/d					1.540			1.330	

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		ኇ			b _i [NE _{scw}] ¹			b ₂ [NE _{wnOme}]	
Model	Ч	÷	9	Ф.	÷		Ч	+	•
[8]: Chamber	3.672	4.202	4.701	1.326	11011	1.213			
	(.021)	(600')	(.065)	(760.)	(.048)	(.258)			
[8]: Field	3.163	3.497	4.035	1.086	.892	.913			
	(020)	(.051)	(.081)	(.265)	(.268)	(.356)			
Walter and	3.058	3.027	3.192	116.	.962	171.			
Mao (1989)	(.055)	(.055)	(.164)	(.034)	(.035)	(.075)			
[9]: Chamber	3.703	4.104	4.782	1.305	1.037	1.191	015	.021	025
	(.025)	(.023)	(990.)	(111)	(960.)	(.264)	(.028)	(.057)	(.017)
[9]: Field	3.038	3.499	3.328	1.133	<u> 006</u>	1.158	.076	.020	.186
	(.062)	(.055)	(+60.)	(.281)	(.280)	(.426)	(.045)	(.054)	(.031)
Walter and	2.90	3.123	3.411	696.	.921	.786	444.	001	1.385
Mao (1989)	(.068)	(.082)	(.137)	(.036)	(.037)	(.067)	(.141)	(.141)	(.370)
NRC (1989)									
Mcal/kg/d		1.540			1.540			1.330	

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		٩			b ₁ [SCM] ¹			b ₂ [WgtChng]²
Model	4	+		۵.	+		٩.	+	
[10]: Chamber	.332	.335	.298	1.137	1.212	1.004	768	582	624
	(.007)	(110)	(.010)	(.051)	(.042)	(.052)	(.259)	(.114)	(161.)
[10]: Field	.286	.291	.259	1.057	1.094	086.	354	454	100
	(.007)	(.007)	(.015)	(.034)	(.033)	(:033)	(960)	(.213)	(.112)
Walter and	.151	.151	.158	.425	.447	.405	1.996	.920	1.996
Mao (1989)	(.003)	(1004)	(900)	(.015)	(.020)	(020)	(.353)	(.243)	(1.120)
[11]: Chamber	1.091	1.165	179.	1.912	1.909	1.485	723	548	581
	(.048)	(660.)	(.049)	(.122)	(.153)	(.105)	(.247)	(.101)	(.175)
[11]: Field	1.014	1.050	.944	1.758	1.738	1.530	318	426	318
	(.031)	(.031)	(.030)	(.147)	(.161)	(.184)	(060.)	(.213)	(060.)
Walter and	.085	.103	.101	.774	.689	.739	2.483	1.864	4.153
Mao (1989)	(.003)	(:003)	(.007)	(.020)	(.018)	(.029)	(.333)	(.354)	(1.234)
NRC (1989)									
Mcal/kg/d		.086			.748			5.12	4.92
¹ SCM = solids-	corrected milk.								

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²WgtChng = average BW loss or gain at every 2 wk during the postpartum period.

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