To the Graduate Council:

I am submitting herewith a thesis written by Clark D. Smothers entitled "The Correlated Response in Feed Efficiency Accompanying Selection for Milk Yield in Jerseys." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Animal Science.

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THE CORRELATED RESPONSE IN FEED EFFICIENCY ACCOMPANYING SELECTION FOR MILK YIELD IN JERSEYS

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ABSTRACT

Feed efficiency data were collected on 353 first lactation Jerseys at the Dairy Experiment Station (DES) from 1971-1982. Feed intake, milk yield, and bodyweight change were recorded for a 28-day period on individual cows during mid- to late lactation. Two-hundred, thirty-two of these cows were from a selection line, developed through use of the highest available A.I. PD milk sires. One-hundred, twenty-one were from a control line originating from 40 foundation cows bred to sires taken randomly from commercial A.I. sampling programs in 1967. The same control sires were used throughout the experiment.

The feeding regime included alfalfa-orchardgrass hay and corn silage fed ad libitum, while grain was fed according to production. Feed samples were taken, by trial, and subjected to ADF analysis to derive estimated net energy values (ENE). Gross feed efficiency was defined as 4% fat-corrected milk/total ENE in feed consumed.

Least squares means were employed to determine if differences existed between genetic lines for estimates of gross feed efficiency. Initially, bodyweight change was used as a covariate to adjust for tissue balance differences. The original model indicated no significant line effects for estimates of gross feed efficiency. However, bodyweight change was considered an inaccurate indicator of physiological status. Thus, a new variable (ENBAL_28) was created and defined as the difference between NRC recommendations and actual energy intake. After dividing the data set into two energy balance groups (positive and negative), analysis indicated an increase of 10% in efficiency estimates for cows in the negative state.

When ENBAL_28 was used as a covariate to adjust for physiological status of cows, the residual variance was reduced and line differences for efficiency became significant (P .01). This indicated that selection line females used a lower percentage of energy intake for maintenance. ENBAL_28 displayed a strong negative correlation with estimates of feed efficiency. Negative relationships with feed efficiency estimates also appeared for intake variables. Results indicated a postive association between efficiency and milk production. It was concluded that gross feed efficiency is a complex trait under the influence of various genetic and environmental constraints.

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CHAPTER I

INTRODUCTION

Selection practices, aimed at increasing milk production, play a vital role in determining the profitability of modern dairies. Measuring response to selection, direct or indirect, is of considerable importance to animal breeders. Researchers have indicated increased production potential for dairy cows selected for higher milk yield. Considerable interest has been shown in examining correlated responses of various related characters. If the response of a correlated character is positive, its improvement would coincide with improvement of the character under direct selection. If the response is negative, an inverse relationship between characters would exist. With the importance of feed costs in determining total expenses for a dairy, the efficiency by which a cow converts feed inputs to milk is of particular interest.

A selection project, originating in 1968 and continuing through 1982, took place at the USDA-University of Tennessee Dairy Experiment Station (DES). The objectives for the entire project are to determine the response to selection for milk yield in Jerseys and determine correlated responses in other traits which accompany selection for yield. The specific objective of this thesis is to evaluate any response in gross feed efficiency accompanying single-trait selection for milk yield in DES Jerseys.

CHAPTER II

LITERATURE REVIEW

Early Investigation

Because of its influence on the profitability of dairy cattle, the economy of feed utilization has been considered a matter of importance to researchers (8, 11, 12, 17, 23, 24, 30, 31, 32) for several years. In 1932, Forbes and Voris (11), investigated efficiency of feed utilization using a series of mineral balance trials. Estimates of feed intake and milk production were obtained from twelve Holstein cows throughout their respective lactations. This study revealed that the most efficient cow converted 23.35 percent of feed energy to milk energy while the least efficient cow had an estimate of 18.04 per cent.

Edwards (8) utilized 2400 cows on test at the London Dairy Show to make inferences about gross efficiency (energy in milk/energy in digestable nutrients consumed) and various related factors. His results demonstrated support for the following conclusions. (1) Little variation in gross efficiency existed between above average cows of the various breeds. (2) Cows, generally, were more efficient than heifers. (3) There was a tendency for live weight increases to be negatively related to gross efficiency. (4) Differences in actual milk yield were most important in determining differences in gross efficiency.

Also, it was recognized that many environmental factors had an influence on gross feed efficiency. This work led to an interest in investigating the genetic parameters concerning this important economic trait. It also led researchers to investigate the genetic relationship between efficiency and other production traits and by what means improvement could be accomplished.

Heritabilities and Genetic Correlations

A summary of heritability estimates, similar to those in Freeman's (13) review on genetic variation in the nutrition of dairy cattle, is listed in Table 1. He noted that even though feed composition differed in these studies, feeding in general was in accordance with need. Differences in management regimes and efficiency measures among studies would change the total pheontypic variance and thus effect the heritability estimate. Also, different methods used in deriving the estimate could have been employed. Thus, small differences among studies for estimates are not surprising. It seems evident, from the heritability estimates, that feed efficiency is a character in which genetic progress could be achieved through selection.

Table 2 lists genetic correlations between milk production and estimates of feed efficiency. The estimates would indicate a strong positive relationship between yield and efficiency. Freeman (13) concluded that the same genes affecting yield seem to have a major influence on efficiency.

Mason *et al*. (27) stated that the positive genetic relationship between yield and efficiency was almost automatic, but none-the-less an important one. This association was partially due to the part-

Table 1. Heritability Estimates of Feed Efficiency Obtained in Various Studies

Feed Efficiency Measure[a]	Estimate	Source
FCM/Mcal ENE Consumed	.56	Hooven _et al_. (1972)
FCM/Feed Units Consumed	.48	Mason _et al_. (1957)
TDN Consumed/kg FCM	.63	Hickman and Bowden (1971)
FCM/Therms ENE Consumed	.46	Hooven _et al_. (1968)
Mcal Milk Energy/Mcal DE Consumed	.47	Lamb _et al_. (1977)

[a]FCM=Fat-corrected milk, DE=Digestable energy, ENE=Estimated net energy, TDN=Total digestable nutrients.

Table 2. Genetic Correlations Between Feed Efficiency and Milk Production Obtained in Various Studies

Feed Efficiency Measure[a]	r_G	Source
Mcal Milk Enengy/Mcal DE Consumed	.95	Lamb et al. (1977)
FCN/Mcal ENE Consumed	.93	Hooven et al. (1972)
FCM/Feed Units Consumed	.95	Mason et al. (1957)
FCM/Therms ENE Consumed	.92	Hooven et al. (1968)

[a]FCM=Fat-corrected milk, DE=Digestable energy, ENE=Estimated net energy.

whole relationship between measures of the traits. He maintained that under a given system of feeding, the highest producing cow would be the most efficient. The increase in efficiency was attributed to the lower percentage of feed intake being used for maintenance.

In the context of apparent positive genetic correlations between yield and efficiency, Meyer and Garrett (29) suggest careful scrutiny in the interpretation of relationships. Feed efficiency is a ratio in which the measure contains two unseparated response criteria. Also, it is assumed that when the output variable is graphically plotted against the input variable, the origin passes through zero. This relationship may or may not be true. Custodio et al. (6) emphasized the need to adjust for tissue balance, making the variance of residuals for feed efficiency measures homogeneous.

Evidence of moderate heritability estimates and large positive genetic correlations between yield and efficiency suggests that feed efficiency is a trait which can be improved through direct or indirect selection practices. Freeman (1967) suggested that indirect selection would be of greater practical value and more beneficial than direct selection for the trait. His reason was that in practice selection intensity for milk production would be greater than that for feed efficiency. Conversely, he noted that provided the selection intensity for the two traits were equal, indirect selection for feed efficiency would be 70-95% as effective as direct selection for the trait. Since production is easier to evaluate than efficiency, direct selection for milk production would be more advantageous. Freeman's theory that selection for milk yield would indirectly improve feed efficiency was supported later by other studies (6, 19, 36, 42).

Correlated Response to Selection Yield

Upon establishment of feed efficiency as a moderately heritable trait which was positively associated both genetically and phenotypically to milk yield, researchers (20, 36) began to investigate the efficiency of feed utilization as a correlated response to direct selection for milk yield.

A correlated response can be illustrated in terms of a direct response. Falconer (9) states that the direct genetic response in a train X is equal to the average genetic merit of the selected individuals and is represented by the equation $R_x = ih\sigma_{ax}$ where R_x=the genetic response of trait X, i=selection intensity, h-the square root of the heritability of X, and σ_{ax}=the genetic standard deviation of X. After direct selection for X, the consequent change of a correlated trait Y is given by regressing the breeding value of Y on the breeding value of X. Therefore, the correlated genetic response in Y is defined as the product of the regression coefficient and the direct response in X. It is represented in the equation $CR_y = b_{(a)yx}R_x$ where CR_y=the genetic correlated response in Y, $b_{(a)}yx$=the regression coefficient, and R_x=the direct response in X.

In terms of phenotypic performance, the association between responses is similar. However, the phenotypic covariance between traits now includes environmental and non-additive genetic components. The influence of environmental factors on the phenotypic regression of Y on X may mask true genetic trends.

Hickman and Bowden (20) utilized Holsteins and Ayrshires to examine the correlated response in feed efficiency accompanying selection for 180-day milk solids yield. Efficiency of feed utilization was defined as total digestable nutrients per unit of fat-corrected milk produced. Holsteins demonstrated a significant increase in feed efficiency whereas Ayshires did not. Holsteins produced more fat-corrected milk than Ayrshires. Efficiency differences resulted from the decrease in total digestable nutrients consumed per unit of fat-corrected milk produced by Holsteins. This decrease did not occur for Ayrshires. The increase in efficiency by Holsteins was accompanied by a decrease in weight gain during lactation. Researchers felt this improvement might indicate an increased ability for Holsteins to partition nutrients more toward production rather than the deposit of adipose tissue.

A similar study by Pearson et al. (36) used purebred Holstein females to study the responses in traits selected under two different criteria. One group was developed using sires with the highest Predicted Difference (PD) milk with a repeatability greater than 40%. A merit group contained female progeny of sires selected on the basis of an udder index. Yield line daughters produced significantly more milk (685 kg) and solids-not-fat (51 kg), but were lower in fat and protein percentages than merit line females. Gross efficiency was significantly higher for the yield group. These results were similar to the study of Hickman and Bowden (20). This result was primarily due to the lack of difference between groups in energy intake under ad libitum feeding of a blended ration. Thus, FCM production seemed a predominant factor in influencing gross efficiency estimate increases, which is in agreement with Weinberg et al. (42).

Recently, Weinberg et al. (42) compared gross feed efficiency estimates across three lines of first parity Randleigh Jerseys. The selection line was developed from daughters of sires selected on Predicted Difference milk. The young sire line contained daughters of unproven sires selected on the basis of pedigree merit for milk production, while the control line originated from six original Randleigh herd sires and remained unselected. The control sires were eventually replaced by male offspring selected at random. Gross feed efficiency was defined as kg FCM produced/therm TENE consumed. Results indicated that selection and young-sire lines were more efficient than controls by approximately 25% and 10% respectively. These results were similar to the Holstein response found by Pearson et al. (36). As in the study of Pearson (36), selection line cows produced more milk on similar feed intakes as controls. Evidence from these studies (20, 36, 42) seems to suggest that selection for milk yield might increase genetic potential for converting feed to milk.

Breed Variation

Variation among breeds for estimates of gross feed efficiency was reported in two studies (7, 20). In a study investigating possible correlated responses in feed intake, body size, and feed efficiency, accompanying selection for 180-day milk-solids yield, researchers (20) found breed differences in the efficiency response. Efficiency estimates increased in Holsteins but not in Ayshires.

Further evidence of breed differences in efficiency of feed utilization was illustrated by Dickinson et al. (7). Data was obtained from 57 Ayshires, 68 Brown Swiss, and 57 Holsteins being used in conjunction with a USDA crossbreeding project. All breeds were managed as a contemporaries in a single herd. Results demonstrated high phenotypic correlations between various measures of production and efficiency. Conversely, mean body weight, gain in weight, and various measures of body size were negatively related to efficiency. Holsteins, as suspected, ranked highest for actual milk production (5302 kg) followed by Ayrshires (4167 kg) and Brown Swiss (3883 kg). After adjustment for breed, year, and season of calving, Brown Swiss were shown to be less efficient utilizers of feed than Holsteins or Ayrshires ($P<.01$). In models which adjusted for body weight, chest girth, or wither height, Holsteins were more efficient ($P<.05$) than Brown Swiss or Ayrshires. Efficiency estimates for Ayrshires were intermediate. The significance of this relationship depended on what adjustments for body and size were used in the models. Examining all models, Holsteins were clearly more efficient than Brown Swiss. Some of this difference was attributed to the Brown Swiss having larger means and ranges in body weight, weight gain, and chest girth.

It was proposed that Brown Swiss used their feed energy more for anabolic tissue gain and less for producing milk than Holsteins when fed according to need.

Results from both studies (7, 20) seem to indicated that variation does exist among breeds for estimates of gross feed efficiency. Production differences appear to play a vital role in determining differences in estimated efficiency. Since the Hickman (20) work was aimed at measuring the correlated response to selection, it was proposed that the two breeds differed in respect to components of productivity increases encountered during selection. The increases were influenced by adaptation to their management regime. The experiment was not designed to measure gross efficiency as a correlated response to selection. However, both studies indicate that differences exist in ability to partition nutrients and to mobilize body tissue.

McDowell and McDaniel (28) used interbreed matings of Holsteins, Ayrshires, and Brown Swiss to determine effects of heterosis on the efficiency of milk production. Every possible two and three-breed cross combinations were utilized in the study. Production and efficiency of cross-breeds was compared to adjusted means for these traits obtained from pure-bred contemporaries. In general, results indicated that heterosis did exist in crossbreds for FCM, SNF, fat%, protein%, and three estimates of feed efficiency. Ayrshire X Holstein and Swiss X Holstein crosses were 8 to 10% improved over parental means for production traits. However, Ayrshire X Swiss crosses were not different. The same improvement, though reduced 50% in magnitude, was observed for feed efficiency measures. Generally, three-breed crosses yielded superior estimates of heterosis as compared to those obtained from two-breed crosses. However, the degree of heterosis reflected in three-breed crosses was partially attributable to arrangement of breeds within the cross.

Implications of Body Size and Weight

Cow size and weight is an important factor involved in investigating the biological efficiency of dairy cattle. Dickinson *et al.* (7) studied relationships between efficiency and various measures of body size, mean body weight, and weight gain on Holsteins, Ayrshires. and Brown Swiss cattle managed as contemporaries. Measures of body size were chest girth, wither height, and body length. A negative relationship existed between feed efficiency and chest girth indicating lower efficiency estimates on cows with larger chest girths. A significant linear effect (-.00485) across breeds was obtained when feed efficiency was regressed on wither height. Although Holsteins were more efficient at any chest girth or wither height, results suggested that within breeds, cattle with lower chest girths or wither heights had higher estimates of feed efficiency. Mean body weight demonstrated a negative linear effect (-00526) across breeds when regressed on feed efficiency. Within breeds, cows of lower body weight were also more efficient. Also, cows gaining the least amount of weight had the highest efficiency estimates. These relationships between feed efficiency, body weight, and gain in weight are in agreement with those found by others (30) and are possibly due to the partitioning of greater amounts of feed toward production by lighter weight cows and cows which gained less weight during lactation. Dickinson _et al_. (7), adjusting for breed, year, and calving season used various body size measurements in combination and in efficiency prediction models. The model combining chest girth and weight gain as independent effects accounted for 30% of the remaining variation in efficiency after adjusting for fixed effects. Weight gain alone accounted for 24% of the variation. The combination of body weight and weight gain accounted for more variation than weight gain alone but less than chest girth and weight gain. When placed in the model separately, chest girth, body weight, wither height, and body length explained 16%, 10%, 6% and 6% of the variation respectively. It was evident that the model which included chest girth and weight gain explained the most variation in feed efficiency while weight gain was the best single explanatory variable.

Investigations into the variation in part vs whole-lactation measures of biological efficiency by Miller and Hooven (30) also revealed the importance of body weight change. The effects considered included year and season of calving, parity, barn, days open, body weight and body weight change. Negative body weight change associations with efficiency were the most consistent across stages of lactation. Also, results indicated a negative relationship between body weight and efficiency which is consistent with findings of other researchers (7, 23, 40, 42). The Hooven and Matthews study (21) involving progeny of six Holstein sires was cited by Hooven _et al_. (23) as one of the first U.S. studies which examined and found a negative phenotypic correlation between body weight and efficiency. Their results indicated that 70% of the variation in feed efficiency could be explained by variability in FCM and body weight. More recent work by Weinburg et al. (42), examining feed efficiency as a correlated response to selection, supports this conclusion as to the importance of body weight. Their results indicated that differences in feed efficiency estimates between different genetic lines of Jerseys decreased in magnitude after adjusting for body weight.

Body weight is due more to additive genetic influence than body weight change. This conclusion is evident in light of moderate to high heritability estimates for body weight obtained by others (23, 27). Hooven et al. (23) estimated the heritability of bodyweight change on 225 daughter-dam pairs to be -.08115. These results suggest that bodyweight change is a good indicator of environmental fluctuations due to its low heritability estimates.

The most recent investigation into the effects of selection for body size on feed efficiency was conducted at the University of Minnesota (44). Purebred Holsteins were bred for either small or large body size for 17 years. The two groups were examined for feed efficiency measured as Total Digestable Nutrients/kg of FCM produced. Cows, within size groups, were not different for estimates of efficiency, however, small group cows were 2.78% more efficient than large group cows over the entire lactation. This supports the conclusion of Dickinson et al. (7) that within breeds, cows of smaller weight or size are more efficient.

Variability in Intake

In most cases, energy ingested from feeds plays a vital role in determining estimates of feed efficiency for dairy cattle. Differences in intake must be taken into consideration. Miller et al. (31) investigated variability among Holsteins for feed intake. Data were collected on daughter-dam pairs over a 19-year period. The feeding regime consisted of alfalfa hay and corn silage fed ad libitum with a 15% protein grain mixture fed in specified proportions. Researchers examined relationships between feed efficiency and the following variables: grain intake, forage intake and total intake. Positive genetic and phenotypic relationships were recorded for feed efficiency and grain as well as total intakes. However, negative phenotypic (r_p=.32) and genetic (r_a=-.11) correlations existed between feed efficiency and forage intake. Heritability, for forage intake, using daughter-dam regression was estimated at $.19\pm.09$. This estimate is in reasonable agreement with the heritability estimate using paternal half-sib analysis reported by Gray et al. (16).

Forage-grain ratios exhibited a negative effect on feed efficiency and results indicated the relationship was stronger for intake and milk production than for intake and feed efficiency. This relationship suggested that yield differences were the primary cause for differences in feed efficiency (16).

Earlier work by Stone et al. (40) found the repeatability of forage intake to be .70 when considered on a within treatment period and year basis. After adjusting for weight change, body weight, and milk production; significant differences were found between cows for forage intake. These differences remained constant across different types of forages. However, only 25% of the variability in forage intake could be expalined by regressing it on weight change, body weight, and milk production in a prediction equation.

The total effect of intake on estimates of feed efficiency differs in some studies. Some researchers (23, 31) have suggested that differences in efficiency estimates are more dependent on milk yield than feed consumption. However, work by Grieve et al. (17) indicated a much stronger association between intake and efficiency. In this work, more efficient cows had higher feed intakes. Researchers (17) speculate that some of the differences in the effect of intake on efficiency might be due to different feeding regimes employed in the studies. Differences between the Hooven (23) and Grieve (17) studies could be due to this difference since cows were fed according to need in one study (23) and were fed complete rations ad libitum in the other (17).

In a study investigating the correlated response in feed efficiency accompanying selection for milk yield, Weinberg et al. (42) found no difference in dry matter intake among selection and control line cows fed a complete ration. In contrast to Grieves et al. (17), dry matter intake was not a key factor in determining the efficiency of production. In work comparing efficiency between daughters of sires selected for PD milk and sires selected on udder conformation. Pearson et al. (36) obtained results similar to those found in the

Weinberg et al. work (42). Although cows selected for yield produced more milk and solids-not fat than those selected for udder conformation, energy intake of ad libitum mixed rations was not significantly different between selection groups. Thus, production played a much larger role in influencing differences in feed efficiency than did intake.

Sire by Ration Interaction

Evidence of a significant sire effects on variation in feed efficiency was gathered in early work by Hooven and Mathews (22). Their data, including observations on 104 cows by six Holstein sires, revealed significant differences in estimates of feed efficiency among sire progeny groups. The establishment of feed efficiency as heritable trait in later work (23) further substantiated this point.

Evaluating the significance of a sire by ration interaction effect on feed efficiency was the partial objective of two studies (25, 38). The first study (38) utilized 228 first lactation Jerseys by 13 sires, two of which were from New Zealand. The progeny were randomly assigned to either an all forage or a forage plus grain ration. The sire by ration interaction only approached significance ($P < .1$) for production of FCM and contributed less than 4% of the total variation. However, for estimates of gross feed efficiency the interaction was significant ($P < .001$). Given that very little intake differences existed in the all forage group, researchers proposed that the significant interaction was due to grain feeding levels being controlled by production. Sires ranked similar under the two feeding regimes with a few exceptions. Three sires had interaction constants which exceeded the standard errors. However in general, researchers concluded that the sire by ration interaction was probably negligible within the environments of commercial dairying in the United States.

One other study (25) investigated sire by ration interaction. One New Zealand-bred sire was used in this study. Results from Trial 1 (the trial most closely resembling work by Richardson et al. (38)) indicated a significant sire by ration interaction for efficiency and production. These results are in agreement with those reported by Richardson et al. (38). However, in this study, when records of daughers by the New Zealand-bred sires were deleted, the interaction effect vanished. Both studies (25, 38) indicated a similar shift in the relative rank of New Zealand-bred sires on the two rations. For these sires, daughters ranked higher for efficiency on the all forage and lower on the forage plus grain rations. Apparently, New Zealand bulls were selected under considerably different management conditions than North American bulls. Both studies (25, 38) seemed to suggest that, for sires bred in North America, the sire by ration interaction effect on feed efficiency was of little importance to commercial dairymen. Similar conlcusions were reached by Rindsig and Freeman (39) in a study utilizing Holstein twins.

Physiological Implications

Past research (23, 24, 27) appears to indicate a pleiotropic effect of genes for milk production on a cow's ability to efficiently convert feed energy to milk energy. This conclusion is due to the high genetic correlations between milk production and gross feed efficiency as measured with a gross input/output relationship. However, more recent work (6) indicated that need to investigate the physiological implications involved in measuring gross feed efficiency. Use of tissue reserves as an energy source is a key factor when considering variation in gross input/output measures of feed efficiency. Tissue catabolism would tend to inflate measures of gross feed efficiency. Coversely, anabolism of tissue may give estimates of feed efficiency which were seriously biased downward. Past researchers have sued body weight change from the beginning to the end of trial periods to partially account for the physiological status of cows on feed efficiency projects. Moe et al. (33) considered the difficulty of defining input/output relationships in their work summarizing 543 energy balance trials on lactating dairy cows. They noted that changes in body weight do not accurately measure the physiological status of a cow. Earlier work by Flatt et al. (10) using respiration and energy balance trials demonstrated that tissue reserves can be mobilized by lactating dairy cattle without reflecting the negative energy status by a decrease in body weight. Conversely, their work also suggested a cow's ability to gain body tissue in large quantities without a corresponding increase in body weight. In light of this previous work, Moe et al. (34) concluded that experiments such as short term feed efficiency trials may be greatly affected by ability to milk and days in milk of project animals. Failure to detect mobilization of body tissue might significantly influence the amount of energy required in feed to produce a unit of milk. Therefore, studies utilizing bodyweight change as a covarate to adjust for tissue balance in feed efficiency models could unknowingly bias estimates of efficiency.

In a study at Texas A & M, Baron et al. (4) suggested a gross measure of feed efficiency would be misleading unless the physiological nitrogen balance was taken into account. Their work found significant errors in the estimation of gross nitrogen efficiency values for cows in both the negative and positive nitrogen balance states. Their results questioned the validity of comparing the efficiency of cows without considering the phyiological status i.e. nitrogen or energy balance.

The complexity of the gross feed efficiency phenomenom also was realized as a result of work by Grieve et al. (17) on 49 first lactation Holsteins. The cows on this project represented a wide range of enstimated transmitting abilities for milk production. Using a milk energy output/feed energy input ratio as a measure of gross feed efficiency, reseachers found the correlation between it and solids-corrected milk yield to be .72. However, data analysis on twenty-four cows used in metabolism trials indicated a cow's estimated transmitting ability for milk was not associated with her ability to digest food components. Researchers concluded that breeding value for milk production is not a useful indicator of ration digestibility, and apparent efficiency increases are mainly attributable to a decreased proportion of total nutrients being used for maintenance. This work agrees with a study by Custodio et al. (6) when Holsteins fed blended rations showed linear increases in energy efficiency when regressed on estimated transmitting ability for FCM. However, cows did not differ in utilization of feed components. Since cows differed only in gross energy efficiency, it was concluded that characters such as milk production, appetite, and the catabolic/analbolic status of the cow are the primary influences affecting returns on feed inputs. Catabolism of tissue might possibly be the means through which increases in energy efficiency were realized. Researchers (6) suggest studies considering the role of growth hormone and other endocrine pathways that could influence catabolic responses to selection.

This hypothesis is supported by Fronk et al. (14) who examined changes in milk yield and feed efficiency after administration of growth hormone to four Holsteins in late-lactation. Their work reported a 47% increase in gross feed efficiency after administration of growth hormone treatments. Additional increments of milk energy secreted were determined to be the result of tissue catabolism. They speculated that these tissues contain high affinity receptors for which the maximum number could be occupied if concentrations of growth hormone were elevated. Similar increases in efficiency of production after administration of growth hormone were reported by others (26, 37). Peel (37) noted efficiency improvements in cows both in early and late lactation. Further evidence lending support to the role of growth hormone in milk production is given by Hart et al. (18). In dietary energy between tissues and milk production, blood samples were taken throughout the lactation of cows with various production abilities. Average GH concentration were much higher in high producing cows than in cows of less production potential. Researchers suggest the lipolytic (energy liberating) role of GH might explain its presence in high-yielding cows. Their results indicated an increased rate of fat mobilization in high producers.

Conversely, Bines and Hart (2) summarize the role of insulin as being associated with processes that inhibit milk synthesis by diverting dietary energy toward deposition of body tissue. In the work of Hart et al. (18), greater plasma concentrations of insulin were noted in low yielding cows as compared to those sustaining higher levels of production. Bines and Hart (1) suggested that variance in energy partitioning is due to differences in the balance of hormones responsible for energy metabolism and is probably controlled genetically. Later work by Hart (19) suggested that the hormone profile may be altered by environmental influences. Brannang et al. (5) reared heifers under a standard feeding regime and at 70% of the standard regime. Results indicated a 10% increase in feed conversion in subsequent lactations for the heifers grown at a slower rate lending support as to the influence of environment. The importance of hormone interaction with other hormones and receptors in the efficiency of feed utilization should be given consideration (1). In conclusion, Blake and Custodio (3) contend that feed efficiency is a composite trait which is an artifact of the response to selection for yield depending on the interactions between genotypes and certain within animal environments.

CHAPTER III

MATERIALS AND METHODS

Experimental Population and Management

The herd at the Dairy Experiment Station at Lewisburg, Tennessee, was divided into two breeding groups. Initially, the herd was ranked according to each cow's estimated breeding value for milk. Animals were assigned to groups in a manner that balanced production. This was accomplished by placing the animals in groups of seven. After starting at a random point, animals ranking second and fifth for production ability were assigned to a control line, while the remaining cows were placed in the selection line. The two lines also were balanced for age, size, type and sire groups. The genetic lines were identified as either selection or control. Each line was placed under an appropriate breeding regime.

Sire Selection and Breeding Plan

Sires used in the selection line were selected based on their Predicted Difference (PD) Milk. Predicted differences of sires used are shown in Table 3. To be eligible for use in the selection line, a sire must have had at least 30 daughters in at least 20 different herds. All sires used had a repeatability of at least 60%. Initially, four sires were used in the selection line. After the projects initiation, a new sire was added and an old sire removed each year until its completion. Any sire discontinued, could be reselected for additional usage if he continued to meet the requirements. Matings

Table 3. Selection Group Sires at DES*

Sire	DOB	Latest (PD74) Predicted Difference[a] Rpt.	Milk	%	BF	Date	PD Type Rpt.	Score
Brigham Confident Infred	12-52	91%	+775	-.22	+18	10-74	63%	-0.0
Sybil Royal Predictor	03-56	95%	+807	-.04	+37	10-74	88%	-0.8
Sybil Carletta's Finalist	05-57	97%	+1018	-.01	+50	5-77	90%	-1.6
Nobleman's Lotus Designer	11-58	99%	+951	-.13	+35	6-69	98%	-0.9
Observer Signal Revival	12-56	96%	+996	-.28	+23	5-77	89%	-0.9
Observer Chocolate Soldier	4-72	98%	+1552	-.25	+53	6-79	97%	-1.6
Milestones Generator	9-64	99%	+1168	-.44	+15	7-82	99%	+1.6
Secret Baronet	9-64	99%	+781	+.02	+41	7-82	98%	+1.1
SS Quicksilver of Fallneva	8-60	99%	+984	-.16	+65	1-79	98%	+2.3
Vaucluse Sleeping Surville	1-66	90%	+712	-.04	+32	7-82	99%	+1.3
Milkboy Happy Hill Abe	10-68	98%	+1132	-.09	+40	7-82	95%	+1.6
Supreme Virginian	4-70	98%	+1236	-.29	+33	7-82	96%	-0.3
Glen Meadows Jeweled Mark	11-65	97%	+1011	-.19	+32	7-81	93%	+0.2
Briarcliffs Bold Torono	5-70	96%	+1539	-.49	+27	7-82	93%	-0.1
Starnes General	2-72	94%	+1898	-.39	+54	7-82	89%	-0.9
Favorite Saint	1-74	55%	+2248	-.49	+59	7-82	53%	+3.2
Briarcliff Soldier Boy	1-72	89%	+1992	-.29	+69	7-82	83%	-0.5

[a] DOB=Date of birth, Rpt=Repeatability, Milk=lbs. milk, %=Percent butterfat, BF=lbs. butterfat.

*Source: (34)

were planned such that progeny's inbreeding coefficients would not exceed 6.24%. Volunteer removals in the selection line were based on production ability. This criteria for culling was considered most conducive to maximization of genetic gains in milk production.

The control line consisted of cattle which originated from 40 foundation cows and associated young stock. Control line sires randomly were chosen from those available in young sire sampling programs in commercial artificial insemination organizations in 1967. Twenty sires were selected for use in the control line. Predicted differences for control line sires are presented in Table 4. A sufficient amount of semen was purchased to use for the duration of the experiment. Matings were planned to keep the inbreeding coefficient of progeny below 6.25%. Removals, other than those for involuntary reasons, were random. This practice eliminated the possibility of bias arising from selective culling of control line cattle on the basis of their production ability.

Selection and control line cattle were bred up to three times using artificial insemination. If after the third service, a cow remained open, she was bred by natural service to a young sire. Young bulls used for this purpose were by a selection line sire and out of a cow which was in the upper 10% of the selection line based on her breeding value for milk yield. Fewer than 10% of the cattle were bred in this manner. All natural service progeny were deleted from the data set.

Table 4. Control Group Sires at DES*

Name	DOB	Latest (PD74) Predicted Differences[a] Rpt.	Milk	%	BF	Date	PD Type Rpt.	Score
Sables Sybil Ira	11-64	65%	+488	-.16	+10	7-81	47%	-1.4
Milestones Bellringer	5-64	81%	-177	-.18	+7	1-79	47%	-0.1
Secret Baronet	9-64	99%	+781	+.02	+41	7-82	98%	+1.1
Headspring Sparkle	11-64	66%	-137	+.09	+1	6-80	39%	+.8
Jester Infred Scotty	12-64	81%	+530	+.08	+19	1-77	69%	-.4
UK Cherry Kelvin	4-65	59%	+906	+.01	+47	1-81	40%	+1.4
Confident Jeweler	2-65	76%	+585	-.05	+25	6-79	56%	+1.0
Stardust Itaska Designer A	4-65	88%	-131	-.28	-31	9-75	65%	-1.2
Marlu Stylist Beacon	4-65	89%	-393	-.04	-23	10-74	76%	-.0
Headspring Sleeping Goliath	3-65	82%	+159	-.03	+17	9-76	64%	-0.7
Pixys Fancy Voyageur	1-65	80%	+309	-.12	+5	5-77	62%	-1.4
Jestermans Standard Basil	3-65	94%	+238	+.17	+27	1-77	85%	-0.8
Marlu Tempo	8-65	94%	+20	-.16	-13	5-77	81%	-0.3
Patience Supreme	3-65	67%	-160	-.25	-30	5-77	53%	-0.3
Beauty's Advancer	8-65	44%	-288	-.04	-18	6-78	38%	-0.3
Borgs B. Etta Preceptor	6-65	57%	-421	-.04	-25	9-75	28%	-0.2
Vaucluse Dazzling Rosemont	11-65	85%	-782	+.14	-28	5-77	66%	+0.0
Cherry Secret Noble	8-65	80%	-26	-.05	-6	6-80	59%	-2.0
Tymor Gipsy Snoball	9-66	73%	-623	+.15	-19	5-77	36%	-0.3
Confident Infred Basil	10-65	66%	-189	-.06	-15	1-81	40%	-0.8

[a]DOB=Date of birth, Rpt.=Repeatability, Milk=lbs. milk, %=Percent butterfat, BF=lbs. butterfat.

*Source: (34)

Data Collection

The feed efficiency experiment covered 21 trials from 1971-1982. During this time span, feed intake and production data were recorded for a 28-day period on cattle in mid-to-late stages (150-270 days) of lactation. Cows were chosen for each trial in a manner which gave equal representation to the sire groups. Body weight changes were recorded on each individual during the trial. The experimental design and total number of observations are presented in Table 5. Both lines were fed in the same manner. Forages utilized in the project included top quality alfalfa-orchardgrass hay and corn silage fed ad libitum. Grain, containing 16% crude was fed according to production of the individual at the rate of 1 lb. of grain per 3 lbs. of milk produced. Feed samples were taken and compiled by trial. The samples were analyzed to derive net energy values. The results of these analyses are presented in Table 6. The 28-day milk production weights were converted to a 4% fat-corrected milk basis as well as a solids-corrected milk basis (41). These correction adjust for the differences in fat and total solids percentages in the milk of individual cows. After adjustment, individual milk yields were converted to therms or units of milk energy. Feed efficiency was defined as the ratio: units of fat or solids-corrected milk energy produced per unit of total estimated net energy in feed consumed.

Table 5. Experimental Design and Total Observations

Trial	Line: Selection n=231	Line: Control n=119	Total per Trial n=350
1	7	4	11
2	5	8	13
3	4	1	5
4	2	0	2
5	17	10	27
6	9	3	12
7	15	2	17
8	7	5	12
9	25	6	31
10	8	7	15
11	17	14	31
12	5	4	9
13	19	8	27
14	5	2	7
15	5	0	5
16	17	10	27
17	2	2	4
18	19	14	33
19	3	0	3
20	20	12	32
21	20	7	27

Table 6. Means of Feed Sample Analyses

Item	Dry Matter Constituents			
	ENE[a]	Crude Protein	ADF[b]	Lignin
	--------------------%			
Hay	48.5	17.3	36.8	7.0
Corn Silage	55.6	9.5	29.8	3.9
Grain Mixture	98.0	18.4	----	---

[a]ENE=Estimated net energy.

[b]ADF=Acid detergent fiber.

Statistical Analysis

The general linear models procedure in the Statistical Analysis System package (15) was employed to perform a least squares analysis of the data. Determining whether differences in gross feed efficiency existed between lines was the primary objective of the analysis. The preliminary statistical model used in the analysis was as follows:

$Y_{ijklm} = u + t_i + b_1 (k_j - \bar{k}) + s_k + l_l + e_{ijklm}$

u=overall mean

$t_i = i^{\underline{th}}$ test effect

$b_1 (k_j - \bar{k})$=regression on weight change during 28-day trial expressed as a deviation from the group mean.

$s_k = k^{\underline{th}}$ stage of lactation effect

$l_l = l^{\underline{th}}$ genetic line effect

e_{ijklm}=random error

Gross feed efficiency, using both fat-corrected milk and solids-corrected milk in the ratio, was the primary dependent variable. Consideration also was given to how independent effects influenced variation in 28-day milk yields (FCM) and total estimated net energy consumed (T_ENE) over the trial period. Bodyweight change in kilograms incurred during each trial period was used in the model as a covariate to adjust for possible differences in the physiological status of cows. These changes in the original model were made: (1) the covariate bodyweight change was deleted from the model, (2) the variable energy balance was created using National Research Council (35) recommended energy requirements for dairy cattle accounting for lactation and growth (3) energy balance, a more precise predictor of physiological status, was added to the model as a covariate.

The energy balance of a cow was determined by comparing NRC recommendations for energy intake to the actual estimated net energy consumed during each trial. The difference in amounts was defined as the variable ENBAL_28. Also, the data was subdivided according to the energy balance status (positive or negative) of the cows. Of those cows in a positive energy balance status 66 were selection cows and 35 were controls. Cows in negative energy balance included 165 and 84 selection and control line females, respectively. A fixed model, including test, stage and line effects, was used for those cows in positive energy balance as well as those in the negative state.

CHAPTER IV

RESULTS AND DISCUSSION

Unadjusted means and standard deviations of parameters relating to measures of gross feed efficiency used in this study are listed in Table 7 by genetic line. Means indicated the high level production of selection line cattle in the Lewisburg herd (6936 kg FCM) as compared to that of the average production of Jerseys in the southeast (5239 kg FCM). Their superiority reflects genetic improvement obtained through intense selection for milk yield and the high management level which was applied to both selection and control line cattle at the Station. Selection line females produced 11% more fat-corrected milk (FCM) and 9% more butterfat than did the control line cows. These differences in production are in agreement with those from a similar study in North Carolina reported by Weinburg et al. (42) whose selection line females produced 20% more mature equivalent milk and 17% more M.E. fat than controls. Selection line superiority for milk production also is reflected in work by Wilk and McDaniel (43). Direct response to selection for milk yield in the Lewisburg herd was evaluated by Hollon et al. (21). Selection line cattle show similar superiority in production of solids-corrected milk (SCM). Control line females did have a higher butterfat percentage than the selection females. Also, control females were heavier. Mean days in milk at the start of trials and weight change over the trial period indicate that most cattle in both lines were in the latter stages of lactation.

Table 7. Means and Ranges by Genetic Line for Milk Production, Milk Compositions, Body Weight, Body Weight Change, Stage of Lactation and Sire's PD.

Variable	Line (1) Selection Mean	Min.	Max.	(2) Control Mean	Min.	Max.
Milk_28 kg/days	425	279	609	370	184	525
FCM[a] kg/28 days	485	318	666	436	237	590
SCM[b] kg/28 days	488	309	613	439	235	594
BF%[c]	5.0	3.5	7.0	5.2	3.7	6.8
BF[c] kg/28 days	21	13.4	28.8	19.2	10.9	25.8
SNF%[d]	9.3	8.7	10.3	9.4	8.8	10.0
BW_INIT[e] kg	385	314	466	393	336	485
BW_END[e] kg	389	319	474	397	324	500
KGCHANGE[f] kg/28 days	4	30	27	4	-33	5
Sire's PD Milk[g] (kg)	556.2	328.6	1021.8	15.7	-335.5	411.8

[a] 4% Fat-corrected milk.

[b] Solids-corrected milk.

[c] Percent butterfat over 28 day trial period, butterfat.

[d] Percents solids-not-fat over 28 day trial period.

[e] Body weight at beginning of trial, body weight at end of trial.

[f] Change in body weight over trial period.

[g] PD74.

F-values and residual mean squares using a model including test, stage, bodyweight change and line effects are presented in Table 8. Stage of lactation effects were significant ($P<.05$) in influencing variation in total energy intake as well as 4% fat-corrected milk. Tese effects were significant ($P<.01$) for all intake and production variables while the effect of bodyweight change was nil. There were significant line effects ($P<.01$) for total estimated net energy (T_ENE) over the trial period as well as for FCM production. Genetic line was not a significant source of variation for our estimate of gross feed efficiency using either 4% fat-corrected or solids-corrected milk in the efficiency measure.

Results differ from those found in the North Carolina study where significant differences in feed efficiency did exist between selection and control lines. In that respect, results obtained at DES also differed from those indicated in other (20, 36) studies using Holsteins.

Least squares means are presented in Table 9. These results partially explain the differences in this study and others (36, 42). Selection line cows produced 483 kg FCM vs 437 kg FCM by control which is similar to the increase at North Carolina (42). However, in contrast to their results, Lewisburg's selection line consumed significantly more T_ENE and therefore, more dry matter over the trial period. Thus, measures of gross feed efficiency remained constant across genetic lines. This relationship was seen for both measures feed efficiency. Management regimes must be taken into account when

Table 8. F-values and Residual Mean Squares for Intake, Production, and Gross Efficiency Measures

Source	DF	T ENE[a] (Mcal)	FCM[b] (kg)	GE[c] %	GESNF[d] %
Test	20	12.64**	3.14**	11.65**	14.2**
Body weight change (kg)	1	2.27	1.33	.08	.46
Stage	5	2.63*	2.58*	.96	.50
Line	1	41.48**	46.13**	.09	.03
Error M.S.	322	4035.9	15691.1	.00388	.00394

[a]T_ENE=[DM(dry matter) hay intake x .826 x (1.044-(.0124 x hay ADF value x 100)) + DM silage intake x .826 x (1.044-(.0124 x silage ADF value x 100)) + .98096 x DM grain intake.

[b]4% Fat-corrected milk.

[c]Energy (Mcal) produced in FCM/Energy (Mcal) consumed in feed.

[d]Energy (Mcal) produced in solids-corrected milk/Energy (Mcal) cons-med in feed.

*P<.05.

**P<.01.

Table 9. Least Squares Means for T_ENE, FCM, GE, and GESNF[a]

Line	n	T_ENE (Mcal)[b]	FCM (kg)[c]	GE[d]	GESNF[e]
Selection	231	560.85**	483.34**	.63	.64
Control	119	512.21	437.37	.65	.64

[a]Adjusted for fixed effects and bodyweight change.

[b]T_ENE=[DM(dry matter) hay intake x .826 x (1.044-(.0124 x hay ADF value x 100)) + DM silage intake x .826 x (1.044-(.0124 x silage ADF value x 100)) + .98096 x DM grain intake].

[c]4% Fat-corrected milk.

[d]Energy (Mcal) produced in FCM/Energy (Mcal) consumed in feed.

[e]Energy (Mcal) produced in solids-corrected milk/Energy (Mcal) consumed in feed.

**P<.01.

considering differences in the results between this and other experiments. In the Weinberg study, cattle were fed a predetermined amount of hay and an ad libitum blended ration of corn silage and concentrate. Since total energy intake and dry matter were not different across genetic lines, the higher producing females were more efficient. Overconsumption of lower ability cattle in relation to production needs might possibly tend to deflate measures of gross feed efficiency in the control line. Cattle in the Lewisburg study were fed grain according to production. Thus, higher producing cattle had an opportunity to consume more energy and did so. This type of feeding program could partially account for the lack of difference between lines in gross feed efficiency in our study.

The initial model included bodyweight change as over the trial period as a covariate. The covariate was intended to adjust for differences in energy balance resulting from various physiological states during lactation. Bodyweight change over the trial period was not a significant source of variation in either measure of gross feed efficiency.

Bodyweight change is an inaccurate indicator of a cow's physiological status. Moe et al. (33) observed this point in work summarizing 543 energy balance trials and warned of the failure of bodyweight change to detect tissue mobilization over the short term. In an attempt to better account for differences in anabolism and catabolism of body tissue by individual cows, the variable ENBAL_28 was created. Table 10 illustrates, by genetic line, the average

Table 10. Means and Standard Deviations by Genetic Lines for NRC Requirements for Maintenance and Milk, Estimated Energy Intake, and Gross Feed Efficiency

	Lines			
	(1) Selection N=231	SD	(2) Control N=119	SD
Estimated net energy intake (T_ENE)[a] Mcal/28 days	567.90	74.04	525.61	97.21
Net energy requirement Mcal/28 days[b]				
Maintenance	234.08		237.72	
Production	351.68		315.00	
Energy balance[c]	-18.46	61.89	-27.21	78.10
Gross feed efficiency[d]	.64	.07	.63	.09

[a]T_ENE=[DM(dry matter) hay intake x .826 x (1.044-(.0124 x hay ADF value x 100)) + DM silage intake x .826 (1.044-(.0124 x silage ADF value x 100)) + .98096 x DM grain intake].

[b]Energy requirements for maintenance and production were computed from NRC recommendations.

[c]Energy balance=Total Energy intake - requirement for maintenance - requirement for production.

[d]Energy (Mcal) produced in FCM/Energy (Mcal) consumed in feed.

energy balance status of cows over the trial period. The method used in determining energy balance status is similar to that used by Custudio et al. (6). Total maintenance (including a 20% increase for growth) and production requirements were calculated using 1978 NRC recommendations (35). The difference between these requirements and the total energy intake over 28 days was termed ENBAL_28. As seen in the unadjusted averages, the energy balance status of selection line females was negative (-18.46 Mcal). On the average, control line females were in more of a negative state (-28.21 Mcal) than those in the selection line. Differences in the catabolic state of these lines would bias results and may be responsible for failure to detect differences in gross feed efficiency using the original model. The energy balance values obtained are for an entire trial period and are not on a per day basis. Cattle were then divided into energy balance gorups. Two-hundred, forty-nine cows were in a negative energy balance status whereas 101 cows were in a positive state. Since most cattle were in the latter stages of lactation, and did increase slightly in bodyweight, the energy balance breakdown was somewhat surprising. One would expect cows in a weight gaining situation to be in the positive state. We may have overestimated energy requirements since the cattle, all first lactations heifers, were housed in stanchions and had essentially no opportunity for exercise. Also, a 20% increase in maintenance requirements was added to allow for growth of the cattle. Possible bias, due to overestimation of energy requirements, might have occurred. Cattle, being of first parity, were probably at different stages in their growth curves. Most cattle were in late lactation at the time of trials. During early lactation, selection females probably used most of their energy for production as opposed to growth. Control females may have grown more in early lactation than selection females. They would not require the same additional nutrients for growth.

Positive Energy Balance

After dividing the cattle into energy balance groups, a model including the effects of test date, stage of lactation, and genetic line was used to examine parameters relating to gross feed efficiency within each energy balance group. Least squares means for cattle in a positive energy balance state are presented in Table 11. There were 66 cows in the selection line and 35 controls in positive energy balance. As expected, 4% fat-corrected milk was significantly different ($P<.05$) between genetic lines. Selection line females produced approximately 26 kg more FCM than did females from the control line. By definition, these cattle were not in a catabolic state. Thus, bias due to catabolism of body tissue, should not inflate measures of gross feed efficiency. Significant selection line increases ($P<.1$) in total energy intake and dry matter intake as a percent of bodyweight are similar to results obtained from the overall data set. No differences between lines are seen for hay or corn silage consumed over the trial period. Thus,

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Table 11. Least Squares Means for Cattle in Positive Energy Balance by Genetic Line[a]

Dependent Variables	Line (1) Selection	Line (2) Control
FCM[b] kg/28 days	487**	461
T_ENE[c] Mcal/28 days	624.4	601.4
HAYENE_C[d] Mcal/28 days	94.4	88.1
CSENE_C[d] Mcal/28 days	232.0	231.8
GRENE_C[d] Mcal/28 days	297.9*	281.5
DMI[e] kg/day	14.8	14.4
DMI%BW[e]	3.8	3.7
ENBAL_28[f] Mcal/28 days	35.9	30.5
KGCHANGE[g] kg/28 days	2.3	2.2
BW_INIT[g] kg	853	860
Gross Efficiency[h] %	58	57

[a]Adjusted for test and stage of lactation effects.

[b]4% Fat-corrected milk.

[c]T_ENE=[DM(dry matter) hay intake x .836 x (1.044-(.0124 x hay ADF value x 100)) + DM silage intake x .826 (1.044-(.0124 x silage ADF value x 100)) + .98096 x DM grain intake].

[d]Hay energy intake, Corn silage energy intake, Grain energy intake.

[e]DMI=Dry matter intake, DMI%BW=Dry matter intake as percent of bodyweight.

[f]ENBAL_28=Total energy intake- requirement for maintenance - requirement for production.

[g]KGCHANGE=Bodyweight change over trial period, BW_INIT=Bodyweight at beginning of trial.

[h]Energy (Mcal) produced in FCM/Energy (Mcal) consumed in feed.

*P<.1

**P<.05

total energy intake differences are due mostly to energy derived from grain intake. It appears that the method of feeding had an influence on the results. F-values and residual mean squares are presented in Table 12. As expected, month and year of each trial had a strong effect ($P<.05$) on most all intake and yield parameters. Stage of lactation effect was nil for all variables, except bodyweight change in which it only approached significance ($P<.1$). Genetic line had its greatest influence ($P<.05$) on kilograms of 4% fat-corrected milk, and its effect approached significance ($P<.1$) in explaining variation in total energy intake, grain energy intake, and dry intake as a percent of bodyweight. The R-square value obtained indicated that 63% of the variation in gross feed efficiency for those cows in the positive energy balance state was explained by the model, stage of lactation, and line effects.

Negative Energy Balance

The same model used on data from positive energy balance cows was used to examine estimates of gross feed efficiency for those cattle in the negative state. There were 165 and 84 cows in a negative energy balance in the selection and control lines, respectively. Least squares means are presented in Table 13. There was a significant difference ($P<.01$) between lines in energy balance over the trial. Control lines females were in more of a catabolic state. Possibly, a lower ability to consume feed in relation to energy requirements is responsible. Again, energy balance status is only

Table 12. F-Values and Residual Mean Squares for Cattle in Positive Energy Balance Relating to Various Intake and Yield Parameters.

Dependent Variables	Independent Effects Test (DF=18)	Stage (DF=5)	Line (DF=1)	Residual M.S.
FCM[a] kg/28 days	1.78**	.81	3.94**	13881.36
T_ENE[b] Mcal/28 days	3.69**	.29	2.78*	3220.24
HAYENE_C[c] Mcal/28 days	8.78**	1.31	1.11	613.41
CSENE_C[c] Mcal/28 days	4.41**	1.20	0.00	1125.85
GRENE_C[c] Mcal/28 days	2.32**	1.46	2.83*	1623.55
DMI[d] kg/day	5.17**	.41	2.23	8.72
DMI%BW[d]	3.23**	.34	2.98*	.000016
ENBAL_28[e] Mcal/28 days	9.27**	.007	.36	1408.25
KGCHANGE[f] kg/28 days	7.44**	3.10**	0.00	51.01
BEINIT[f] kg	.70	.97	.24	3492.14
Gross Efficiency[g] %	6.37**	1.90	.79	.00167

[a]4% Fat-corrected milk.

[b]T_ENE=[DM(dry matter) hay intake x .826 x (1.044-(.0124 x hay ADF value x 100)) + DM silage intake x .826 (1.044-(.0124 x silage ADF value x 100)) + .98096 x DM grain intake].

[c]Hay energy intake, Corn silage energy intake, Grain energy intake.

[d]DMI=Dry matter intake, DMI%BW=Dry matter intake as a percent of bodyweight.

[e]ENBAL_28=Total energy intake - requirement for maintenance - requirement for production.

[f]KGCHANGE=Bodyweight change over trial period, BW_INIT=Bodyweight at beginning of trial.

[g]Energy (Mcal produced in FCM/Energy (Mcal) consumed in feed.

*P<.1

**P<.05

Table 13. Least Squares Means for Cattle in Negative Energy Balance by Genetic Line[a]

Dependent Variables	Line (1) Selection	Line (2) Control
FCM[b] kg/28 days	482**	425
T_ENE[c] Mcal/28 days	533.8**	475.0
HAYENE_C[d] Mcal/28 days	67.6*	62.9
CSENE_C[d] Mcal/28 days	197.7**	180.9
GRENE_C[d] Mcal/28 days	268.5**	231.2
DMI[e] kg/day	12.5**	11.2
DMI%BW[e]	3.2**	2.8
ENBAL_28[f] Mcal/28 days	-50.05**	-72.05
KGCHANGE[g] kg/28 days	6.5	7.7
BW_INIT[g] kg	386	399
Gross Efficiency[h] %	68	68

[a]Adjusted for test and stage of lactation effects.

[b]4% Fat-corrected milk.

[c]T_ENE=[DM(dry matter) hay intake x .826 x (1.044-(.0124 x hay ADF value x 100)) + DM silage intake x .826 (1.044-(.0124 x silage ADF value x 100)) + .98096 x DM grain intake].

[d]Hay energy intake, Corn silage energy intake, Grain energy intake.

[e]DMI=Dry matter intake, DMI% BW=Dry matter intake as a percent of bodyweight.

[f]ENBAL_28=Total energy intake - requirement for maintenance - requirement for production.

[g]KGCHANGE=Bodyweight change over trial period, BW_INIT=Bodyweight at beginning of trial.

[h]Energy (Mcal) produced in FCM/Energy (Mcal) consumed in feed.

*P<.1

**P<.05

an estimate based on NRC recommendation for maintenance, growth, and production as compared to estimates of total energy intake. As in the previous subset, 4% fat-corrected milk was higher for selection line females. Estimated total energy intake was also higher ($P<.01$) for these cows. Selection line females consumed more energy from all three dietary sources instead of only grain. Also, dry matter intake as a percent of bodyweight was higher ($P<.01$) for selection cows. Thus, increased appetite seemed to accompany increases in milk production for this group or at least, selection line females were more aggressive in attempting to fulfill their nutrient requirements. Gross efficiency was unchanged across genetic lines. Control line females were in more of a catabolic state. Thus, they received a higher percentage of their nutrient requirements for production through catabolism of body tissue. This catabolism might tend to inflate estimates of gross feed efficiency to a greater extent in the control line. If all cows were at the same stage of catabolism, higher producers might be more efficient for reasons suggested in the work of Grieve et al. (17).

F-values and residual mean squares for independent effects used in the model to analyze data on cows in negative energy balance are presented in Table 14. Test period is again highly significant ($P<.01$) in influencing variation for most dependent variables considered. Stage of lactation significantly affected ($P<.01$) energy balance over trial period, dry matter as a percent of bodyweight, and

Table 14. F-Values and Residual Mean Squares for Cattle in Negative Energy Balance Relating to Various Intake and Yield Parameters.

Dependent Variables	Independent Effects			
	Test (DF=18)	Stage (DF=5)	Line (DF=1)	Residual M.S.
FCM[a] kg/28 days	2.76**	1.76	46.26**	16141.64
T_ENE[b] Mcal/28 days	3.09**	1.56	57.84**	2892.84
HAYENE_C[c] Mcal/28 days	15.36**	1.03	4.11*	262.25
CSENE_C[c] Mcal/28 days	11.94**	1.74	17.87**	761.57
GRENE_C[c] Mcal/28 days	2.98**	.75	4379**	1538.4
DMI[d] kg/day	2.99**	1.66	50.55**	7.43
DMI% BW[d]	2.50**	5.83**	58.65**	.000015
ENBAL_28[e] Mcal/28 days	2.67**	2.77**	20.87**	1164.17
KGCHANGE[f] kg/28 days	8.75**	.65	1.3	50.67
BW_INIT[f] kg	1.49	5.70**	8.61**	3937.9
Gross Efficiency[g]	2.48	1.24	.10	.0036

[a]4% Fat-corrected milk.

[b]T_ENE=[DM(dry matter) hay intake x .826 x (1.044-(.0124 x hay ADF value x 100)) + DM silage intake x .826 x (1.044-(.0124 x silage ADF value x 100)) + .98096 x DM grain intake].

[c]Hay energy intake, Corn silage energy intake, Grain energy intake.

[d]DMI=Dry matter intake, DMI% BW=Dry matter intake as a percent of bodyweight.

[e]ENBAL_28=Total energy intake - requirement for maintenance - requirement for production.

[f]KGCHANGE=Bodyweight change over trial period, BW_INIT=Bodyweight at beginning of trial.

[g]Energy (Mcal) produced in FCM/Energy consumed in feed.

*P<.05

**P<.01

body weight at beginning of the trial. For cattle in this physiological state, line differences became apparent (P<.01) for most intake and production parameters measured. Comparing results from analyses of both data sets, it would appear that cattle do behave somewhat differently relative to their physiological energy balance status. An approximate increase of 10% for estimates of gross feed efficiency was realized for cows in negative energy balance as opposed to those in the positive state. This increase was expected and was similar to the increase found between trimesters of lactation by Custodio et al. (6) and reflects that catabolism inflates estimates of gross feed efficiency. Also, large differences in R-square values were obtained using the same model on the two data sets, suggesting a larger portion of unaccountable variance in gross feed efficiency for cows in a catabolic state. Presumably, some of this variance was attributable to catabolism of body tissue. This result somewhat supports Blake and Custodio's (6) contention that feed efficiency is a composite trait relating to various genetic and environmental interdependencies.

Analysis on All Cows Adjusting for Energy Balance

Upon consideration of results obtained by dividing the cows into energy balance groups, a model was conceived to test for genetic line differences in gross feed efficiency. This model, as in the one used originally, consisted of test period, state of lactation, and genetic line effects. However, energy balance over the trial period was placed in the model as a covariate to account for tissue balance differences in the cows (6). An approximate 33% increase in the R-square value resulted, the increase is partially due to the part-whole relationship between variables used in defining feed efficiency and energy balance. This relationship exists since the intake and production variables used to estimate gross feed efficiency also are used in determining the energy balance status of cows. F-values and residual mean squares from this analysis are in Table 15. The energy balance variable was highly significant (P<.01) for gross feed efficiency and most all dependent variables. Test period effects were also significant (P<.01) for most dependent variables, similar to previous analyses. Genetic line, again, was significant (P<.01) in affecting production of 4% fat-corrected milk, total energy intake, dry matter intake, and dry matter intake as a percent of bodyweight. However, using this model, genetic line was significant (P<.01) for gross feed efficiency. The differences, encountered in feed efficiency estimates for cows differing in genetic ability for milk production, are supportive of those in similar studies (6, 36, 42). Leas squares means for intake and production parameters are seen in Table 16. Line differences for total energy intake are contrary to findings by Pearson et al. (36). They found energy intake between lines nearly identical under ad libitum feeding of a blended ration. Increases in energy intake for selection line females in our study appeared to result from increased grain energy intake. This result is not surprising given that grain was fed according to production. Dry matter intake and dry matter intake as a percent of bodyweight were different (P<.01) between

Table 15. F-Values and Residual Mean Squares Adjusting for the Energy Balance State of Cows.

Dependent Variables	Independent Effects Test (DF=20)	Stage (DF=5)	ENBAL 28[g] (DF=1)	Line (DF=1)	Residual M.S.
FCM[a] kg/28 days	3.12**	2.33*	3.79*	40.56**	15572.98
T_ENE[b] Mcal/28 days	3.07**	.95	461.14**	33.02**	1671.14
HAYENE_C[c] Mcal/28 days	18.89**	1.71	104.40**	.13	356.93
CSENE_C[c] Mcal/28 days	12.14**	1.73	140.93**	1.82	704.55
GRENE_C[c] Mcal/28 days	6.11**	1.13	108.47**	29.32**	1260.15
DMI[d] kg/day	2.99**	.85	527.17**	22.86**	4.30
DMI%BW[d]	2.27**	4.80**	453.41**	36.48**	.000008
KGCHANGE[e] kg/28 days	13.95	1.78	.92	.43	52.63
BW_INIT[e] kg	1.36	4.78	5.72	6.16	3710.46
Gross Efficiency[f] %	3.22**	4.05**	519.31**	24.0**	.00149

[a]4% Fat-corrected milk.

[b]T_ENE=[DM(dry matter) hay intake x .826 x (1.044-(.0124 x hay ADF value x 100) + DM silage intake x .826 x (1.044-(.0124 x silage ADF value x 100)) + .98096 x DM grain intake].

[c]Hay energy intake, Corn silage energy intake, Grain energy intake.

[d]DMI=Dry matter intake/day, DM%BW=Dry matter intake/day as a percent of bodyweight.

[e]KGCHANGE=Weight change in kilograms, BW_INIT=Initial bodyweight at beginning of trial.

[f]Energy (Mcal) produced in FCM/Energy consumed in feed.

[g]Energy balance over the trial period was placed in the model as a covariate.

*P<.05

**P<.01

Table 16. Least Squares Means by Genetic Line for Related Intake and Production Parameters[a]

Dependent Variables	Line (1) Selection	Line (2) Control
FCM[b] kg/28 days	483**	439
T_ENE[c] Mcal/28 days	564.1**	535
HAYENE_C[d] Mcal/28 days	78.2	77.3
CSENE_C[d] Mcal/28 days	208.6	204.2
GRENE_C[d] Mcal/28 days	277.3**	254.1
DMI[e] kg/day	13.3**	12.7
DMI%BW[e]	3.4**	3.2
KGCHANGE[f] kg/28 days	5.6	6.2
BW_INIT[f] kg	386**	395
Gross Efficiency[g] %	65**	62

[a]Adjusted for fixed effects and energy balance.

[b]4% Fat-corrected milk.

[c]T_ENE=[DM(dry matter) hay intake x .836 x (1.044-(.0124 x hay ADF value x 100)) + DM silage intake x .826 x (1.044-(.0124 x silage ADF value x 100)) + .98096 x DM grain intake].

[d]Hay energy intake, Corn silage energy intake, Grain energy intake.

[e]DMI=Dry matter intake, DMI%BW=Dry matter intake as a percent of bodyweight.

[f]KGCHANGE=Weight change in kilograms, BW_INIT=Initial bodyweight at beginning of trial.

[g]Energy (Mcal) produced in FCM/Energy consumed in feed.

*P<.05

**P<.01

lines. This finding is contrary to results obtained by Weinberg et al. (42) who found no difference in dry matter intake among genetic lines of Jerseys. Differences in feeding methods might also account for this discrepancy. As in the Weinberg study (42), bodyweight was different ($P<.01$) between lines. Differences ($P<.01$) for gross feed efficiency between lines suggested that lighter weight selection line females were more efficient producers of milk. This result supports the conclusions of Miller and Hooven (30) and Dickinson et al. (7). Other work (6, 17) indicated that variation among cows in the ability to digest dietary components is small. After adjusting for energy balance status of cows in our experiment, it seems that differences detected in estimates of gross feed efficiency are due to the lower percentage of nutrients in feed being used for maintenance as suggested by Grieve et al. (17). As indicated by Custodio (6), our study suggested responses in gross feed efficiency seem to depend on relationships between milk yield, feed consumption, and the tissue energy balance status of the cow. Also, differences in feed efficiency suggest differences in cows' ability to efficiently utilize body reserves and to partition more nutrients toward milk production, not in digestion of feed components.

Correlations between measures of gross feed efficiency and related parameters are presented in Table 17. Similar to the study of the Weinberg et al. (42), estimates of gross feed efficiency using 4% fat-corrected milk and solids-corrected milk were close to identical ($r=.99$). A strong negative association ($r=-.84$) between energy

Table 17. Partial Correlation Between Measures of Gross Feed Efficiency and Related Parameters[a]

	2	3	4	5	6	7	8	9	10
Gross Efficiency[a]	.99**	.35**	.38**	.09	-.51**	-.17**	-.85**	-.57**	-.46**
Gross Efficiency[b]		.39**	.39**	-.04	-.50**	-.11	-.85**	-.59**	-.48**
4% Fat-corrected milk			.99**	-.07	.61**	-.23**	.11*	.51**	.56**
Solids-corrected milk				-.14*	.58**	-.20**	.08	.47**	.50**
Weight Change KGCHANGE					-.13*	-.08	-.13*	-.11*	-.14**
Total Estimated Net Energy Consumed						-.07	.84**	.97**	.97**
Initial Bodyweight							-.12*	-.02	-.42**
Energy Balance								.87**	.84**
Dry Matter Intake									.91**
Dry Matter Intake as a Percent of Bodyweight									

[a]4% Fat-corrected milk measure, n=350.

[b]Solids-corrected milk measure, n=268.

*P<.05

**P<.01

balance status of cows and our measure of gross efficiency would seem to suggest that efficiency increases are in part due to catabolism of tissue as indicated by Custodio et al. (6). Although consistent with findings of other studies (6, 23, 40, 42), the degree of association between 4% fat-corrected milk produced and gross feed efficiency was somewhat less (r=.35) than in those studies. However, dry matter intake (r=-.57), dry matter intake as a percent of bodyweight (r=-.46), and total energy intake (r=-.51) had a significant negative association with estimates of gross feed efficiency. This result is inconsistent with Grieve et al. (17) who found a positive relationship (r=.60) between dry matter intake and a slightly different measure for gross efficiency of lactation. The work at Randleigh (42) indicated no association between dry matter intake and estimates of gross feed efficiency. The association between intake and efficiency in our study indicates that intake is more influential in controlling variation in gross feed efficiency than in other studies (36, 42).

CHAPTER V

SUMMARY AND CONCLUSIONS

Feed efficiency data were collected on two genetic lines of Jerseys at the Dairy Experiment Station. Females, selected for milking ability, were compared with unselected control line females to determine any differences in estimated gross feed efficiency occuring as an indirect response to selection.

Bodyweight change, the original covariate, was replaced by a variable defining the difference between WRC recommendations and actual energy intake. The energy balance variable seemed a better indicator of physiological energy status. Energy balance over the trial period displayed a strong negative association with the estimate of gross feed efficiency. It was concluded that a cow's energy balance status had greatly influenced her efficiency measured as an input/output relationship. Negative relationships were also encountered between dry matter intake, dry matter intake as a percent of bodyweight, total energy intake over trial, and estimates of gross feed efficiency.

Cows in negative energy balance demonstrated an increase of approximately 10% for estimates of gross feed efficiency as compared to those in the positive state. It was concluded that this increase was primarily due to catabolism of tissue.

Upon use of the energy balance variable as a covariate in the model, line differences became significant for estimates of gross feed efficiency. Although selection line females consumed more energy than controls, they produced more milk per unit of feed input. Results indicated that in this respect, selection line females were more efficient producers of milk.

Although production of 4% fat-corrected milk was positively related to efficiency, it appears that variation in this trait was only partially attributable to differences in yield. The results suggest a need to consider physiological tissue balance in studies involving estimates of gross feed efficiency. It seems that feed efficiency is a complex trait influenced by genetic and environmental parameters such as intake, production, and physiological status.

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