EFFECT OF BODY CONDITION AND RATION PROTEIN SOURCE ON PERFORMANCE OF HIGH PRODUCING COWS DURING EARLY LACTATION

by

William Matthew Seymour

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APPROVED:

C.E. Polan, Chairman

J.H. Herbein

R.M. Akers

J.M. White, Department Head

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ABSTRACT

Forty-two high producing Holstein cows were paired by body condition and mature equivalent milk production and fed either a high or low energy complete ration ad libitum during the last 16-20 weeks of lactation. Cows fed the high energy ration ate more feed, produced more milk and gained more body condition than cows fed the low energy ration. Cows were fed to maintain condition during the dry period. During weeks 3-15 of the next lactation, half the cows in each condition group (fat or thin) were fed a mixed ration with soybean meal (SBM) as the major protein source. The remaining cows were fed a ration with dried brewers grains (DBG) as the main protein source.

Fat cows produced more 3.5% fat corrected milk during weeks 1-15 of lactation, more actual milk in weeks 1-7, ate less feed and lost more bodyweight than thin cows. Cows fed DBG had slightly higher milk production than cows fed SBM despite a high level of bound, unavailable nitrogen in the DBG. Differences in milk production, feed intake and body-

weight change between the four treatment groups (FB, FS, TB, TS) were not significant. Ruminal acetate and ammonia were higher and butyrate lower for cows fed DBG. Rumen ammonia was higher in thin cows than in fat cows. Plasma urea was highest in TB cows. Plasma growth hormone, insulin and the response areas of each hormone after intravenous arginine were affected by stage of lactation (6 or 15 weeks), body condition and ration.

The data show that the lack of adequate body condition results in decreased milk production, especially at peak lactation. Differences between fat and thin cows in feed intake and milk production compensated for changes in energy balance imposed during the previous lactation. DBG were equal to soybean meal as a protein source for lactating dairy cows. Metabolite and hormone data indicated an interaction of body condition and ration in the case of TB cows. Effect of stage of lactation on hormonal parameters was consistent with the proposed roles of growth hormone and insulin in the control of nutrient partitioning in lactating cows.

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INTRODUCTION

The ruminant animal is unique in its ability to convert non-nutritive substances into food and fiber for man. Thus the ruminant has become an important part of human agriculture. The complex digestive physiology and intermediary metabolism of the ruminant animal has made it difficult to establish nutrient requirements. At the same time genetic selection has been producing animals with greater abilities to transform feed into meat and milk. Thus the nutritionist is faced with the problem of meeting the requirements of high producing ruminant animals without sacrificing feed efficiency.

This problem becomes obvious in the case of the high producing dairy cow. At low levels of milk production the cow's nurtrient requirements are met by the products of the ruminal fermentation. However, special manipulation of the diet may be needed in order to meet the cow's nutrient requirements during early lactation (Clark and Davis, 1983.) Cows producing in excess of 65 lbs of milk per day often consume feed at 3 to 4 times maintenance levels and still cannot meet their nutrient requirements for milk production (Clark and Davis, 1983). Therefore high producing cows mobilize body tissue to supply extra nutrients needed for peak

lactation. Because total lactation performance is strongly associated with peak milk production (Broster and Broster, 1984) it is critical to establish clear relationships between long term feeding practices and milk production efficiency in the dairy cow.

In the high producing cow, body reserves may account for one third of the milk produced during the first month of lactation (Bauman and Curry, 1980). Fat tissue is heavily depleted with smaller losses of nitrogen and minerals from the tissues (Bines and Hart, 1982; Tyrrell and Haaland, 1983). Therefore it has been proposed that cows mobilizing body tissue will require more dietary amino acids to adjust for the fatty acids being released from adipose tissue (Orskov et al., 1977). Infusion of casein into the abomasum of lactating cows in negative energy balance increases the energy deficit, suggesting that fat mobilization is stimulated by an increased protein supply (Orskov et al., 1977). Konig et al. (1982) found that under similar conditions casein infusion increased the turnover of plasma palmitate and acetate.

Other research has shown that more protein can be supplied to the ruminant animal if the extent of dietary protein degradation in the rumen is reduced (Armentano et al., 1984; Stern et al., 1984; Tamminga et al., 1979). Thus when

an animal's amino acid requirements are not being met by a conventional diet, substitution of less degradable protein into the ration could be a means of meeting the need.

Excessive degradation of feed protein in the rumen results in high levels of rumen ammonia. Ammonia then enters the portal blood and must be converted to urea by the liver. The net result is inefficient utilization of both nitrogen and energy by the animal (Chalupa, 1972). Therefore controlling the rate and extent of protein degradation in the rumen could be a means of improving the feed efficiency of ruminants. However the crude protein system of protein evaluation measures only the total nitrogen in the feeds and not their rumen degradability. Newer systems of protein evaluation are being developed which take account of protein degradability and can predict protein supply to the animal (Satter and Roffler, 1975).

The in situ rumen bag technique (Orskov, 1979; Nocek et al., 1979) and accompanying equations allow measurement of the rate and extent of protein degradation and estimation of the net degradation of feed protein in the rumen of a lactating dairy cow. Research (Santos et al., 1984; Rooke et al., 1984) has verified the ability of the in situ bag technique to predict the degradability of nitrogen sources in vivo. These techniques can be used to formulate rations

differing in protein degradability and, presumably, in the protein supplied to the animal.

Data from feeding trials suggests a beneficial effect of feeding less degradable protein sources to lactating cows (Forster et al., 1980; Herrington, 1983). However more evidence is needed to confirm the value of resistant proteins in dairy rations.

If the mobilization of body fat in lactating dairy cows is linked to the supply of certain limiting amino acids, then increasing the protein supply to the animal should stimulate milk production and efficiency of cows with adequate body fat reserves. Cows lacking adequate fat reserves should be less responsive to protein supply than cows in good body condition.

In this study, fat and thin cows were fed two rations, high or low in rumen degradable protein. Thus the effects of body condition, protein degradability and the interaction of these two factors were studied in high producing cows during early lactation. Rumen and blood analysis were undertaken in order to better understand the metabolic adjustments occurring in response to treatments.

REVIEW OF LITERATURE

LACTATIONAL RESPONSES TO PROTEIN SUPPLEMENTATION

Responses to Level of Dietary Crude Protein

Clark and Davis (1984) defined the crude protein (CP) requirement as the minimum concentration of dietary nitrogen which will support maximum milk production. Attempts to define such a requirement for high producing cows in early lactation have yielded values of 13 to 16% of dry matter (Oldham, 1984). Rations containing less than 12% crude protein (CP) depress digestibility, intake and the efficiency of energy utilization in lactating cows (Huber and Kung, 1981). Lactating cows initially fed a low protein ration (9-10% CP) show marked increases in dry matter intake, digestibility and milk production as crude protein is increased to 14% of ration dry matter (Polan et al., 1970; Cowen et al., 1980). Non-protein nitrogen was as effective as preformed protein at these levels of dietary nitrogen (Wohlt et al., 1978; Polan et al., 1976). As the CP content of the diet is increased, milk production responses are smaller and less consistent. Polan et al. (1976) reported increases in fat corrected milk (FCM) and dry matter (DM) intake as the CP content of corn silage based diets was raised from 9.4 to 16.2% of DM using soybean meal and/or

urea. Kung and Huber (1980) found increasing production and intake in response to ration CP levels of 11, 14 and 17%. Roffler et al. (1978) demonstrated increased production and intake when the CP content of alfalfa-grass silage rations was changed from 12.2 to 16.2% during early lactation. Wohlt and Clark (1978) found greater 310 d FCM yields when ration CP was increased from 11.5% to 13 or 14% using a mixture of soybean meal (SBM) and urea. Grieve et al. (1980) found no benefit from increasing the CP content of hay or haycrop silage based rations from 14 to 16% using soybean meal. The results of 13 experiments were summarized by Van Horn et al. (1979). They concluded that 14% crude protein was most effective and economical level of supplementation for corn silage-corn-SBM rations.

In another experiment Van Horn et al. (1979) showed that when ration CP was raised from 13.5 to 16.3% using cottonseed meal, milk production and intake were increased while the same increase in ration CP using SBM had no beneficial effects. These workers further showed that a corn silage-corn-SBM ration containing 13.5% CP was equivilent to a corn silage-corn-cottonseed meal ration with 16.3% CP when fed to lactating cows. Accordingly, cows responded to an increase of ration CP from 13.5 to 16.5 % when cottonseed meal, but not when SBM was used as a supplement (Roffler et al.,

1983). Dry matter intake was increased by both supplements. Therefore the source as well as the amount of crude protein affected animal response. Oldham et al. (1981) fed urea, SBM, treated SBM or fish meal at levels of 10.3, 12.3, 14.3 and 16.3% CP to lactating cows. FCM production was higher for cows fed the three higher protein levels. Actual milk and milk protein on the 16.3% CP ration exceeded that on the 14.3% and 10.3% but not the 12.3% CP rations. Fishmeal, SBM and treated SBM proved superior to urea for milk production, while responses to fishmeal and SBM were similar.

When milk production has increases in response to CP levels greater than 13% it is almost always associated with increased intake and digestibility of dry matter (Oldham, 1984). Cowen et al. (1980) attributed 70 to 80% of the increases in production observed when ration crude protein level was raised from 11.1 to 14.7% of dry matter to increases in metabolizable energy intake. Thomas et al. (1980) found that increased energy intake could explain the production response of cows to protein supplementation of low protein rye silage diets. Data of Holter et al. (1980) show that increased milk production in response to higher CP levels was associated with greater intake of metabolizable energy. When increased protein in the diet has failed to increase milk production it has also failed to affect intake

and digestibility of the diet (Van Horn et al., 1979). These results suggest that the primary effect of added protein is to alleviate a shortage of some nitrogen compound in the rumen, thus improving carbohydrate digestion and increasing microbial cell growth.

A few studies have shown positive effects of high crude protein levels (17-18%) for lactating cows (Kung and Huber, 1980) while most studies have not (Oldham, 1984). Treacher et al. (1980) reported no difference in milk production or DM intake between cows fed rations of 13.5 or 18% CP. Feeding rations containing more than 18% CP to dairy cows can result in more days open and services per conception (Jorden et al., 1984).

Other Dietary Factors Affecting Response to Crude Protein

Source and amount of forage in the ration will affect the response to protein supplementation. When the proportion of forage in the ration is reduced, the level of readily fermentable carbohydrates is increased. Thus the microbial demand for nitrogen compounds is increased (Van Soest, 1982). Poor quality forages have low energy values (Waldo et al., 1982) and high levels of acid detergent insoluble (bound) nitrogen(ADIN). Sniffen et al. (1975) reported markedly reduced amino acid absorption, as measured by arterio-venous

difference, with poor vs. high quality alfalfa hay. Gordon et al. (1980) found that the response of lactating cows to protein supplementation of silage diets was proportional to the digestibility of organic matter in the ration.

Forage species and method of preservation can affect response to ration protein. Waldren et al. (1982) reported poorer nitrogen utilization with grass vs urea treated corn silage. The grass silage had a lower energy value and higher % ADF and % ADF-N. Silages with high levels of soluble protein may be less responsive to protein supplementation especially when a highly degradable protein source is used (Kung and Huber, 1983).

Silage dry matter can affect the response to ration CP. Craig et al. (1984) detected a milk production response when SBM-meat meal was added to a low (36%) DM alfalfa haylage diet but no response when a high (55%) DM silage was fed.

Variation in the results of feeding trials are also due to the limitations of the crude protein system. Crude protein is merely an expression of the total nitrogen present in a given amount of feed dry matter multiplied by 6.25, a factor which reflects the average % nitrogen in plant proteins. The system does not distinguish between true protein and non-protein nitrogen, nor does it account for differenc-

es in the rate and extent of ruminal degradation of nitrogenous feed components. Both of these factors have been shown to affect animal response to protein supplementation (Huber and Kung, 1981; Orskov, 1982) and have been incorporated into the newer systems of protein evaluation (Waldo and Glenn, 1984). The majority of the ruminant's amino acids are supplied by microbial proteins synthesized in the rumen (Armstrong and Weekes, 1983). Therefore variations in microbial protein yield could account for different production responses within the same range of ration CP.

Animal Factors Affecting Response to Crude Protein

Other factors not directly related to the chemical and physical properties of feedstuffs such as cow age, producing ability, stage of lactation and level of feed intake influence the response to protein supplementation.

Different responses to ration crude protein level have been observed between cows and heifers. Cressman et al. (1980) fed cows and heifers rations of 10:30:60 hay:corn silage:concentrate, varying the ratio of corn to soybean meal to give crude protein levels of 12.4, 15.1 and 17.7%. The higher levels of CP increased production in cows but not in heifers during weeks 1 to 12 of lactation. Thomas et al. (1980) supplemented the rye silage diets of cows and heifers

with soybean meal and found a positive milk production response in cows but not heifers. Cowen et al. (1982) compared crude protein levels of 11.1 and 14.7% in hay-barley diets fed to Holstein cows and heifers during weeks 1-16 of lactation. Milk production was increased in both groups by higher crude protein in the ration. Dry matter digestibility and intake were increased both groups. The positive response of heifers in this study may be related to the use of white fishmeal as protein source. Fishmeal has been shown to support a high rate and efficiency of gain in dairy bull calves (Zerbini and Polan, 1985). The effect of fishmeal on the milk production of heifers may be due to its contribution towards the growth requirement of these animals. However the rations fed by Cowen et al. contained less than 12% CP. Addition of protein to the rations increased DM digestibility and intake and this could have accounted for the increased milk production of the heifers.

Oldham et al. (1981) reported lower intake, DM and fiber digestibility, milk yield, fat and protein yield, serum albumin and greater bodyweight losses during d 1 to 62 of lactation in heifers fed 10.8 kg of a low protein concentrate vs those fed according to CP requirements. Roffler et al. (1982) found that decreasing dietary CP from 17.3 to 13.5% decreased milk production in mature cows but not in heifers.

Heifers were shown to respond to increased energy and ration CP by McLeod et al. (1983) who found that the largest increase in production occurred when CP level was raised from 12 to 15% as compared to 15 to 18% of DM. Like the mature cow the heifer is sensitive to low ration CP, but appears less responsive to CP levels above 13% of DM.

Stage of lactation, producing ability and level of feed intake are related animal factors affecting the response to CP supplementation. In early lactation nutrient requirements exceed those supplied by the diet. Higher producing animals consume more feed per unit bodyweight but also experience greater energy deficit during peak lactation. Thus, high producing cows will mobilize the largest amounts of body fat to correct their energy deficit (Bines and Hart, 1982), and may require larger amounts of protein in order to efficiently utilize body fats for milk production (Orskov et al., 1981).

Hypertrophy of the gut and other organs (liver) during early lactation increase the dam's absorptive and metabolic capacity to match lactational demands (Cripps et al., 1980). This may increase the animal's sensitivity to ration protein. Whether proliferation of gut tissue parallels the pattern of intake during lactation or is proportional to the producing ability of the cow is unknown.

Dairy cows are most responsive to changes in dietary protein during early lactation when positive milk production responses have been observed with crude protein levels as high as 16-17% (Polan et al., 1976; Kung et al., 1983). However in most cases ration CP levels of 13.5 to 15% have been adequate. Cows producing 14,000 lbs of 305 day (ME) milk performed as well on rations containing 12% CP as cows fed similar rations containing 14.5% CP (Van Horn et al., 1976).

According to Satter and Roffler (1977), when ration CP exceeds 13% of DM, more ammonia is released in the rumen than can be used by the micorflora. Nitrogen wasting occurs with energy costs to the host animal. Rate of ammonia release is reduced as the degradability of ration protein is reduced. Therefore, variable responses to CP levels greater than 13% of ration dry matter may be due to differences in protein degradability. Rate of carbohydrate digestion in the rumen must also be considered as this determines the rate of ammonia utilization by rumen bacteria (Van Soest, 1982).

Results of other studies (Roffler et al., 1982; Barney et al., 1980) suggest that adaptive changes to high protein diets may be important. Cows initially fed a high CP ration, (17%), decreased milk production and intake when ra-

tion CP was reduced to 13.5 or 13% (Barney et al., 1980). The earlier in lactation that ration CP was reduced the greater was the reduction in milk production. Adaptation of rumen and/or host animal metabolism to ammonia may be important in determining responses to changes in ration CP.

After peak lactation, % CP requirements decline due to decreasing milk production and high level of intake. Cows are in positive energy and nitrogen balance and tissues lost during early lactation are replaced. The tissue losses of early lactation are mainly fat, therefore the protein requirements for their replacement should be low. This decreases the protein requirement relative to energy during late lactation.

During the declining phase of lactation, ration CP levels of 11 to 12% are sufficient to support milk production (Thomas et al., 1980; Clark and Davis, 1984). Burgess et al. (1982) compared rations with 10,13 or 16% crude protein fed ad libitum to cows in midlactation. Wilted timothy silage was the forage source while soybean meal was the protein supplement. Cows fed the 10% crude protein ration consumed less DM and lost more bodyweight than cows fed the higher protein rations. Milk production and 4% FCM was increased in one of two trials as ration CP was increased from 10 to 13%. Milk fat and protein were depressed by the low protein

ration in both trials. The authors concluded that for cows producing 22 kg of milk daily, a CP level of 13% is adequate to maintain intake and body weight.

Thus the nitrogen requirement of dairy cows depends on the level and stage of lactation, the rates of dry matter intake and fermentation in the rumen and the age of the animal. Variation in the results of feeding trials testing the effect of crude protein on milk production indicates the need to consider other properties of feed proteins.

EFFECT OF PROTEIN DEGRADABILITY ON MILK PRODUCTION

The rationale for limiting the rumen fermentation of feed protein is that "excessive" protein degradation in the rumen liberates more free ammonia than can be utilized by the microbial flora (Satter and Roffler, 1975). Excess ammonia then enters the portal blood and is converted to urea by the liver. Some urea can be recycled into the rumen or cecum, but when the ammonia concentration in these compartments is already high, the rate of recycling is decreased (Kennedy and Milligan, 1980). By reducing the rate of protein degradation in the rumen, ammonia overflow can be reduced and the total protein supply to the intestine increased (Stern et al., 1984).

Abomasal infusion of casein, soybean meal and cottonseed meal increase milk production in lactating cows (Clark et al., 1977; Rogers et al., 1984.) Casein elicits a growth response in ruminants when given via the abomasum but not when given orally (Hatfield, 1977). Intraperitoneal injections of essential amino acids increased growth and N balance in growing sheep (Hall et al., 1974). Gelatin, monosodium glutamate and other poor quality proteins do not improve milk production and growth when given postruminally showing the importance of protein quality (Hatfield, 1977). These data suggest that milk production and/or growth in ruminants may be limited by the supply of certain amino acids. Therefore feeding trials have been conducted to test the value of less degradable protein sources for growth and production in ruminants, on the grounds that reducing protein degradability will increase protein supply to the animal. (note: solubilty of proteins in mineral buffer, used as a measure of rumen degradability (Huber and Kung, 1981), is referred to as NSOL.)

Majdoub et al. (1978) fed rations containing 13 or 15% CP and 22 or 52% NSOL to cows in mid-lactation for 9 weeks. Feeds included sorghum silage, beet pulp, wheat bran and middlings, CSM, oats, corn meal and dried whey. The ratio of forage:concentrate was 40:60. Cows fed the 15% CP/22%

NSOL ration produced more milk and FCM than the other treatments groups. The lower NSOL rations improved production and N utilization. Grieve et al. (1980) found that lowering ration NSOL by substituting haycrop silage and ensiled corn with dry hay and corn increased percent conversion of dietary N to milk. Formic acid-formaldehyde treatment of alfalfa silage (which lowers NSOL) has improved animal performance, mainly due to increased intake(Glenn et al., 1983). Holter et al. (1982) conducted two trials where ration CP was increased in high (46%) or low (20%) NSOL rations. Increasing ration CP increased milk production only when the low NSOL ration was fed. Higher producing cows were used in the high NSOL trial. Janicki (1983) found no significant effect of ration NSOL (40 vs 48%) on milk yield, although gross energy intake and metabolizable energy value of the rations were improved by lower NSOL. Lowering NSOL had more benefit when ration CP was 15.8 vs 13.8% of DM.

In several experiments heat or formaldehyde treatment of SBM was used to alter NSOL and protein degradability. Grummer and Clark (1982) found no difference in milk yield of cows fed five diets varying from 21.7 to 34.4% NSOL during early lactation. Diets were based on corn grain/corn silage with regular or heat-treated SBM as the protein source. Ahrar and Schingoethe (1979) fed corn silage, alfalfa-brome

hay and SBM or heated SBM to cows during weeks 9 to 25 of lactation and found no response of milk production to NSOL, although digestibility and nitrogen utilization were slightly improved by HSBM. Netemeyer et al. (1980) compared the in vitro digestiblity and feeding value of regular vs heated SBM at two ration CP levels. Heat treatment of SBM increased milk production by 0.7 kg per day while increasing ration CP from 14 to 22% had no effect on milk yield. Dry matter intake was not affected by treatments. Kung and Huber (1983) tested combinations of SBM or HSBM and regular or ammoniated corn silage at 11.3, 14.5 and 17.5% ration CP for lactating cows. The combination of HSBM and ammoniated corn silage at 17% CP was best for production and most economical. The authors suggested that this combination allowed greater escape of SBM from the rumen while supplying adequate nitrogen for rumen bacteria.

In two studies, feeding formaldehyde treated SBM (Crooker et al., 1983; Folman et al., 1980) had no significant effect on milk production. Crooker et al found that the digestability of CP was lower for the treated SBM, suggesting that the protein may have been rendered indigestible by the formaldehyde. Heating can also damage proteins making them unavailable to both microbes and the host animal (Van Soest, 1982). This can occur in dried brewers grains which are

heated during processing Heat damaged protein is reflected in the ADF-N fraction of feeds. Oldham et al. (1982) reported that protected SBM was equal to SBM and inferior to fishmeal fed at four levels of CP during early lactation.

A recent study found that treatment of soybean meal with sodium hydroxide significantly increased milk yield, fat-corrected milk, solids corrected milk and efficiency of protein utilization in dairy cows when compared to untreated SBM (Mir et al., 1984). This suggests that the method of treatment may be a critical factor in determining the response of lactating cows to protected protein.

Several investigators have fed rations formulated based on the predicted rumen degradability of protein as determined by the in situ rumen bag technique (Orskov, 1982). In most cases protein sources known to be resistant to rumen degradation, such as brewers and distillers grains, fishmeal, corn gluten meal and cottonseed meal, were used. Recent work (Rooke et al., 1984; Orskov et al., 1983) has shown good agreement between the in situ and in vivo estimates of ruminal protein degradation. Forster et al. (1982) fed isocaloric, 50% roughage diets containing 14% CP with either soybean meal or corn gluten meal as the protein source. Nitrogen disappearance as estimated by the in situ rumen bag method were: 2.8, 2.3, 1.9 and 3.2 percent per

hour: for rations based on SBM, CGM + urea, and CGM at 14% CP and SBM at 17% CP. The rations were fed for 8 wk beginning at 35 d postpartum. Lowering degradability at 14% CP increased production but decreased milk protein percent. Average production was 30-32 kg per day. Milk yield and protein percent were higher for the 17% CP ration.

Erdman and Vandersall (1983) formulated two rations containing 14.3% CP, with estimated net degradabilities of 52.9 and 72.8%. Protein sources were: corn, CSM, brewers grains, and CGM for the low, and corn, barley and SBM for the high degradability diets. Rations contained 40% roughage (corn silage). All cows (24) were fed a balanced ration with 16.5% CP and a net degradability of 72.7% during weeks 1-4 of lactation. The cows were then randomly assigned to the two experimental rations for 12 weeks. Neither milk yield nor FCM were affected by ration. Protein percent and yield were decreased by the low degradability ration. Rumen degradable dry matter matched RDN in the high but not the low degradability ration. No digestability values were reported. Herrington (1983) fed rations based on SBM and wet and dry brewers grains to cows in mid-lactation. Milk and protein yield were increased when brewers grains replaced SBM over a range of 12.2 to 18.1% CP. Increasing ration CP above 15% using brewers grains increased milk yield while no

such response was found with SBM. Fiberous, less degradable proteins such as brewers grains and cottonseed meal elicit production responses at higher CP concentrations than SBM. This contrast between the protein sources may be obscured in early lactation when high rumen outflow rates increase the escape of dense concentrates such as SBM (Orskov et al., 1983).

Orskov et al. (1981) found that FCM was increased by lowering protein degradability of the ration only when cows were in early lactation and energy intake was restricted. Protein sources were fishmeal and peanut meal and cows were producing 27-28 kg per day.

In a growth trial, Cummins et al. (1982) found no difference in intake, gain or feed efficiency of calves fed rations of 30, 45 or 60% RDN as defined by the in situ bag technique. Dietary nitrogen was more efficiently utilized by calves fed the low vs the high RDN diets. Protein degradability has the potential to be a useful means of improving feed efficiency and milk production if a greater understanding of ruminant digestion can be reached.

RUMEN ECOLOGY

General Scheme of Rumen Fermentation

In the rumen, feedstuffs undergo anaerobic fermentation prior to gastric and intestinal digestion. Carbohydrates are partially oxidized to VFA's and the ATP generated is used for maintenance and growth by the microbial flora. Proteins, nucleic acids and amines are partially or completely digested by bacteria, yielding peptides, amino acids and ammonia. These compounds are incorporated into microbial cells. Thus through the action of rumen microbes the host animal derives energy and protein from otherwise indigestible materials. Vitamins are also synthesized while certain toxic plant compounds are detoxified (Van Soest, 1982).

Goals in ruminant nutrition are to maximize the feeding of forages, byproducts and poor quality nitrogen sources while maintaining high levels of production. Feeding high quality proteins to ruminants is wasteful unless they are protected from ruminal degradation. However, several rumen bacteria, among them the fiber digesting species require peptides, amino acids and branch chain isoacids (Russell and Hespell, 1981). Therefore some true protein must be included in ruminant diets. Selective protection of feed proteins and judicious use of non-protein nitrogen could satisfy both

microbial and animal nitrogen requirements while maximizing feed efficiency.

Under normal feeding conditions pathways of substrate oxidation and end product production and utilization in the rumen follow fairly predictable patterns. However, the microbial ecology underlying these reactions is very complex and can vary considerably. Figure 1 shows the general scheme of rumen fermentation. Intense competition for secondary fermentation products such as mono and di-saccarides and the transfer of hydrogen from cellulolytic to methanogenic bacteria are important components of rumen ecology (Baldwin and Allison, 1983). The rate of fermentation of carbohydrate and nitrogen compounds in the rumen affects the efficiency of microbial growth. If supplies of ammonia or other required building blocks are lacking, microbes will dispose of ATP by avenues other than growth. This is refered to as energetic uncoupling (Russell and Hespell, 1981). Competitive advantages are gained by species which exhibit a wide range of substrate affinity and preference, fast growth rates, low maintenance requirements and pH tolerance (Russell and Hespell, 1981). Starch and sugar fermenting organisms have these properties while fiber digesting and methanogenic species are relatively slow growing, have complex nutrient requirements and are inhibited by pH

below 6.0 (Hynd et al. 1984). Cellulolytic activity requires low partial pressure of hydrogen gas and is thus affected by the activity of the methanogens (Wolin, 1981).

High roughage diets favor acetate, butyrate and methane production and higher microbial cell yields. Roughage stimulates saliva flow which increases liquid turnover and buffering capacity. These conditions favor the growth of celluloytic and methanogenic species in the rumen. The growth of amylolytic species is kept in check by the relative lack of soluble sugers (Baldwin and Allison, 1983). High grain feeding allows the fast growing starch fermenting species to multiply. Rapid production of lactate and propionate along with decreased salivation lowers rumen pH and results in a less stable fermentation (Barry et al., 1984). Cellulolytic and methanogenic species are inhibited by the low pH, thus fiber digestion is depressed (Colucci et al., 1983). However the efficiency of milk production increases as the proportion of grain in the ration increases (Coppock et al., 1964). Addition of buffers to high grain diets helps to increase liquid turnover rate, improving fiber digestion, fat test, intake and the efficiency of milk production (Wolin, 1981). Rumen fermentation patterns and factors affecting microbial efficiency are complex. Further study is required before the goals of ruminant nutrition can be met.

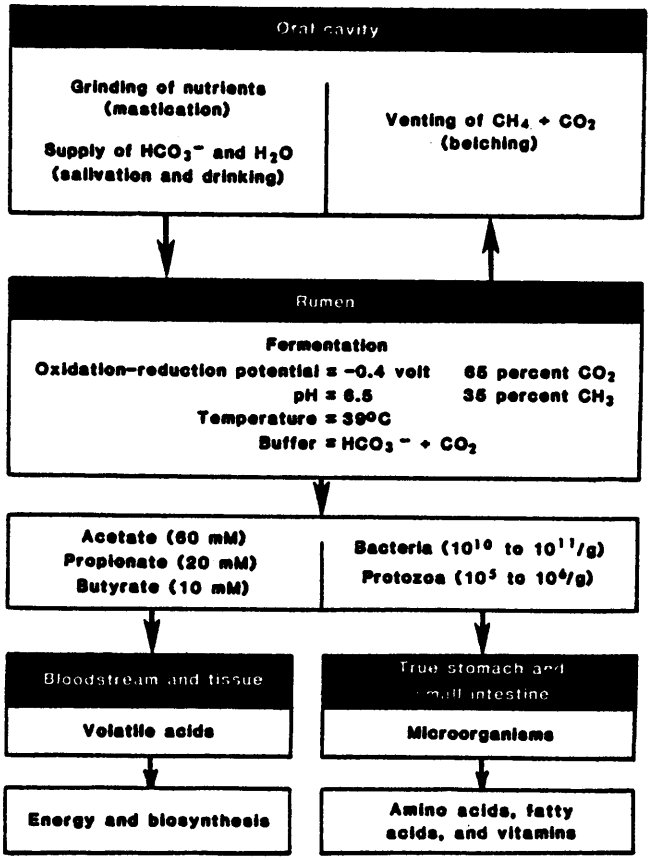

Fig. 1. Schematic representation of the ruminant as a factory for conversion of food to animal products. [From Wolin (*3*)]

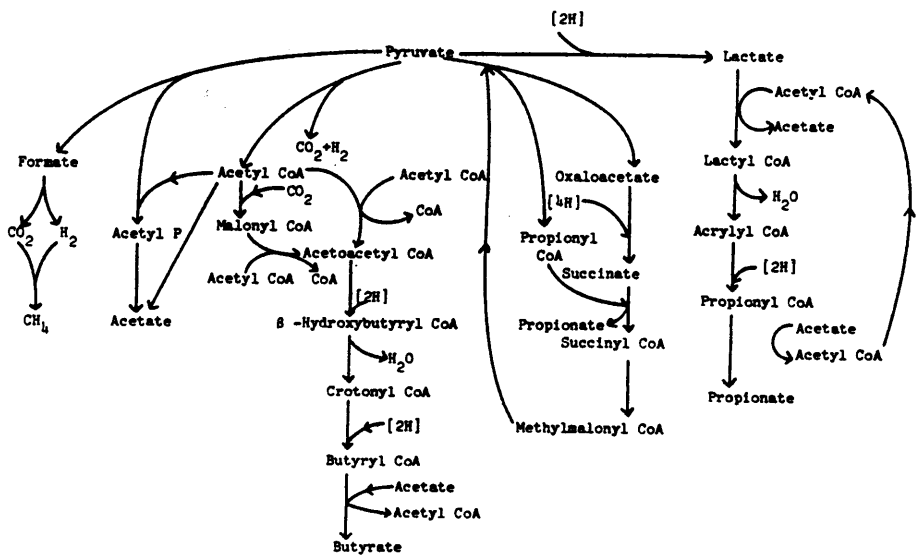

Figure 1: General Scheme of Rumen Fermentation

Nitrogen Metabolism in the Rumen

The relationships between fermentation of organic matter and nitrogen use in the rumen are shown in Figure 2. Energy released during fermentation of organic matter is partitioned between heat of fermentation (relatively constant), microbial maintenance costs, VFA production and synthesis of micobial cells (Russell and Hespell, 1981). Maintenance costs are reduced as the rate of cell passage from the rumen increases. Increased washout of bacteria selects for faster growing species and a younger, more efficient bacterial population (Van Soest, 1982). Increased liquid turnover also reduces nutrient recycling in the rumen. Theoretically, microbial cell yield and escape of feed protein should increase as well (Orskov, 1982). High quality fiber is important as a stimulus for liquid turnover and as an energy source to support high rates of microbial growth and animal production. Attachment of bacteria to feed particles serves as a harvesting device (Orskov, 1982).

Feed proteins and other nitrogenous compounds such as nucleic acids undergo varying degrees of digestion in the rumen. Ammonia, amino acids and peptides are released and re-assimilated into microbial proteins and nucleic acids. Total degradation is a function of rate of hydrolysis vs the rate of outflow of the protein from the rumen (Orskov,

1982). Rate of hydrolysis depends on the physical and chemical accessability of the protein to bacterial proteases. The outflow rate of protein is affected by its physical form and density and the rate of liquid and solid phase turnover (Orskov, 1982).

Mixed rumen bacteria have a high proteolytic activity associated with the glycocalyx or cell coat (Kopecny and Wallace, 1982). Peptidases and proteases are also present on the inner face of the cell membrane. The latter enzymes probably degrade small proteins and peptides released by proteases in the cell coat. Cytosolic proteases are also present. The external proteases display a wide range of pH tolerance (Hazelwood et al., 1981).

Although the proteases of certain species of rumen bacteria such as Bacteroides Ruminicola are subject to substrate or end product inhibition (Blackburn, 1968; Hazelwood et al., 1981) the proteolytic activity of the total microbial population is always high (Russell and Hespell, 1981). Most of the proteolytic species identified are gram negative. Protozoa displayed relatively low proteolytic activity on azocasein but have a high rate of endogenous activity which is consistent with their engulfment and digestion of whole bacteria (Forsberg et al., 1984).

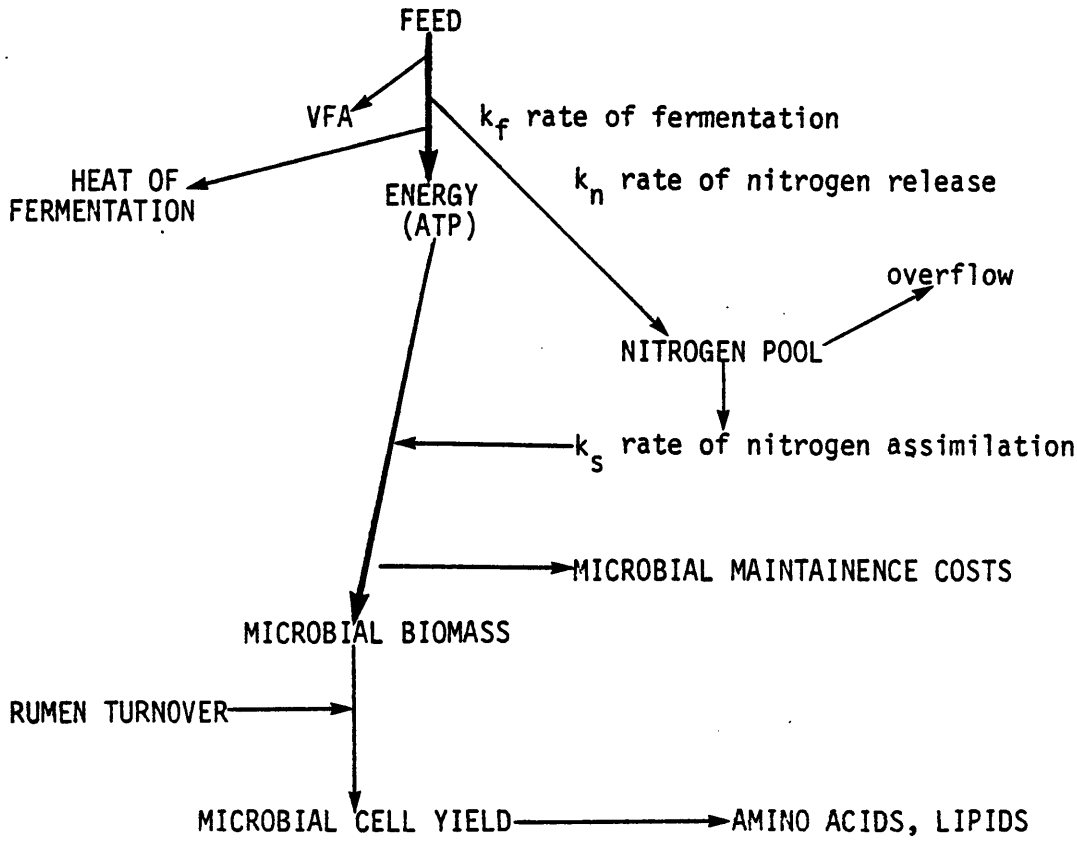

Figure 2: Energy and Nitrogen in the Rumen

Certain proteins are resistant to ruminal hydrolysis due to denaturation by heat or chemicals or by virtue of their natural structure. Disulphide bonds and other crosslinking between polypeptide chains decreases susceptibility to hydrolysis in the rumen (Mangan, 1972; Wallace, 1983). Formaldehyde treatment reduced rumen degradability of soybean meal by 36% without impairing its digestibility in rats (Rooke et al., 1982). Performic acid treatment increased degradation of some proteins (Wallace, 1983). Excessive heating or chemical treatment may render proteins undigestible. Generally proteins less soluble in rumen fluid are more slowly degraded in the rumen. However, while casein and ovalbumin have high solubilities, the latter is very slowly degraded in the rumen (Mangan, 1972). Feed nitrogen insoluble in acid detergent (ADF-N) is essentially unavailable. Protein insoluble in neutral detergent but soluble in acid detergent may comprise the slowly degraded fraction of feed protein (Muscato et al., 1983).

Incorporation of ammonia, amino acids and peptides by rumen bacteria links the energy yielding process of fermentation with the synthesis of the host animal' protein supply. Ammonia is the preferred nitrogen source for the many of the rumen species. This includes several proteolytic species in which peptide and amino acid transport has been demonstrated

(Hazelwood et al., 1981). Several important cellulolytic and methanogenic species have an absolute requirement for ammonia (Chalupa, 1972). However, when diets of natural protein are fed, 50-60% of microbial protein may arise directly from amino acids and peptides (Armstrong and Weekes, 1983). Addition of natural protein to protein free diets markedly increases microbial cell yields (Maeng et al., 1976). Bacterial counts were stimulated to a much greater degree when protein vs NPN was added to basal (9.4% CP) rations of lactating cows (Teather et al., 1980). The greatest increase in bacterial counts was in species known to require branched chain VFA (BCVFA), derived from branched chain amino acids (ibid). Similar results were obtained in vitro when C-4 and C-5 BCVFA were added to rumen fluid from hay fed cows (Russell and Sniffen, 1983). Satisfaction of microbial N requirements may explain why protein supplementation often improves energy utilization (Tyrrell, 1983).

Ammonia arising from rumen hydrolysis of amino acids and urea diffuses across the rumen wall into the portal blood. The rate of diffusion increases with increasing ammonia concentration and with rumen pH (Leng and Nolan, 1984). Research (Boilla and Milligan, 1980) has shown that rumen epithelial cells are capable of incorporating ammonia into amino acids. The potential physiological significance of this finding is unknown.

Blood ammonia is converted to urea which re-enters the rumen from the blood or the saliva (Kennedy and Milligan, 1980). Re-entry rate increases with blood urea concentration and rate of carbohydrate fermentation and is inhibited by increasing rumen ammonia (Kennedy and Milligan, 1980; Armstrong and Weekes, 1983). Bacteria attached to the rumen wall and exhibiting high ureolytic activity appear to be involved in the transfer of urea from blood to rumen (Wallace et al., 1979).

Optimal ammonia concentrations for rumen microbial protein synthesis have yet to be defined. Ammonia utilization requires 3 to 4 ATP per mole of NH_4, and the lack of either ammonia or energy results in the uncoupling of VFA production from microbial growth and loss of efficiency (Russell and Hespell, 1981). This may explain why continuous cultures (Satter and Slyter, 1974) have given lower optimal ammonia concentrations for microbial growth than have in vivo studies (Wallace, 1979). The former study found that 1.0 to 1.2 mM ammonia concentrations was the minimum required and levels of 2.0 to 5.0 mM were cited as optimal for microbial protein synthesis. Wallace (1979) using sheep fed barley or barley + 3% urea found that 12-15 mM ammonia was needed to support maximum microbial growth. Rate of degradation of barley was increased 90% when barley+urea was fed, and the

rate of enzyme catalyzed incorporation of ammonia into alanine was increased.

Ammonia utilization is related to the energy supply within the microbial cells (Van Soest, 1982). Activities of the major ammonia fixing enzymes (glutamate synthase, glutamate dehydrogenases) are high, suggesting that activity of these enzymes is not the rate limiting step in ammonia utilization (Chalupa, 1972; Wallace, 1979). The effects of many other factors, such as intake, rate of fermentation and ammonia release, on microbial protein yield are poorly understood.

There are wide variations in microbial cell yields measured in vivo. The main determinants of yield are rate of fermentation and liquid turnover rate (Russell and Hespell, 1981). Variation arises due to differences in experimental conditions, i.e. the comparison of lactating cows, sheep and in vitro systems, and errors inherent in liquid and solid phase markers (Whitelaw et al., 1983). Teather et al. (1983) reported a negative correlation between levels of protozoal and bacterial protein in rumen fluid with considerable variation between animals. These authors concluded that microbial protein values should be corrected for the bacteria/protozoa ratio. The data of Merry and McAllen (1983) shows that marker systems will underestimate microbial protein yield because bacteria attached to solid phases

of digesta have a lower content of marker compounds than do the liquid phase bacteria used in most studies.

For cows, values range from 18 to 40 g of microbial N synthesized per kilogram of organic matter (OGM) apparently digested in the rumen (Orskov, 1982). Greatest yields occur with high quality roughages supplemented with moderate amounts of concentrate (Van Soest, 1982; Hogan, 1975). In early lactation, when intake is high and rumen digestibility of dry matter depressed, fiber quality and rate of fermentation are important in determining microbial yield.

POSTRUMINAL DIGESTION AND ABSORPTION OF PROTEIN

Protein entering the intestine of the cow is a mixture of microbial and undegraded feed protein. Microbial protein may contribute 80-85% of the total intestinal supply in animals fed conventional diets (Armstrong and Weekes, 1983). Nitrogen constitutes 5 to 12% of microbial biomass and 75-80% of this N is true protein (Orskov, 1982). Storm and Orskov (1982) reported true digestibility of microbial protein of 0.85. The biological value of microbial protein is high, although amino acid availability may vary with protein source and diet (Burris et al., 1974). Salter and Smith (1984) infused N-15 labeled rumen bacterial protein into the duodenum of steers and found a true digestibility of 0.74.

Microbial nucleic acids appear to have a low biological value (Hale, 1979).

Mathers et al. (1982) tested fish meal, sunflower meal (SFM) and their residues recovered after 6 h of in the rumen against casein/methionine as protein sources for growing rats. Rumen incubation decreased the biological value of SFM but not of fish meal. Because digestibility was not affected by incubation in the rumen, the authors concluded that the pattern of absorbed amino acids was poorer for the SFM residue than for intact SFM. Therefore the quality of protein entering the intestine of cows may vary, depending on the source of protein and roughage fed and rumen fermentation patterns.

Secretion and properties of digestive enzymes of the ruminant are similar to those of monogastrics. Digestion and absorption of protein appears to occur more distal to the true stomach of the ruminant due to slower neutralization of digesta (Johns and Bergen, 1973). Work in vivo and in vitro has shown efficient absorption of essential amino acids (EAA), with methionine being most efficiently absorbed and least inhibited by other amino acids (Armstrong and Weekes, 1983; Moe, 1984). Tagari and Bergman (1978) used cannulated sheep fed high or medium protein diets to study amino acid absorption. Total amino acids, as a percentage of those

fed, were lower when measured at the duodenum, higher at the jejunum, and declined steadily toward the terminal illeum. Duodenal amino acid N and percent absorbed were greater for the HP diet. Portal appearance of amino acids was 30-80% of that disappearing from the intestine. Koeln and Webb (1982) reported that large quantities of amino acids may appear in the portal blood in the form of short peptides. They found that peptide fractions accounted for the greatest net splanchnic output of amino acids in fed calves. Sumner et al. (1979) found that duodenal infusions of methionine increased both plasma cystine and erythrocyte glutathione (GSH) concentrations in sheep. Baumrucker and Pocius (1978) reported possible extraction of blood GSH by the mammary gland of dairy cows. Metabolism of glutamate accounts for its net uptake by the gut tissue of ruminants (Lindsay, 1982). Digestion, absorption and gut metabolism of amino acids by ruminants requires further study before rations can be formulated to meet amino acid requirements.

INTERMEDIARY AMINO ACID METABOLISM AND REQUIREMENTS

Nutrients absorbed from gut enter the portal vein which passes through the liver. The ruminant liver extracts propionate, butyrate, lactate, free fatty acids and amino acids which serve as precursors of glucose, ketones, triglycerides

and proteins (Baird, 1982). The liver exerts control over the blood levels of the various metabolites and synthesizes serum proteins and urea. All free amino acids except glutamate, citrulline and ornithine undergo net extraction by the liver (Bergman and Heitmann, 1978). Fluxes in peptide and erythrocyte amino acid pools also occur (Koeln and Webb, 1982).

Ammonia, Urea and Nitrogen Cycling

Ammonia is toxic and must be converted to urea by the liver at a cost of 4 ATP per mole (Visek, 1984). Activities of enzymes of the urea cycle are increased by high protein diets and in particular by high dietary alanine, methionine and lysine. Glucagon and corticosteroids are also involved (Visek, 1984). As in monogastric animals, arginine, ornithine and citrulline play an important role in the urea cycle. Excess ammonia may in some cases be converted to ornithine by the ruminant liver (Chalupa, 1972). If the balance between ammonia(NH_4) production and utilization in the rumen is upset, blood ammonia levels can rise. High blood ammonia results in an insulin resistant hyperglycemia in rats, and seems to impair gluconeogenesis in ruminants (Visek, 1984). Therefore high protein or urea diets could disturb the balance of glucose production/utilization, which is especially

delicate in the lactating cow. Non-lactating cows have the capacity to extract up to 1.8 mmol NH_4/min/kg liver (Symonds et al., 1981). Intoxication symptoms appear when carotid NH_4 exceeds 0.8 mmol and portal NH_4 1.0 mmol/liter but rate of infusion had more effect than total NH_4 infused (Symonds et al. 1981).

Bruckental et al. (1981) noted a reduction in the irreversible loss of urea in cows when nitrogen demand was high i.e., during early lactation. Activity of argininosuccinate synthetase, thought to be the rate limiting enzyme in the urea cycle, was markedly reduced in the livers of lactating as compared to virgin rats (Naismith et al., 1981).

Role of Amino Acids in Glucose Homeostasis

The role of amino acids in ruminant gluconeogenesis is poorly understood. Several studies (Lindsay, 1982; Bruckental et al., 1981; Macrae and Egan, 1980; Heitmann et al., 1979) suggest a glucose sparing effect of amino acids, with little direct incorporation of amino acid carbon into glucose. Whenever it has been measured in ruminants, the rate of oxidation of labeled amino acids to CO_2 has exceeded their incorporation into glucose (Macrae and Egan 1980). However, tracer studies of glucose synthesis in ruminants have often failed to account for net glucose synthesis with-

out large contributions from amino acids (Armentano et al., 1982; Bergman and Heitmann, 1978). Alanine and glutamine appear most important in gluconeogenesis in ruminant and monogastric species, acting as shuttles for nitrogen and carbon between muscle and liver (Lindsay, 1982).

The carbon of alanine and glutamine released from muscle is derived from glucose and amino acids respectively (Goldberg and Chang, 1980). Glutamine may be converted to alanine by the gut tissues. In non-ruminants, release of amino acids from muscle is linked to the oxidation of branched chain amino acids (BCAA) (Snell, 1981; Goldberg and Chang, 1980). Leucine is uniquely able to stimulate protein synthesis in non-ruminant muscle (ibid), but this has not been shown in ruminants. The catabolism of BCAA by ruminant muscle is less than in non-ruminants (Lindsay, 1982; Coward and Buttery, 1982). Omission of valine from intravenous infusions of amino acids increased blood urea and urinary N losses in sheep (Mesbah, 1984). Mammary tissue of cows oxidizes BCAA, possibly as an energy source for milk synthesis (Mepham, 1982).

The studies of Black and Kleiber (1957) and Egan and Black (1968) showed extensive conversion of glutamic acid to glucose, of glucose to milk proteins and of acetate into glutamic acid in lactating cows. Clearly, the intermediary

metabolism of amino acids by the lactating cow is complex. A better understanding of the role of amino acids in ruminant metabolism is required in order to define the amino acid requirements for lactation.

Amino Acid Requirements for Milk Production

Smith (1980) suggested the pattern of amino acids presented to the mammary gland at a given time is a more meaningful concept than absolute amino acid requirements. This enforces the idea of regulation of blood amino acid balance. Mepham (1982) assigned amino acids to classes based on their extraction and metabolism by the lactating mammary gland. Group 1 are those essential amino acids (EAA) with a high rate of extraction and transfer to milk. Group 2 are EAA taken up in excess of their occurrence in milk and used for energy or synthesis of other milk componeants. Group 3 are the non-EAA not extracted in sufficient quantities to account for their appearance in milk, and therefore synthesized within the gland from group 2 amino acids or other sources. Candidates for group 1 are lysine, especially for corn based diets, methionine, tryptophan, phenylalanine and possibly histidine and tyrosine (Clark et al., 1977; Polan, 1978). Milk production of cows increased when tyrosine was added to rations thought to be low in available tyrosine (Rae et al., 1984).

Group 2 may include the branched chain amino acids (Mepham, 1982), as well as arginine, which is converted to proline by the lactating mammary gland (Mepham, 1982). Milk production responses to the addition of branched chain VFA to dairy rations suggests that supply of BCAA may be involved. The importance of a balanced supply of non-essential amino acids (NEAA) for milk production in ruminants has not been studied extensively, but may be related to the response to casein infusions. Serum albumin concentration was correlated to milk production of rats fed diets of varying protein quality (Grimbal, 1980) and may have value as an indicator of protein status in dairy cows.

Protein Reserves

Dairy cattle have reserves of labile protein (Botts et al., 1979) which may supply key amino acids during early lactation. Glucocorticoids stimulate proteolysis in muscle (Guyton, 1982) and are elevated during the early post-partum period in cows (Tucker, 1979). Leucine stimulates protein synthesis in non-ruminants (Goldberg and Chang, 1980) and could be important in the mobilization of protein reserves in the lactating cow.

Paquay et al. (1972) reported that cattle had a potential reserve equal to 20% of total body protein. Reserves con-

sist of short term labile sources such as serum proteins, liver and gut proteins, and long term stores in skin and muscle which are mobilized during extended protein starvation (Swick and Benevenga, 1976). Botts et al. (1980) depleted nitrogen stores of cows from 2-3 weeks post-partum until 8 or 16 weeks post-partum by feeding a 9% crude protein ration. Nitrogen balance during repletion indicated reserves of 25-27% of total body protein. Smith et al. (1980) found extensive mobilization of muscle lipids even in well fed lactating ewes along with losses of nitrogen. RNA:DNA ratios of tissue samples suggested decreased protein synthetic activity during early lactation. The authors cited other research showing a 25% reduction in muscle fibril diameter during early lactation in sheep. Trigg et al. (1980) measured energy and nitrogen balance in well fed cows and their underfed twins during early lactation. They found that both groups catabolized 85-95 grams of tissue protein per day. These data support the conclusion of Reid (1964) that cows could mobilize up to 0.36 kg of protein per day during lactation. Although the energetic value of this protein is small, its contribution of essential amino acids could be important during early lactation.

RUMINANT ADIPOSE TISSUE METABOLISM DURING LACTATION

Fatty Acid Synthesis

Metabolism in ruminant adipose tissue differs from non-ruminants in several aspects of fatty acid synthesis and responses to metabolic hormones. Energy flux through adipose tissue in fed, lactating cows may equal 32% of metabolizable energy intake (Emery,1979) illustrating the possible impact of this tissue on efficiency.

Adipose tissue is the major site of fatty acid synthesis in ruminants while the liver is the primary site in many non-rumininants (Emery, 1980). The role of the liver in metabolism of free fatty acids and formation of lipoproteins becomes critical in lactating cows during fat mobilization (Reid et al., 1979). As in other species, most free fatty acids taken up by ruminant adipose tissue are derived from triglycerides in plasma lipoproteins via the action of lipoprotein lipase (Vernon, 1980).

In ruminants, the main precursor for de novo synthesis of fatty acids is acetate, not glucose and reducing equivalents are generated by both the pentose pathway with partial oxidation of glucose (Baldwin et al., 1973) and the isocitrate dehydrogenase pathway (Bauman, 1976). This is consistent with the ruminant's need to conserve glucose. Low activities of ATP-citrate lyase and NADP-malate dehydrogenase pre-

vent incorporation of glucose carbon into fatty acids (Bauman, 1976) and appear to force extra-mitochondrial citrate through the isocitrate dehydrogenase pathway. However there is evidence for a functional ATP citrate lyase:NADP-malate dehydrogenase pathway in bovine adipose tissue (Smith and Prior, 1981) associated with fatty acid synthesis from lactate. Prior and Jacobson (1979) demonstrated lactate incorporation into fatty acids, stimulation of lipogenesis from acetate by lactate and inhibition of lactate incorporation by acetate in ruminant adipose tissue. Involvement of lactate in generation of reducing equivalents and effects on citrate lyase activity were also reported (Prior and Scott, 1980). Thus lactate appears to be an important intermediate in lipid metabolism of ruminants. Insulin appears neccesary for lipogenesis from acetate, but its influence on rates of lipogenesis in vivo is less than in non-ruminants (Smith et al., 1981).

Lipolysis and Changes During Lactation

Lipolysis and release of free fatty acids into the blood occurs when the appropriate hormonal or neural stimulus increases the activity of hormone sensitive lipase in the adipocyte (Vernon, 1981). Hormone sensitive lipase is transformed to its active form by a cyclic AMP dependent protein

kinase (Vernon, 1980). Most lypolytic hormones are thought to activate adenylate cyclase while inhibiting phosphodiesterase, thus increaseing the concentration of c-AMP in the cytosol of the target cell (Bauman, 1976). Epinephrine stimulates lipolysis in isolated bovine adipocytes (Yang and Baldwin, 1973) although its role in lipolysis during lactation is unclear. Data from rats suggests a minor role for epinephrine during lactation in that species (Aitchison et al., 1982).

Growth hormone increases lipolysis in lactating dairy cows (Peel et al., 1980), perhaps by antagonizing the effects of insulin in adipose tissue (Vernon, 1980; Kahn et al., 1978).

Butyrate and beta-hydroxy butyrate at physiological concentrations inhibited basal and epinephrine stimulated lipolysis in bovine adipose tissue, apparently by inhibiting adenylate cyclase (Metz and Van de Bergh, 1972; Metz et al., 1974).

In ruminants and other species, fats stored during pregnancy are mobilized to supply energy during lactation (Vernon, 1980). In sheep, lipoprotein lipase activity, rate of fatty acid and acylglycerol synthesis, number of high affinity insulin receptors and adipocyte volume all were decreased during early lactation (Vernon et al.1981). Lipo-

lytic activity of isolated adipocytes from sheep increased five fold during early lactation and was associated with increased plasma free fatty acids (Pike and Roberts, 1980a). Incorporation of labeled acetate was markedly decreased during this period (Pike and Roberts, 1980b). Lipolytic activity of adipocytes from lactating cows was greater than from dry cows (Yang and Baldwin, 1973). Lipolysis during lactation in cows is likely controlled by the growth hormone/insulin ratio which is highest during early lactation and decreases as milk production declines (Aiello et al., 1981; Vasilitos and Wangness, 1980). In non-ruminants prolactin increases the activity of lipoprotein lipase in mammary gland while decreasing it in adipose tissue (Collier et al., 1984). In rats prolactin and progesterone prevent the increases in adipose insulin receptors and lipogenic rates which occur in late lactation (Flint et al., 1984).

Possible relation of protein status to serum albumin levels during lactation (Grimbal, 1980) is interesting in view of evidence that the ratio of FFA to serum albumin limits lipolysis in lactating cows (Bines and Hart, 1980). Adipose tissue is an important energy source for lactating cows and further information is needed as to the nutritional and metabolic factors controlling fat deposition and mobilization in dairy cows.

BODY CONDITION IN DAIRY CATTLE

Body Condition as Related to Fat Metabolism and Health

Subcutaneous fat deposition in dairy cattle has been estimated by a subjective body condition scoring system, scaled 1 (thin) to 5 (fat), based on the amount of tissue cover over the spinal processes and tail head (Wildman et al.1982). Body condition scores for beef and dairy cattle derived from similar British scoring systems were shown to be highly correlated to actual fat content of the carcass (Wright and Russel, 1984). "Adequate" body condition at calving is important in high producing cows because of the extensive fat mobilization which occurs during early lactation (Bauman and Curry, 1980). However, overconditioned cows are subject to a greater incidence of metabolic and reproductive disorders referred to as the fat cow syndrome (Morrow, 1976). Fatty infiltration of the liver is characteristic of fat cow syndrome (Morrow, 1976) although it also occurs in cows which are ketotic (Grohn et al., 1983), underfed or high producing cows in early lactation (Reid et al., 1979), but apparently to a lesser degree. Reid et al. (1979) found that severity of fatty liver in cows was directly related to the degree of fat mobilization. These authors also reported significantly lower blood glucose and serum albumin and higher free fatty acids during the first 8

wk of lactation in the severe vs mild fatty liver groups. Furthermore cows in the severe fatty liver group had a history of fertility problems, evidenced by longer calving intervals and more services per conception, suggesting a link between liver function and fertility. Energy balance during days 1-20 of lactation is related to the onset of ovarian activity in cows (Butler et al., 1981).

Effect of Body Condition on Production and Intake

Cows overconditioned by overfeeding during the dry period have an increased incidence of postpartum health disorders and reproductive problems (Fronk et al., 1980). Overconditioning cows from day 120 of lactation then feeding normally during the dry period had no affect on reproductive traits or milk production in dairy cows (Perkins et al., 1983). However the condition score of control cows (4.0) was high, although statistically lower than fat cows (4.5 and 4.7). Boisclair et al. (1984) found that overfeeding during late lactation and/or the dry period had no detrimental effects on production or health. Cows had been overfed for about the last 90 d of lactation.

Body condition at calving can affect milk production and feed intake of lactating cows and ewes. Mature cows tend to lose more body condition during early lactation than cows in

their 2nd or 3rd lactation (Kaim et al., 1983). An extensive field study (Wildman et al., 1982) found that cows whose body condition increased significantly during lactation were less efficient producers and had a greater number of days open. The more efficient high producing cows showed no increase in body condition during lactation.

Yadava et al. (1973,1974) fed Jersey and Holstein cows for four months prepartum to attain high, medium or low condition scores at calving. Jerseys calving in medium condition produced more milk, FCM and protein than those calving in high or low condition. Production was highest in Holsteins calving in high body condition. In Holsteins, DM intake was lowest in the medium condition group while among Jerseys the fattest cows had the lowest intake. Digestibility was unaffected by body condition. Garnsworthy and Topps (1982a,b) reported lower intake, greater loss of bodyweight and condition , and higher plasma FFA in cows with higher condition scores at calving. Cowen et al. (1982) found by comparative slaughter that ewes fatter at lambing lost more body fat than thin counterparts. Boisclair et al. (1984) reported that fatter cows produced more milk than thinner cows while FCM, milk fat, plasma FFA and glucose and intake during early lactation were not affected by treatments.

Bines et al. (1969), Bines and Morant (1983) showed that cows ate 24% more feed when thin than when fat. Based on rumen and blood analysis they proposed that the rate of fatty acid synthesis was greater in the adipose tissue of thin cows. Thus free fatty acids would be cleared more quickly from the plasma and have less inhibitory effect on feeding in thin cows. Plasma FFA were higher in fat cows before feeding but decreased to levels similar to thin cows after feeding. When cows were thin, blood glucose fell more rapidly while propionate rose faster after feeding. This may indicate higher postprandial insulin levels in thin cows. The higher intake of thin cows was due to higher intake of concentrates (3-4 kg/day) which has been shown to result in higher postprandial serum insulin in cows (Jenny et al., 1973).

Degree of fatness affects intake, production and health of dairy cows but the metabolic basis for these effects as well as the nutritional factors affecting utilization of body fat during lactation are not well understood.

PROTEIN REQUIRMENTS DURING FAT MOBILIZATION

Postruminal infusion of casein has increased milk and milk protein production in cows (Clark et al., 1977) and goats (Ranawana and Kellaway, 1977; Gow et al., 1979). However, the beneficial effect of casein has usually been found in high producing animals near peak lactation. The greatest increases; 38% in milk and 25% in protein production; have been observed when cows receiving the infusion were in a state of negative energy balance. Furthermore, casein infusion increased the extent of negative energy balance and the concentration of FFA in plasma (Orskov et al., 1977). Evidence suggests that labile protein reserves of dairy cows are small relative to fat reserves (Orskov et al., 1977). Therefore when cows are in negative energy balance and thus mobilizing fatty acids, extra protein would be needed to balance the supply of nutrients presented to the mammary gland (Orskov, 1982). In well fed cows the response to postruminal casein is diminished, especially after peak lactation (Peel et al., 1982). In these cases more of the infused nitrogen is excreted in the urine, indicating poorer utilization (Ranawana and Kellaway, 1977).

Several studies have sought to establish the mechanism behind the response to postruminal casein infusions and the possible stimulation of lipolysis by increased protein sup-

ply. Clark et al. (1977) noted a small increase in glucose entry rate and a small decrease in glucose oxidized to CO_2 in response to postruminal casein. However the changes in glucose kinetics were not of sufficient magnitude to account for the increased milk and protein production observed. No significant change in pool size or irreversible loss of glucose was found in response to postruminal infusions of casein or glucose in goats at mid-lactation (Ranawana and Kellaway, 1977). The authors concluded that milk production was not limited by glucose in this case (goats at mid-lactation) and that infused casein did not enhance gluconeogenesis. However, Konig et al. (1984) using cows in early lactation found that casein infused into the abomasum increased, in addition to milk yield, the mean flux rates of glucose, palmitate and acetate, suggesting that protein status affected metabolism of these nutrients. Unlike Orskov et al.,these workers did not impose negative energy balance on the cows by limiting intake, but the animals were in energy deficit. The protein content of the basal ration was low, 11% crude protein. Gill and Beaver (1982) reported that when the postruminal protein supply of steers was increased 80 g per day by supplementing ryegrass silage diets with fishmeal, no change occured in glucose irreversible loss, or conversion of propionate to glucose.

Daily injections of growth hormone (GH) increase milk production and efficiency of nutrient utilization in dairy cows (Peel et al., 1982). In one case plasma GH was increased in goats infused postruminally with casein (Oldham et al., 1977) while in another study it was not (Gow et al., 1979). Plasma growth hormone was increased in Holstein heifers in mid-lactation fed formaldehyde treated casein or soybean meal as compared to untreated proteins (Oldham et al., 1982). Insulin, prolactin and thyroxine were not affected by treatment. However no increase in milk yield was observed in response to feeding protected proteins.

Milk production of cows in mid-lactation increased in response to both postruminal casein and injections of growth hormone (Peel et al.1982). Growth hormone injections significantly increased milk production without increasing feed intake. Casein infusion did not increase plasma growth hormone concentration. None of the above studies have duplicated the conditions used by Orskov et al. (1977), making it difficult to draw conclusions.

Postruminal casein may supply certain limiting amino acids for milk production (Clark et al., 1977). Casein infusions increase plasma concentrations of essential amino acids, especially the branch chain amino acids (Gow et al., 1979). Effect of infusion of branch chain amino acids on milk production has not been investigated.

Plasma non-essential amino acids increase in response to increased dietary energy or glucose infusion in goats (Ranawana and Kellaway, 1977). The balance between essential and non-essential amino acids absorbed from the intestine may determine the milk production response to postruminal infusions. Attempts to mimic the effects of casein with mixtures of essential amino acids have failed (Gow et al., 1979). Nitrogen balance in men consuming casein was greater than in men consuming a mixture of essential amino acids patterned after casein with glutamate and citrate added as precursors for non-essential amino acids (Anderson et al., 1969). Postruminal infusion of branch chain amino acids and of amino acid mixtures patterned after the non-essential amino acids of casein should be tested for their effects on milk production. Infusion of certain essential amino acids along with a complement of NEAA may enhance production.

While progress has been made in our understanding of protein nutrition of dairy cattle, key information concerning the control of postruminal protein supply and quality, and the metabolism of absorbed amino acids is required to implement more effective systems of ration formulation. Greater understanding of ruminant amino acid metabolism and its relation to lipid and carbohydrate metabolism is needed in order to determine the optimum balance of amino acids required for efficient milk production.

OBJECTIVES

1. To test the response of fat and thin dairy cows to rations high or low in rumen degradable nitrogen during early lactation.
2. To compare milk production, dry matter intake and bodyweight changes of cows fed high or low energy rations during late lactation.
3. To compare soybean meal and dried brewers grains as protein sources for high producing cows fed silage based rations during early lactation.
4. To test the effects of body condition and protein source on plasma growth hormone and insulin and the response of these hormones to an intravenous infusion of arginine.

EXPERIMENTAL PROCEDURES

SELECTION, FEEDING AND HANDLING OF ANIMALS

Forty two multiparous Holstein cows, confirmed pregnant and averaging 190 d in lactation, were selected from the Virginia Tech research herd. DHIA records were reviewed and low producing cows disqualified. Cows were scored for body condition using the Virginia Tech system where 1=very thin and 5=obese (Wildman et al., 1981). Initial scores, those assigned at drying off and at 6 weeks postpartum were the concensus of the same three individuals. Initially the cows were also scored for bone structure; 1=fine, 3=coarse. Cows were paired by body condition and projected 305 day mature equivalent milk production (ME), and randomly assigned to either a high or low energy total mixed ration for the remainder of their lactation. Composition of the rations are found in table 1. Cows were housed in free stalls, fed at 700 and 1430 h (30% and 70%) in Calan doors and milked at 0100 and 1300 h. Cows were dried off to allow for at least a 60 d dry period. Milk production was recorded daily, milk composition analyzed monthly, and feed samples were analyzed weekly for dry matter, acid detergent fiber and crude protein. Appropriate adjustments were made in the ration based on analysis. Cows were weighed bi-weekly and feed intake

measured four consecutive days in five separate weeks for each cow.

During the dry period all cows were fed medium/good quality orchardgrass hay ad libitum and had access to a small pasture. Fat cows were given an additional 13 kg/d of alfalfa haylage:high moisture corn to insure maintenance of body condition. Beginning 2-3 weeks prepartum the cows were gradually adapted to milking ration S, which contained soybean meal (SBM). At two weeks post-partum, half the cows in each body condition group were randomly assigned to milking ration B, which contained dried brewers grains (DBG). This resulted in a 2x2 factorial arrangement of treatments. Composition of rations S and B are given in Table 2. Total mixed rations were fed throughout the experiment. Previous work in this laboratory showed that DBG were more resistant to ruminal degradation than SBM. The flow of non-ammonia nitrogen to the intestine was greater for cows fed DBG than those fed SBM as a protein supplement(Armentano et al.1984). Dried brewers grains are a better source of "bypass protein" for ruminants than are more readily degraded proteins such as soybean meal (Merchen et al., 1979).

Cows were fed their assigned ration through week 15 of lactation according to the same daily schedule as during the previous lactation. Thirteen of the cows were housed in a

TABLE 1

Composition of Rations Fed During Late Lactation

High Energy Ration	DM[1] kg	ADF[2] kg	CP[3] kg	NE[4] Mcal
Silage Mixture[2]	40.1	12.4	3.9	58.4
High Moisture Corn	38.1	1.7	3.4	78.1
Protein Supplement	21.8	2.0	7.7	34.8
	100.0	16.1	15.0	171.3
Low Energy Ration				
Silage Mixture	79.9	24.8	7.8	116.1
Protein Supplement	20.1	1.8	7.1	32.0
	100.0	26.6	14.9	148.1

Silage mixture was 2:1 corn silage:alfalfa haylage.
Protein supplement contained vitamins and minerals.
[1] dry matter
[2] acid detergent fiber
[3] crude protein(N x 6.25)
[4] estimated net energy for lactation

TABLE 2

Composition of Rations Fed During Early Lactation

Feed (%DM)	Ration S	Ration B
Alfalfa Haylage	20.5	20.5
Corn Silage	34.5	34.5
Soybean Meal	10.0	--
Dried Brewers Grains	--	19.0
High Moisture Corn	29.0	20.0
Vitamin-Mineral Premix	6.3	6.3
Total	100.0	100.0

tie stall barn, the remainder in freestalls with access to Calan doors for feeding. Rations were mixed in a portable feed cart. Free choice minerals and fresh water were available to the cows. The total ration was sampled weekly, a sample submitted for immediate analysis and another frozen at -20 C for later analysis. Ingredients were sampled every 2-3 weeks and whenever a new batch of feed or silage was offered. Appropriate adjustments of the rations were made based on dry matter and chemical analysis of the rations.

Milk production was recorded twice daily. Samples for milk fat and protein analysis were taken monthly by the DHIA supervisor. Feed intakes were measured for four consecutive days during weeks 3-15 of lactation with some extra measurements during weeks 1-2. Cows were weighed weekly from calving through week 15 of lactation. Body condition scores were assigned at week 6.

SAMPLING AND PRESERVATION OF BLOOD AND RUMEN FLUID

Rumen fluid was aspirated via stomach tube and blood was taken by tail vein/artery puncture approximately 2.5-3.5 hours after the afternoon feeding during weeks 3, 9 and 15 of lactation. Two 7 ml aliquots of strained rumen fluid were placed in plastic test tubes on ice, taken to the laboratory and frozen at -20 C. One aliquot was preserved with

25% orthophosphoric acid (1ml per 5ml rumen fluid) for ammonia analysis. The second aliquot was later analyzed for volatile fatty acids. Ten ml of blood was taken into an evacuated plastic tube containing benzamidine-EDTA to prevent coagulation and red cell metabolism, then placed on ice. At the laboratory, blood was centrifuged for 20 minutes at 3000 x g (Beckmann model J2-21) to separate plasma, which was frozen in plastic tubes at -20 C until analysis for urea.

ARGININE INFUSION

An arginine infusion was given to each cow at 6 and at 15 weeks of lactation. On the day of the infusion cows were moved from the freestalls to a sampling barn prior to their morning feeding(0600 h). Cows were then fitted with an indwelling jugular catheter (DelMed, Canton,MA). Following a brief rest period, 15 ml blood samples were taken at intervals of (-120,-90,-60,-30,-15 min) and placed in plastic tubes containing benzamidine-EDTA. Waste blood (5 ml) was removed from the catheter prior to each sample. After each sample was taken the catheter was flushed with sterile saline and filled with heparinized saline (100 units per ml in sterile saline). Within 2 min of the zero time sample a sterile aqueous solution of arginine hydrochloride, pH 7, (0.075 g arginine/kg bodyweight) was injected through the

catheter, which was then rinsed with saline. Samples were taken at 5,10,15,20,25,35,45,75 and 120 min from zero. Blood samples were placed on ice, transported to the laboratory, centrifuged at 3000 x g for 20 min and the plasma frozen in plastic tubes at -20 C until analysis for growth hormone and insulin.

LABORATORY ANALYSIS

Feeds

Feed samples were frozen at -20 C, except protein concentrates which were room temperature. Samples of rations S and B were composited at 4 wk intervals, dried at 50 C for 48 h, then ground to pass through a 1 mm screen in a Wiley mill. Duplicate samples of feeds were analyzed for nitrogen by the Kjeldahl procedure. Acid and neutral detergent fiber and acid detergent insoluble nitrogen were analyzed by the methods of Goering and Van Soest (1978) and Van Soest and Robertson (1981). Absolute dry matter was determined by drying 1 g of air equilibrated sample at 100 C in a forced air oven to a constant weight. Composite samples of dried brewers grains and soybean meal used in the experiment were analyzed in a similar manner. Analysis of the feedstuffs and rations from the Virginia Tech Forage Testing Laboratory were used to monitor ration composition during the study.

The rumen degradability of nitrogen and dry matter in rations S and B and soybean meal and dried brewers grains were determined by the in situ rumen bag method. Bag specifications were the same as Zerbini and Polan (1985). Samples of DBG, SBM or wet ground (6mm screen) samples of rations S and B (9-12 g) were placed in quadruplicate bags and tightly closed with plastic ties. A pair of bags for each feed were suspended in the rumen of each of two fistulated, lactating cows fed a corn silage/SBM based total mixed ration twice daily at 700 and 1430 hours. Pairs of bags were tied to a 400 g weight with nylon string, then attached by a second string to the rumen fistula. Bags were then pushed through the mat of fiberous digesta down into the liquid phase of the rumen contents. The bags were inserted 72, 48, 36, 24, 12, 6, and 2 h prior to removal, beginning at 2100 hours. Upon removal, the bags were rinsed in cold running tap water until squeezing released no more color into the rinse water. Bags were then opened and dried in a forced air oven at 100 C until a constant weight was obtained. The dried residues were ground to pass through a 1mm screen. Duplicate samples were analyzed for nitrogen and dry matter by the methods described above. Based on the composition and weight of the original samples, the percent disappearance of nitrogen and dry matter for the various incubation times was calculated for each feed and ration.

Degradability of dry matter and nitrogen were estimated by the equations of Orskov et al.(1979) where percent nitrogen or dry matter disappearance is related to incubation time as follows:

$p = a + b(1-e^{kt})$ equation I where;

(p) is the percentage of feed or ration nitrogen or dry matter degraded at time (t).

(a) is the readily solubilized fraction assumed to have an infinite rate of degradation in the rumen.

(k) is the rate constant for degradation of the fraction (b)

(b) is the fraction degraded at variable rates depending on rate of hydrolysis and rate of flow out of the rumen. A third fraction "c" , the residual after 72 hours incubation, is assumed undegradable and indigestable and is accounted for as follows;

Fraction of feed remaining in the rumen at any given time

$(t) + b\ e^{kt} + c$ therefore;

$(\text{fraction of feed remaining}) - c = b\ e^{kt}$

Taking the natural logarithm of both sides of the equation;

$\ln(\text{fraction feed remaining} - c) = \ln(b) - kt.$

This is graph of a straight line; $y = mx + b$.

If the in situ bag data is graphed accordingly (i.e. natural log of percent disappearance vs. time of incubation) then the slope of the resulting straight line is the (k) rate of degradation for fraction (b). The value of (b) in the original feed is equal to the y intercept. The value of (c) is already known, and that of (b) derived, so that (a) can be found by subtracting (b+c) from unity. Net degradability in vivo is then estimated using the value for fraction (b) and assumed values for outflow rate of the feed from the rumen;

$D = a + (bk)/(k+T)$, where (T) is outflow rate.

In this experiment the calculations were made using outflow rates of 5, 7 and 9 % per h (Orskov et al., 1983).

Analysis of Rumen Fluid and Blood

One ml of plasma was deproteinized by adding 9 ml of a 1:9 mixture of 10% sodium tungstate and 0.083 N sulphuric acid, and then filtering through Whatman 42 filter paper. Urea was determined on duplicate aliquots of filtrate using the colorimetric assay of Coulombe and Favreau (1963). The reagents were mixed just prior to use. Optical density was read at 540 nm on a Beckman model 35 spectrophotometer.

Rumen fluid was centrifuged for 15 min at 3000 x g and the supernatant filtered through a 125 um millipore filter. A 3 ml aliquot of filtrate was combined with 0.5 ml of 30uM isocaproic acid as internal standard. Concentrations of acetic, propionic, isobutyric, butyric, isovaleric and valeric acids were measured on a Bendix 2600 gas chromatograph. A 183 cm by 2 mm glass column packed with 10% SP-1200 1% H3PO4 liquid phase on 80/100 chromosorb WAW packing was used. The column was conditioned at 200 C for 48 h and determinations of acids made at 125 C. A standard solution of 51.18 acetic, 38.80 propionic, 6.3 isobutyric, 10.57 butyric, 6.38 isovaleric, 6.02 valeric um/ml acids was injected prior to every third unknown, in duplicate. The ratio of peak heights was used to calculate the concentration of each VFA in the unknowns.

Rumen ammonia was determined in duplicate samples of acid preserved filtrate using a modified procedure of Chancey and Marbach,(1962). Optical density was read at 660 nm.

RADIOIMMUNOASSAYS FOR INSULIN AND GROWTH HORMONE

Insulin and growth hormone were determined in plasma using a double antibody radioimmunoassay (Barnes et al., 1985) For growth hormone, standards were prepared using NIH-GH-B18 bGH. Anti-ovine growth hormone(NIAMDD-AoGH-1) was used as

first antibody (Eisenman and Chew, 1983). All samples were analyzed in triplicate and intra- and interassay coefficients of variation calculated from a pooled plasma sample were 21% and 26% respectively. Assay for plasma insulin used purified bovine insulin and anti-bovine insulin (Barnes et al., 1985). Samples were analyzed in triplicate with intra- and interassay variation calculated from a pooled plasma sample were 12.1% and 41%.

STATISTICAL ANALYSIS

Milk production, feed intake, bodyweight change, milk fat and protein, rumen VFA's, rumen ammonia and plasma urea were analyzed by analysis of variance (general linear model of SAS) with a split plot design. Main treatment effects (body condition and ration) were tested using the mean square for cow nested within body condition and ration(see appendix, model A). Orthogonal contrasts were used to test differences between combined treatment effects i.e. body condition x ration.

Body condition change, days open and services per conception were tested using a two factor randomized design(model B). Treatment effects were tested by the mean square error.

For the arginine challenge, basal and peak concentrations of insulin and growth hormone, time to peak and area under

the response curve were tested using model B. Data were also analyzed using a split plot design (model A), including all 15 values from each challenge. With this analysis, differences in the shape of the response curve are tested by the interaction term (treatment*time). For example, a significant (ration*time) interaction indicates that the shape of the response curve of the hormone in question to arginine was significantly different between ration groups.

Data from the in situ rumen bag trial (percent disappearance vs time) was analyzed using linear regression to establish the rate of degradation (k) of fraction (b) for nitrogen and dry matter in soybean meal, dried brewers grains and rations S and B.

RESULTS AND DISCUSSION

CONDITIONING PERIOD

Means for selected productive traits for the two groups of cows assigned to the high energy and low energy rations are given in table 3, showing the similarity between the two groups. Analytical description of the fattening and thinning rations fed are given in Table 4. The forage:concentrate ratios of the high and low energy rations were 40:60 and 80:20, respectively. Reported values for net energy of lactation were 1.71 and 1.51 mcal/kg dry matter, respectively. This is in contrast to the NRC recommendation of 1.62 mcal/kg for cows in late lactation and producing 18-20 kg of milk per day.

Performance traits for the 4 to 5 month conditioning period are shown in table 5. Milk production and dry matter intake were significantly higher in cows fed the high energy ration. Bodyweight change was positive in both groups and not significantly affected by treatment. While milk fat and milk protein percents were not significantly affected by ration energy level, cows fed the high energy ration showed a trend toward milk fat depression.

Cows fed the high energy ration consumed significantly more dry matter than cows fed the low energy ration. Often

TABLE 3

Pre-experimental Mean Productive Traits of Cows

Trait	Ration Energy			
	High	se	Low	se
Body Condition				
Thin = 1 Obese = 5	3.1	.4	3.1	.3
Bone Score				
Fine = 1 Coarse = 3	1.9	.1	1.9	.1
Bodyweight, kg	588	15	586	12
Age at Calving, months	37	3.1	38	3.3
Days in Milk	187	8.3	196	9.0
Daily Milk, kg	24	1.1	23	0.9
Mature Equivalent Milk[1], kg	8844	210	8851	171

[1] 305 day mature equivalent milk of cows prior to start of trial.

TABLE 4

Laboratory Analysis of Rations Fed in Late Lactation

	DM[2](%)	ADF[3](%)	CP[4](%)	NE[5](Mcal/kg)
High Energy	60.2	17.9	16.5	1.71
Low Energy	50.6	27.7	16.4	1.51

[1] analysis by Virginia Tech Forage Testing Lab
[2] percent dry matter
[3] acid detergent fiber, percent of dry matter
[4] crude protein(N x 6.25), percent of dry matter
[5] estimated net energy for lactation

TABLE 5

Performance Traits of Cows Fed High or Low Energy Rations During Late Lactation

Productive parameter	Ration		
	High	Low	Significance
Change in Body Condition Score	0.78	0.25	.01[1]
Milk Production kg/d	21.6	17.6	.001
Milk Fat %	3.4	3.7	--
	(.2)	(.2)	
Milk Protein %	3.4	3.3	--
	(.1)	(.1)	
Bodyweight Change kg/d	0.72	0.64	--
	(.1)	(.4)	
Dry Matter Intake kg/d	19.7	18.7	.05[2]
Change in ME Milk[3]kg	+200	-315	.01

[1] significant interaction of ration x starting date
[2] significant effect of starting date
[3] intial projected ME milk - final ME milk production

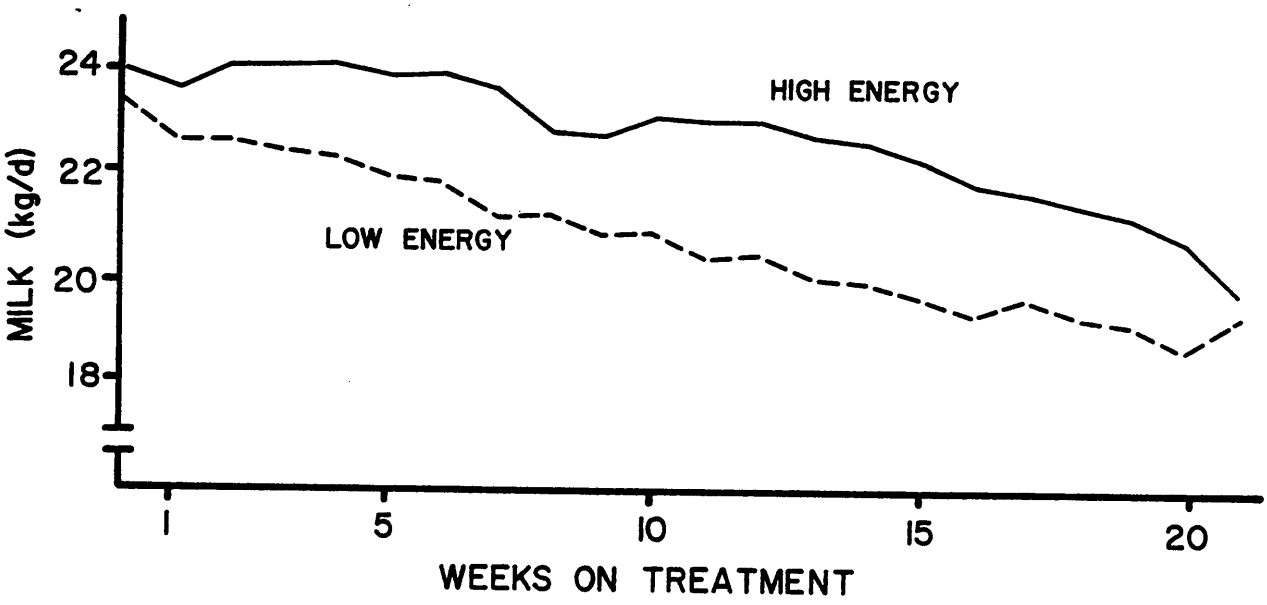

Figure 3: Effect of High or Low Energy Ration on Milk Production of Cows During Late Lactation

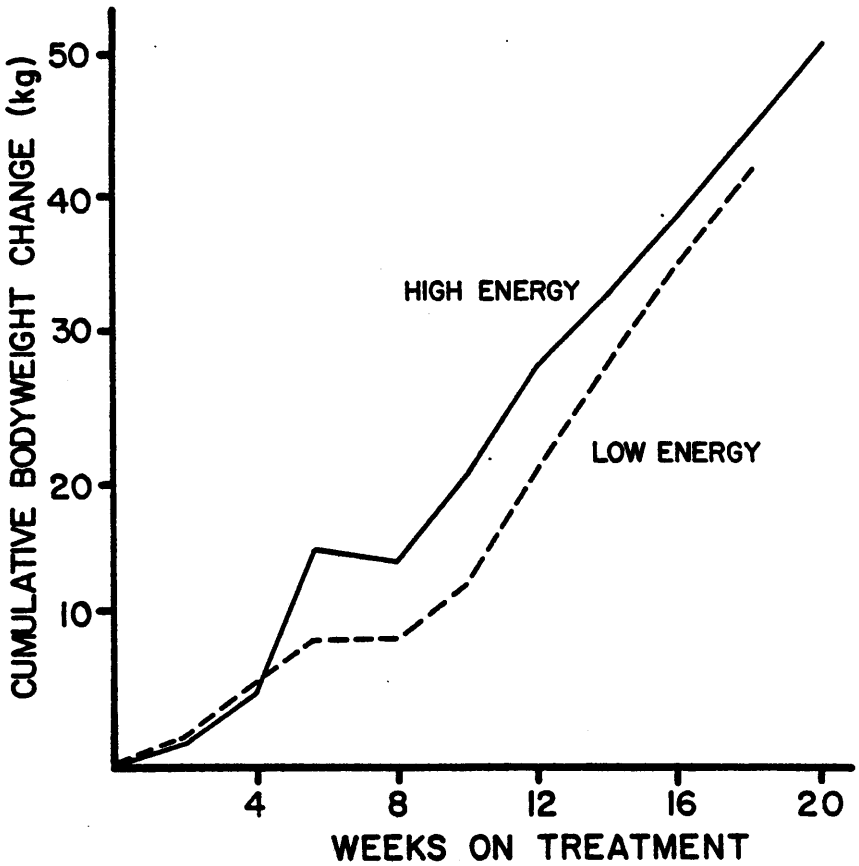

Figure 4: Effect of High or Low Energy Ration on Bodyweight Change of Cows During Late Lactation

it is said that dairy cows regulate their energy intake, when possible, relative to requirements. Therefore, cows in late lactation should decrease intake in response to increasing energy density of the ration. The difference in the intake of cows fed the high or low energy rations in this study may have been due to inability of cows fed the low energy ration to compensate for energy dilution of their diet. Based on the high forage content, it is likely that rumen fill limited intake of the low energy ration (Van Soest, 1982). Conversely, cows fed the high energy ration may have been overeating. Both factors may have contributed to the differences in intake.

Body condition increased significantly more in cows fed the high energy ration. Change in body condition was also affected by the interaction of ration x date started on experiment. Average body condition at drying off was 3.88 for fat and 3.35 for thin cows.

The total 305 d ME of the fattening cows exceeded the 305 d ME projected at the start of the experiment. The 305d ME of the cows fed the low energy ration decreased relative to projected ME at the start of the study. The effect of ration was significant. Thus cows fed the low energy ration were less persistent in their lactation than those fed the high energy ration. Based on milk production responses and

changes in bodyweight and body condition it appears that milk production was more adversely affected by energy restriction during late lactation than was body tissue gain.

Krohn et al. (1982) fed cows high, medium or low energy rations until week 24 of lactation, when all cows were switched to the low energy ration. Cows previously fed high or medium energy rations decreased intake and milk production after being switched to the low energy ration. Rumen fill was increased from 58.4 to 80.3 kg in cows switched from high or medium to low energy. Bodyweight gain during late lactation was significantly less for the cows fed at a medium or high energy level during weeks 1-24 of lactation. The authors cited evidence that more milk is produced when ration energy is decreased at about the eighth week of lactation. Changes before or after this point diminish total lactation yields. However Everson et al. (1976) found that a moderate decrease in ration energy at week 23 of lactation did not decrease milk production. The cows entering the previous study had been fed one of several silage based rations which averaged 50% forage. Therefore the change in forage:concentrate ratio was most abrupt for the cows assigned to the low energy ration. The reduction in feed intake and milk production by this group are consistent with the findings of others (Broster and Broster, 1984). Rumen

fill probably increased in cows fed the low energy ration and this may have contributed to bodyweight gain by that group.

Cows switched to low energy rations in late lactation appear to resist loss of body tissue by decreasing milk production. The energy intake of the thinning group was less than recommended by the NRC for their initial level of milk production. However, the natural decline in production during the experiment should have made energy progressively less limiting in these cows. As seen in figure 3, production of the cows fed the low energy ration fell relative to the high energy group during the initial 2-3 weeks of the study. This difference between the groups remained throughout the lactation, similar to the carryover effects of energy restriction observed in other studies (Broster and Broster, 1984). Further study of the economics of the effects of such feeding is needed.

LABORATORY ANALYSIS OF FEEDSTUFFS AND RATIONS

Results of laboratory and in situ rumen bag analysis performed on samples of the milking rations and protein concentrates are shown in Table 6. Dry matter and crude protein content of rations S and B were similar. Neutral detergent fiber (NDF) and acid detergent fiber (ADF) were higher in

ration B. Acid detergent insoluble nitrogen (ADF-N) was higher in ration B. Net energy of lactation was higher for ration S due to its lower fiber content. Herrington (1983) cited evidence that the energy value of DBG is actually higher than reported in the tables of feed composition. Therefore the true energy value of the rations were probably closer than the predicted value for NE lactation would suggest. Because the forage content of the rations S and B were equal, differences in fiber and ADF-N were due to differences in the composition of the protein supplements. Dried brewers grains are lower in protein and higher in fiber than soybean meal.

The most significant differences between the rations were in the nitrogen fractions, due primarily to the different protein sources used. Dried brewers grains are usually high in ADF-N, 10-18% of total nitrogen (Muscato et al., 1983). The brewers grains fed in this study were especially high in ADF-N, 26% of total nitrogen. Nitrogen in the ADF-N fraction of feeds is almost totally unavailable to the animal (Van Soest, 1982). Therefore ration B had less available nitrogen even though its crude protein content was equal to ration S.

Neutral detergent insoluble nitrogen (NDIN) was higher in ration B. NDIN minus ADIN has been proposed as a measure of

TABLE 6

Analysis of Rations Fed During Weeks 1-15 of Lactation

	Ration S		Ration B	
Item	mean	s.e.	mean	s.e.
Dry Matter(%)	60.7	2.0	61.5	1.9
NDF(% of DM)	32.8	1.9	43.8	2.8
ADF(% of DM)	17.4	1.5	20.8	2.1
NE[1](mcal/cwt)	77.3	1.1	75.0	1.5
CP(% of DM)	14.7	1.2	14.7	0.9
RDP[2](%)	69.5	--	55.0	--
ADIN[3]	4.1	0.7	7.7	1.4
NDIN-ADIN[4]	8.1	3.6	16.7	4.1

Ration S: protein source is soybean meal.
Ration B: protein source is dried brewers grains.
[1] estimated net energy for lactation
[2] estimated percent rumen degradable protein
[3] acid detergent insoluble nitrogen, % of total nitrogen
[4] neutral detergent insoluble nitrogen-ADIN

the slowly degraded, available feed nitrogen (Van Soest, 1982). Ration B, which contained the more slowly degraded protein source, contained the larger NDIN-ADIN fraction.

Degradability was estimated for both rations using the in situ bag method described previously. Values shown in Table 6 were calculated using three different rumen outflow rates. In most cases a close correlation has been reported between in situ and in vivo determinations of nitrogen degradability (Orskov et al., 1983; Rooke and Armstrong, 1984). In situ data from this experiment agrees with findings in vivo that DBG are a better source of bypass protein than SBM in mixed rations fed to dairy cows (Armentano et al., 1984). Total protein flow to the duodenum was also higher with DBG (ibid). Therefore the total protein flow to the intestine may have been greater for cows fed ration B. However the high level of ADF-N in the DBG and in ration B suggests that not all the feed protein escaping the rumen was available.

EFFECTS OF BODY CONDITION AND PROTEIN SOURCE ON LACTATIONAL PERFORMANCE

Dry Matter Intake

Dry matter intake, milk production, composition and body-weight change are shown in Table 7. Figures 3-8 show changes in performance traits of the treatment groups over the course of the study. Thin cows consumed significantly more

dry matter than fat cows. An inverse relationship between body condition and dry matter intake has been observed in dairy cows (Garnsworthy and Topps, 1982; Yadava et al., 1973; Bines and Morant, 1983; Bines et al., 1969), and lactating ewes (Cowen et al., 1982). However others have found no effect of body condition on the dry matter intake of lactating dairy cows (Davenport and Rakes, 1969; Fronk et al., 1980; Boisclair et al., 1984). These differences are difficult to explain because the physiological mechanisms involved are unclear. Bines and Davey (1978) reported that cows ate 24% more feed when thin than when fat. Based on the mass of rumen contents the authors concluded that intake of the fat cows was not limited by rumen fill. Plasma free fatty acids were higher in fat cows before feeding. Thin cows had a more rapid drop in plasma glucose and higher plasma propionate concentrations after feeding. The authors suggested that more rapid utilization of metabolites by the adipose tissue of thin cows diminished the inhibitory effect of these substances on feed intake. The post-prandial rise in plasma insulin could have been greater in the thin cows.

In two trials each covering week 1-16 of lactation, dry matter intake of fat cows was lower and peaked later compared to medium or thin cows. Serial blood samples taken each week revealed a significant positive correlation bet-

TABLE 7

Production and Body Condition of Cows During Weeks 1-15 of Lactation

	Body Condition		Protein Source	
	Fat	Thin	SBM	DBG
Milk kg/d	32.2	31.4	31.4	32.3
Milk kg/d week 1-7	32.3	30.9*	31.1	32.1
3.5% FCM kg/d	33.8	31.3*	32.0	33.1
Fat %	3.9	3.5**	3.7	3.7
Fat kg/d	1.2	1.1**	1.2	1.2
Protein %	3.2	3.2	3.2	3.2
Intake kg DM/d	23.2	24.4*	23.9	23.7
B.W. change kg/wk	-2.7	0.9***	-1.0	-0.9
Body condition change	-1.3	-1.1	-1.0	-1.3

* $p<.05$
** $p<.01$
*** $p<.001$

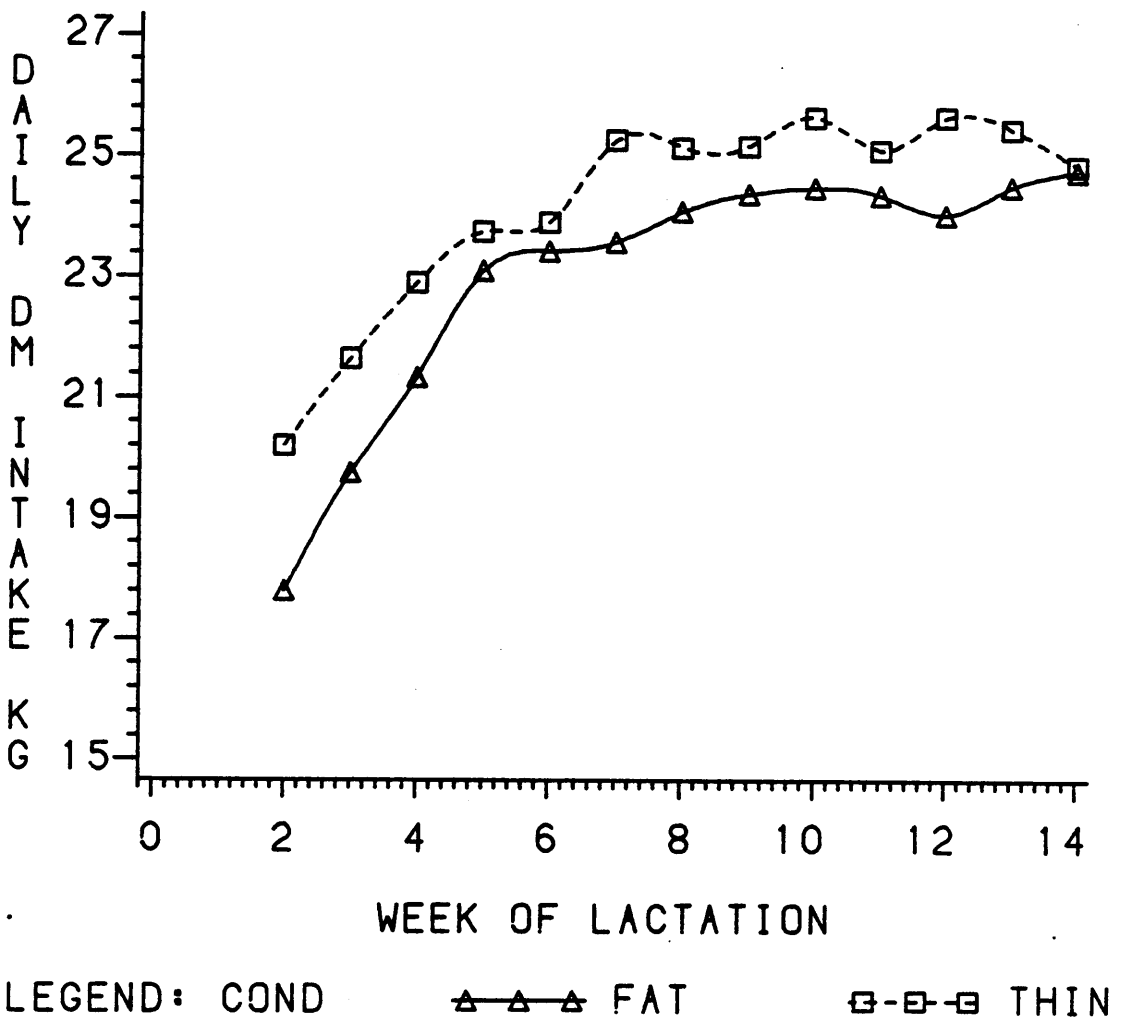

Figure 5: Effect of Body Condition on Dry Matter Intake

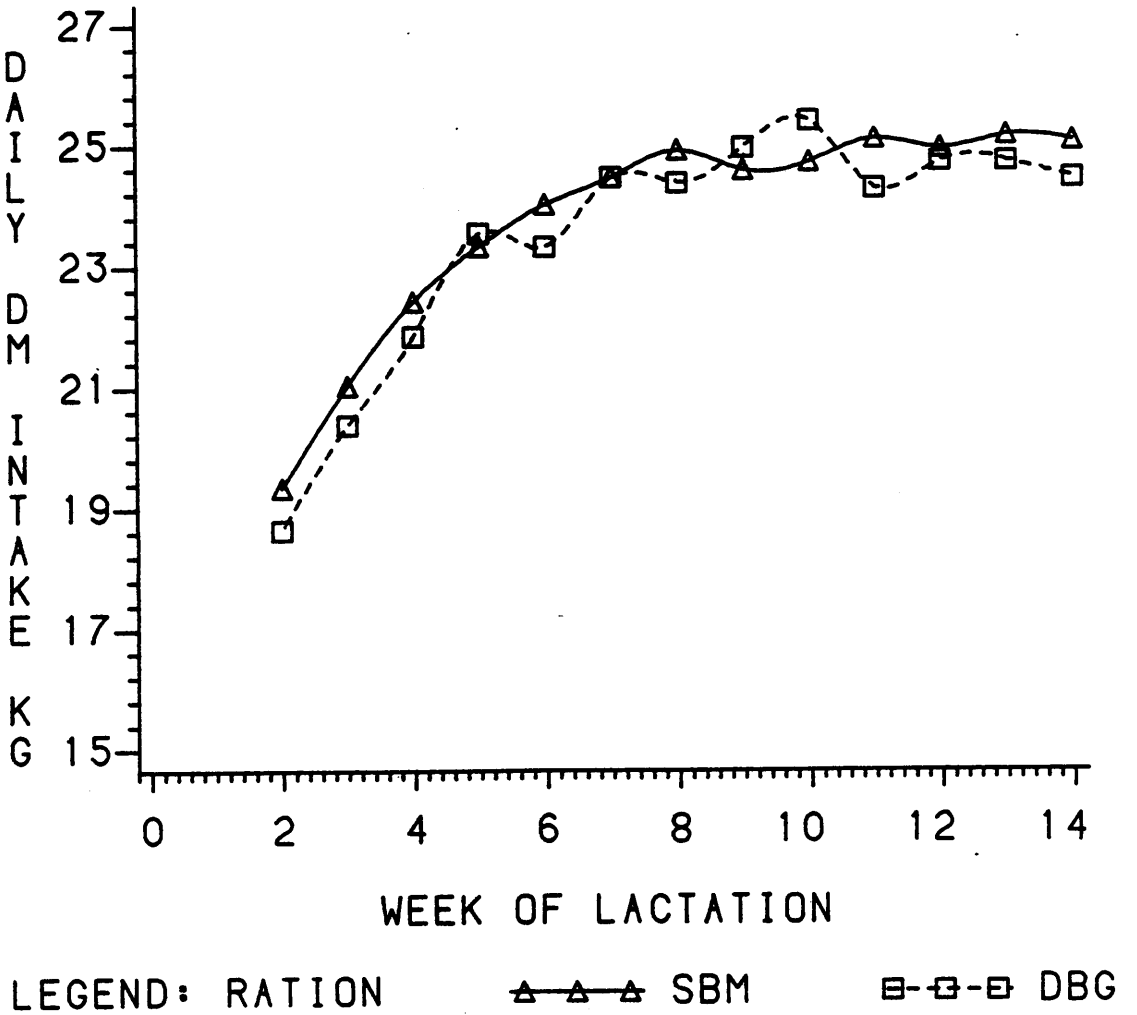

Figure 6: Effect of Ration on Dry Matter Intake

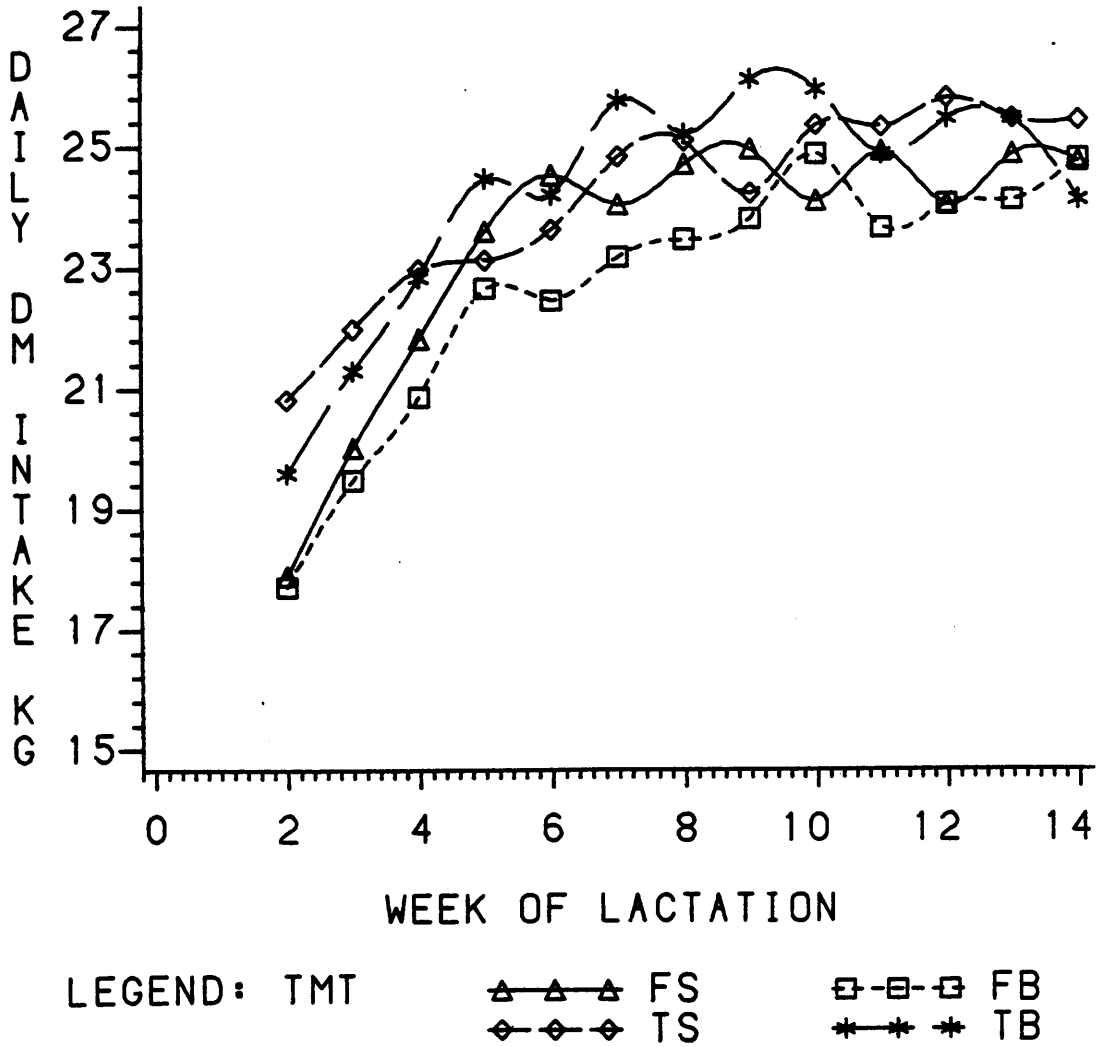

Figure 7: Effect of Body Condition and Ration on Dry Matter Intake

ween intake and both plasma glucose and progesterone. Plasma insulin and free fatty acids were negatively related to intake.

A metabolic signal originating from adipose tissue is thought to regulate energy balance in rodents (La Magnen, 1983). Bines and Davey (1978) concluded that changes in rumen metabolites corresponded more closely to feeding behavior than did blood metabolites. This suggests that changes in the production and/or absorption of rumen VFA would have the greatest influence on feeding in ruminants. Rumen VFA may affect intake via binding specific sensory receptors in the rumen wall and liver or by the release of hormones from the gut and pancreas (Bines and Davey 1978; Baile and Della-Ferra, 1981). Protein source had no significant effect on dry matter intake. This agrees with previous findings (Herrington, 1983; Danielson et al., 1981). Dried brewers grains were readily consumed by dairy cows in this study.

Effect of Body Condition on Fat Corrected Milk Production

Weeks 1-3 of lactation served as a control period. During this time, cows later switched to ration B produced more milk than those which remained on ration S. This was especially pronounced within the fat cow group. Because these differences would introduce bias into the analysis of treat-

ment affects, the average milk production for weeks 4-15 were corrected for production during week 3, before statistical analysis. Production during weeks 1 and 2 was highly variable.

Fat cows (cows fed the high energy ration in the previous lactation) produced slightly more milk during weeks 4-15 of lactation ($p<.07$). The effect of body condition was more pronounced during weeks 1-7($p<.03$). Larger energy reserves allowed the fat cows to reach a higher level of production during early lactation. Fat corrected milk (3.5%), fat percent and fat production were significantly higher for fat cows. This further emphasizes the importance of body reserves as an energy source during early lactation.

Others have reported higher milk production and/or milk fat percent by cows fed higher energy levels pre-partum (Boisclair et al., 1984; Yadava et al., 1973; Davenport and Rakes, 1969). A study of thirty Virginia dairy herds concluded that milk production was highest by cows calving in body condition score 4, followed by cows scoring 3, 2 and 5 (Wildman et al., 1982). Average condition scores of cows in the present study were 3.88 and 3.35. Wildman and co-workers also found an inverse relationship between body condition gain during lactation and efficiency of milk production.

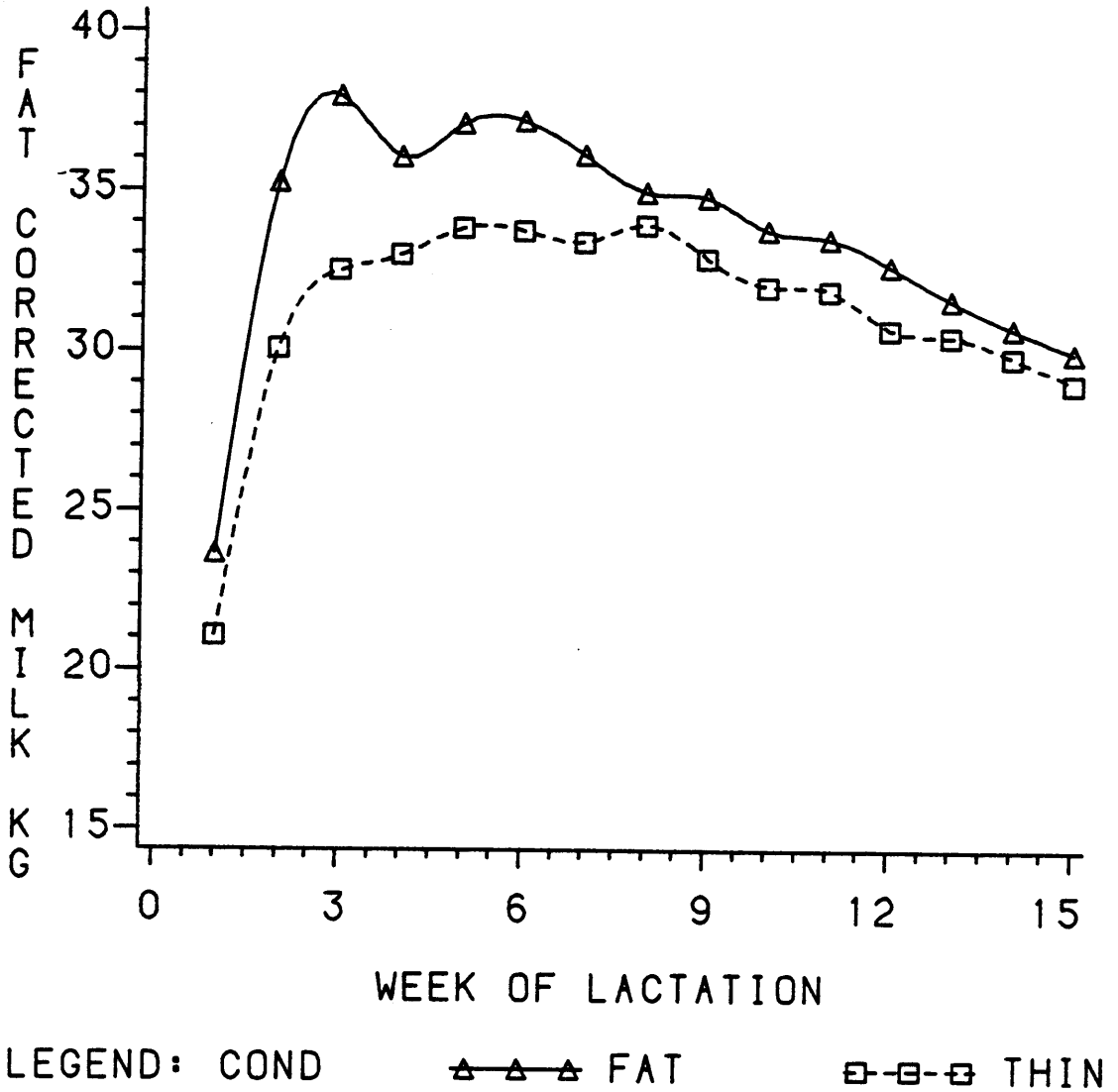

Figure 8: Effect of Body Condition on 3.5% Fat Corrected Milk Production

Some studies have found no effect of body condition on milk production of dairy cows (Fronk et al., 1980; Perkins et al., 1983). Garnsworthy and Topps (1982) found in one of two trials that thin cows produced more milk than fat cows, while in both trials intake was greater for thin cows. These authors concluded that thin cows produced more milk directly from feed and were therefore more efficient than fat cows. However the cows had been fattened by overfeeding during the dry period. Other studies have shown that the partial efficiency of fattening is lower in dry as compared to lactating cows (Moe, 1981). Furthermore, overfeeding during the dry period is associated with an increased rate of post-partum health disorders (Morrow, 1976). In studies where fattening was accomplished by overfeeding during the dry period, the production of fatter cows was equal to or lower than thinner cows. In the present study feeding a high energy ration during late lactation increased the milk production of cows in their next lactation when compared to cows fed at lower energy levels during late lactation. If inadequate body condition limits peak and total lactation milk production, the advantage in feed efficiency noted in thin cows (Garnsworthy and Topps, 1982) would be nullified.

Effect of Ration and Interaction with Body Condition

Milk production during weeks 4-15 was not significantly affected by ration or by an interaction of body condition and ration. Orskov et al. (1982) found that negative energy balance and milk production increased in response to feeding bypass protein only when the energy intake of the cows was restricted. Trigg et al. (1980) found that underfed cows mobilized equal amounts of tissue protein but significantly less fat than well fed cows. This suggests that under conditions of energy restriction, protein supply limits tissue mobilization and milk production in dairy cows. Therefore an interaction of body condition and protein source might have occurred if the energy intake of the cows in the present study had been restricted. In the present study, fat cows ate significantly less feed than thin cows. Strictly speaking this does not represent feed restriction, but rather a physiological change within the fat cows resulting in lower intake. Even so, cows with different body condition may respond differently to bypass protein. Danielson et al. (1981) reported greater milk production response to brewers grains by fat as compared to thin cows, Unlike the present study the fat cows used were picked directly from the research herd and were likely to be animals with a propensity for fattening. This type of cow may be more responsive to bypass protein.

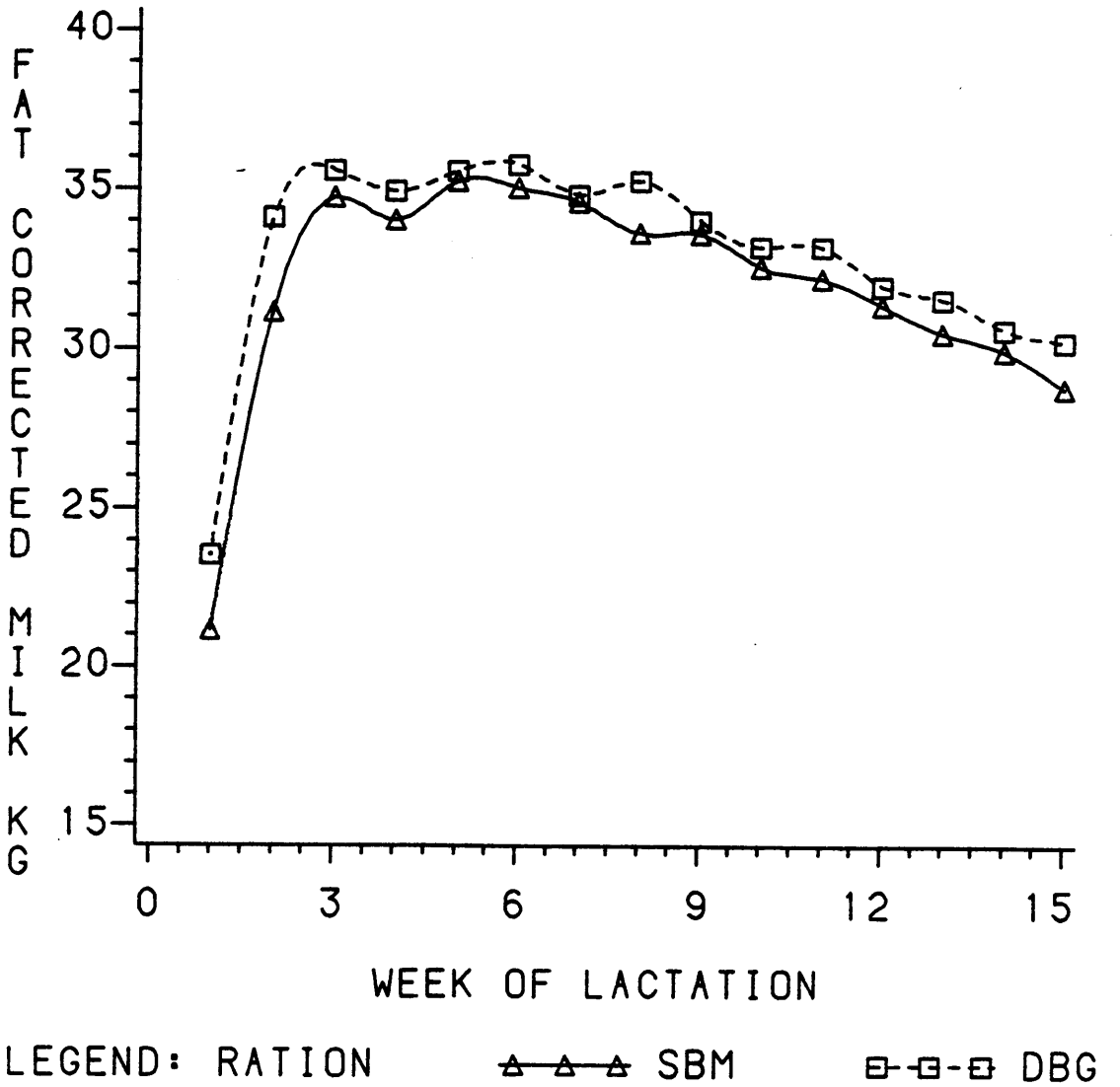

Figure 9: Effect of Ration on 3.5% Fat Corrected Milk Production

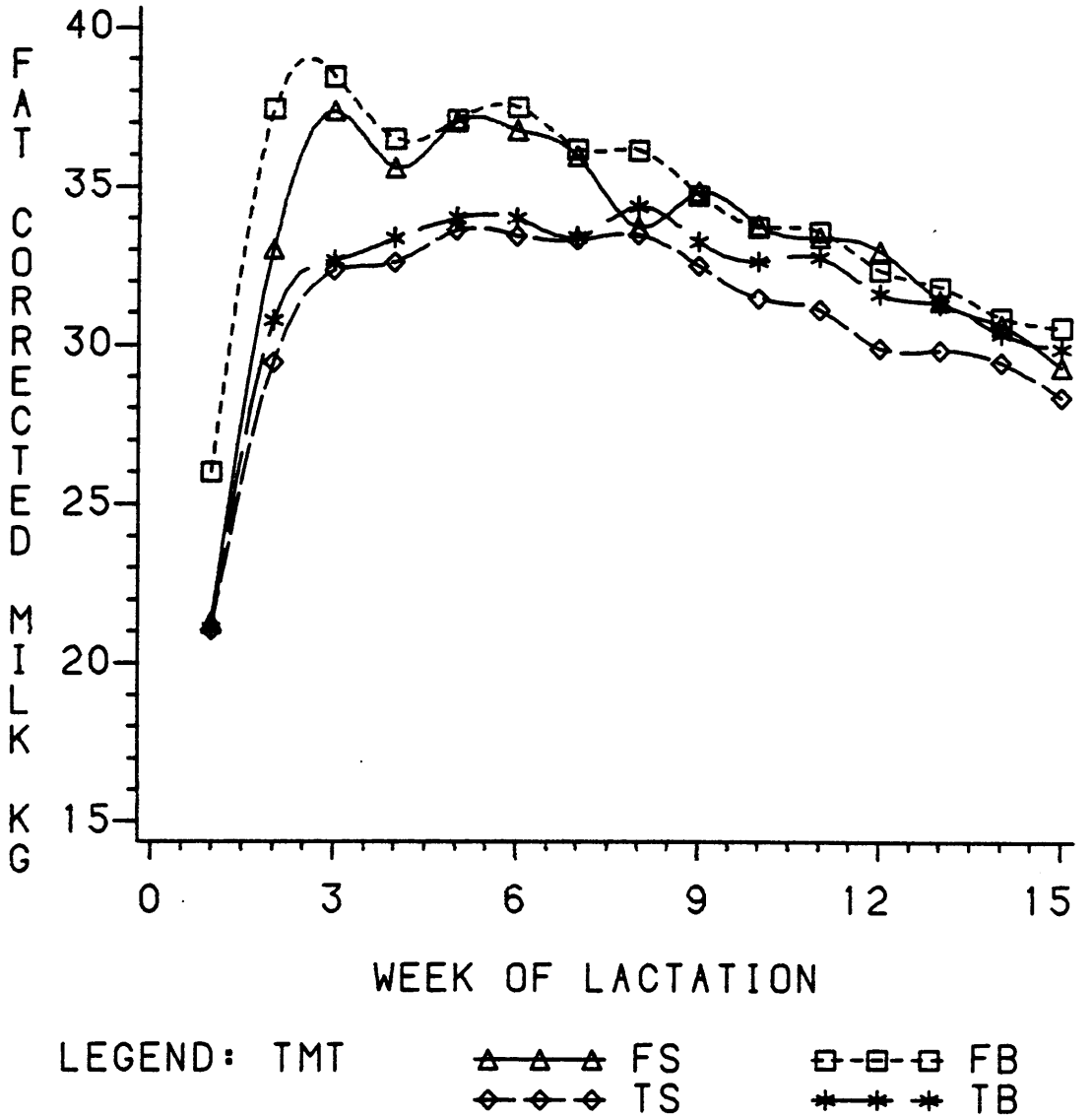

Figure 10: Effect of Body Condition and Ration on 3.5% Fat Corrected Milk Production

In the present study milk production was similar between fat cows fed soybean meal or dried brewers grains. However feed intake tended to be lower and bodyweight loss greater for the fat cows fed DBG. Energy balance, calculated from weekly group averages for FCM and intake, would be more negative for the fat cows fed DBG. This trend is consistent with the findings of Danielson et al. (1981). However the FB cows were producing more milk prior to being switched to ration B. Furthermore, negative energy balance is usually greater in high producing cows (Bines and Hart, 1982).

Past studies have demonstrated the value of DBG as a source of bypass protein in the rations of lactating cows (Armentano et al., 1984). However heat damaged protein, reflected in the ADF-N fraction, was quite high in the brewers grains used in this study. Therefore the digestibility of feed protein escaping the rumen was likely to have been decreased relative to a ration with typical brewers grains. Significant portions of the total essential amino acids were found in the ADIN fraction of dried brewers grains (Muscato et al., 1983). The high ADIN content of the brewers grains used in this study, the slower than normal rate of degradation of SBM (Armentano et al., 1983) and high levels of intake may have diminished the difference in postruminal protein supply expected from the two rations. These data could

explain the lack of agreement between the results of the present study and Danielson et al. (1981). Other studies (Orskov, 1977; Konig et al., 1983) have increased protein supply by infusing casein directly into the abomasum. The resulting increases in milk production and fat mobilization may be unique to the amino acid complement of casein.

In addition to being used for milk synthesis, amino acids contribute to the glucose economy of the ruminant (Egan and Macrae, 1980). During early lactation the demand for glucose is very high. At the same time fatty acids mobilized from adipose tissue must be balanced by sufficient supplies of amino acids and glucose in order to be used by the mammary gland. Therefore the demand for certain gluconeogenic amino acids may be very high and may limit the rate of milk synthesis during early lactation. Supplying the limiting amino acids would signal the body's regulatory systems that adequate nutrients were available for more milk production. Therefore more body fat could be directed towards milk synthesis. Direct incorporation of long chain fatty acids into milk fat is more efficient than de novo synthesis of fatty acids from acetate. The use of long chain fatty acids by the mammary gland could allow diversion of acetate from fat synthesis to oxidation for energy. The response to a particular protein source will depend on its delivery, via

changes in microbial protein synthesis or bypass of feed protein, of limiting amino acids to the host animal. In this study, damage to the protein in the dried brewers grains as measured by the ADF-N fraction of the feed, probably reduced its digestibility in the small intestine. Therefore the amino acid supply to the animal would be reduced compared to animals fed typical DBG.

Effect of Body Condition and Ration on Bodyweight Changes

Fat cows lost more bodyweight and regained weight at a slower rate than thin cows (figure 11). Loss of body condition was numerically greater in fat cows and in cows fed ration B (Table 7). These differences were not statistically significant. Others have reported that fatter animals lose more bodyweight and body condition during early lactation than do thinner animals (Yadava et al., 1973; Cowen et al., 1982; Davenport and Rakes, 1969; Garnsworthy and Topps, 1982). In the present study two groups of cows quite similar in bodyweight and body condition were fed high or low energy rations during late lactation. In the next lactation fat cows produced more fat corrected milk while eating less feed and losing more bodyweight than thin cows. Thus both groups of cows appeared to compensate for body fat gained or lost during the previous lactation. This resembles the regu-

lation of energy balance in laboratory animals (La Magnen, 1983). Mean bodyweights of the two treatment groups at 190 d of lactation, at the end of that lactation, at the next calving and at 105 d of lactation are shown(appendix). It can be seen that initially the mean bodyweights of the two groups were quite similar. During the conditioning period both groups gained similar amounts of bodyweight, but after calving the bodyweight of cows fed the high energy ration in the previous lactation was higher. By week 15 of lactation, the bodyweights of the two groups were again similar and slightly higher than at the beginning of the study.

While not significantly different, the reproductive performance of fat cows (days open and services per conception) equaled or exceeded that of thin cows(see appendix). A positive relationship has been reported between energy balance and ovarian activity in dairy cattle (Butler et al., 1980). Therefore conception may be delayed by prolonged periods of negative energy balance. In the present study negative energy balance was greater for fat cows but reproductive performance was not different from thin cows. However such parameters such as days to first heat or days to first breeding were not measured. The incidence of health disorders was similar in fat and thin cows.

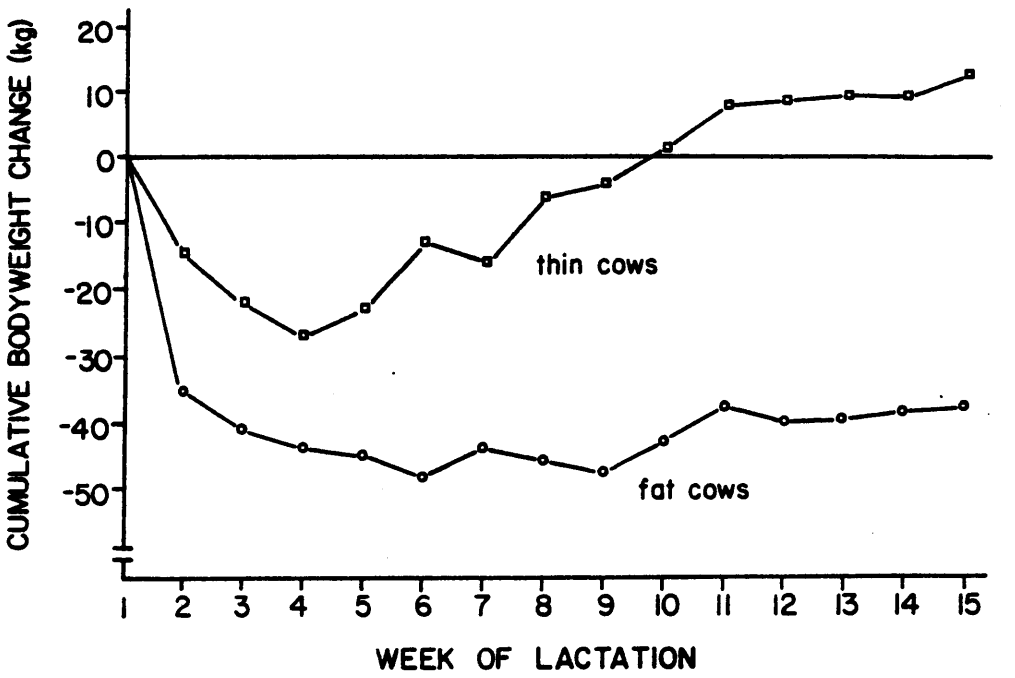

Figure 11: Effect of Body Condition on Bodyweight Change

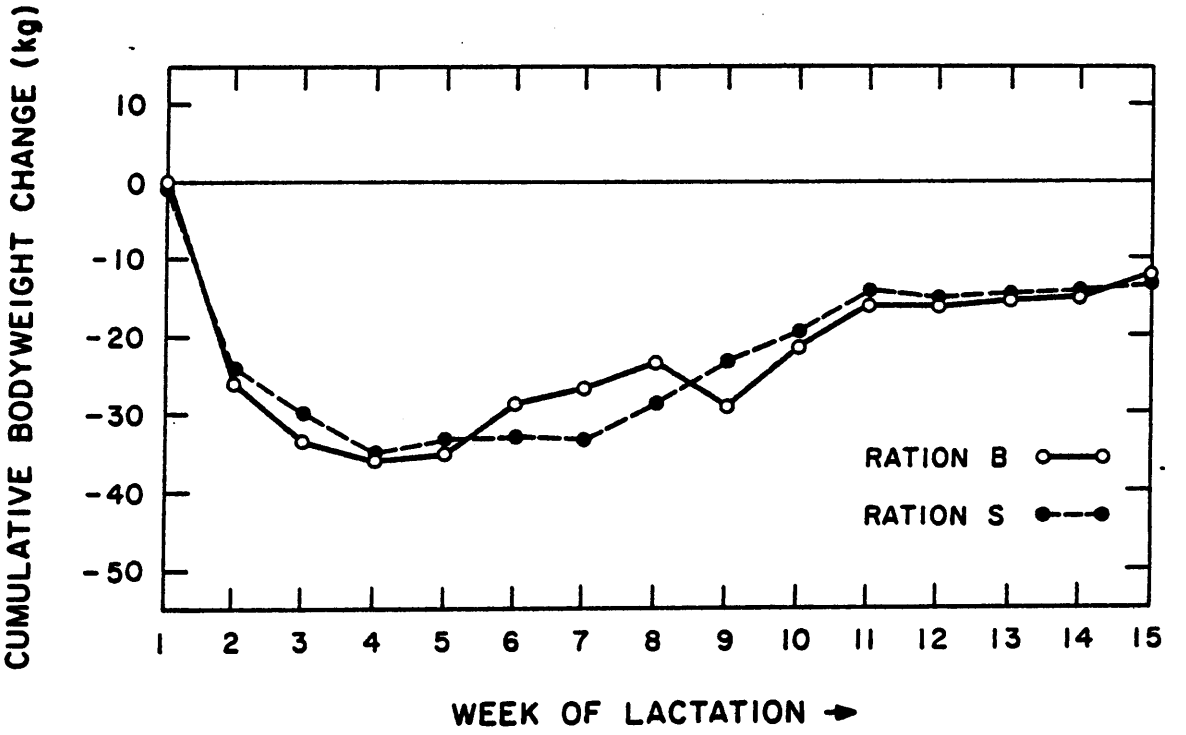

Figure 12: Effect of Ration on Bodyweight Change

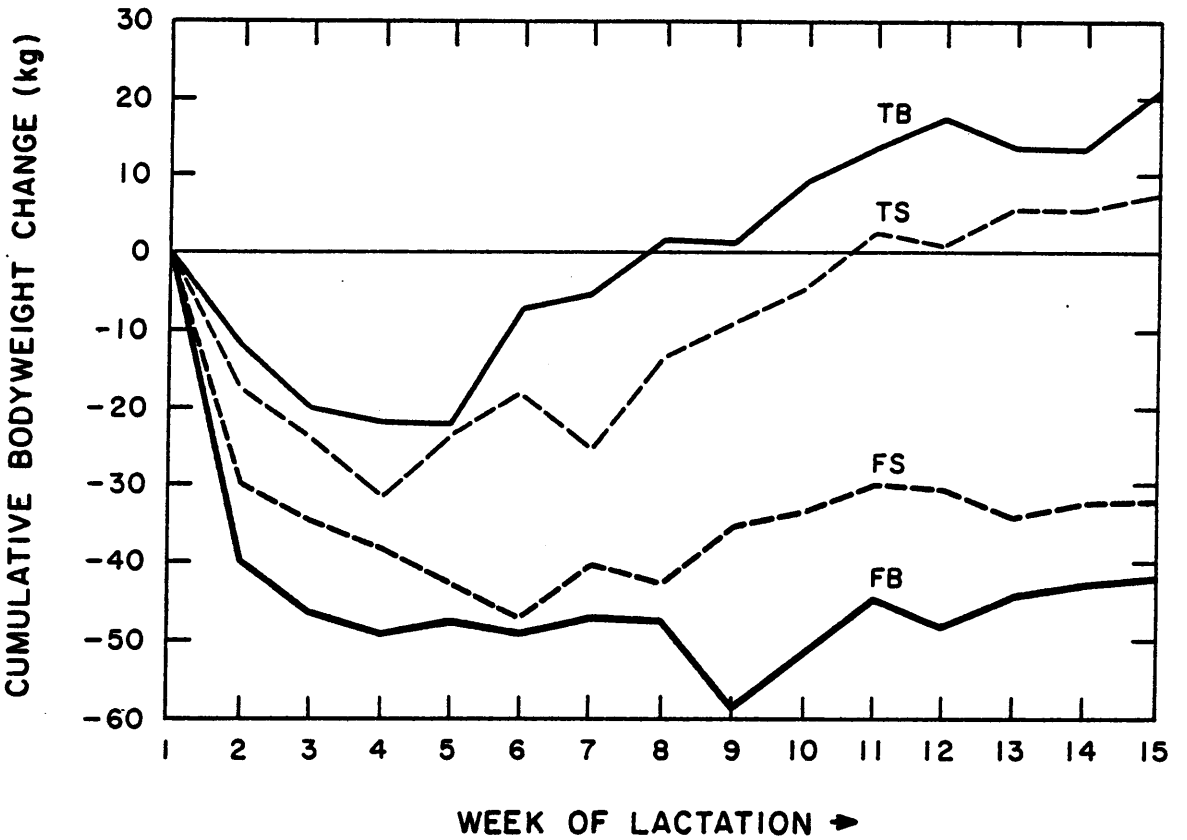

Figure 13: Effect of Body Condition and Ration on Bodyweight Change

RUMEN AND BLOOD METABOLITES

Rumen and blood metabolites are shown in Table 8 and 9. Feeding ration B resulted in a larger molar percentage of rumen acetate while molar percent butyrate was greater for cows fed ration S. Molar percent isobutyrate and total volatile fatty acids were higher in the rumen of thin cows. Valerate and isovalerate increased significantly in all cows as lactation progressed. Acetate/propionate ratio was not significantly affected by treatments. Overall, the proportions of VFA's were within the range of values reported for lactating cows (Oldham, 1984).

The larger molar percentage of acetate in response to ration B is consistent with the higher fiber level of this ration. Higher butyrate levels observed with ration S may reflect the fermentation of soy protein or differences in NDF. Increases in rumen valerate and isovalerate coincide with increasing intake. The higher concentration of total VFA'a in rumen fluid from thin cows may be due to the higher dry matter intake of these cows. Fiberous components of the ration exert the most influence on the proportions of rumen VFA (Van Soest, 1982), however the level of intake and protein source could also influence fermentation patterns.

Bines et al. (1983) found similar proportions of VFA's in the rumen of the same set of cows when thin and again when

fat. Samples were taken at three times post-feeding. In the present study one sample was taken 3 h post-feeding to coincide with the maximum rate of fermentation.

Rumen ammonia (NH_3) concentrations were higher for cows fed ration S, and in thin as compared to fat cows. Rumen ammonia concentration is proportional to the crude protein content of the ration (Polan et al., 1976). At a given level of crude protein, rumen ammonia increases as more readily degraded nitrogen sources are added to the ration. Rate of ammonia absorption increases with rumen pH (Leng and Nolan, 1984). Blood urea nitrogen usually increases with rumen ammonia concentration (Chalupa, 1972). Thus ration S would be expected to result in higher rumen ammonia levels than ration B because the rate and extent of degradation of soybean meal is greater than that of dried brewers grains. Differences in rumen ammonia between fat and thin cows may be explained by the greater feed intake of thin cows in this experiment.

Within both body condition groups, rumen ammonia tended to be higher for cows fed ration S. Plasma urea usually increases with increasing rumen ammonia concentrations. In the present study plasma urea was higher in thin cows fed ration B than thin cows fed ration S. This caused a significant body condition x ration interaction. High blood urea

TABLE 8

Rumen Volatile Fatty Acids

Effect of Body Condition and Protein Source on Ruminal VFA's

VFA (molar %)		Fat	Thin		SBM	DBG
Acetate		65.2	65.2		64.2	66.2*
Propionate		20.4	20.2		20.9	19.6
Butyrate		11.6	11.6		11.9	11.2*
Iso-Butyrate		0.5	0.7*		0.6	0.6
Valerate		1.1	1.1		1.1	1.2
Iso-Valerate		1.2	1.3		1.3	1.2
Total VFA's (mMoles)	S 94.3 B 88.3	91.3	92.5	S 99.1* B 85.8	96.7	87.1*

* $p<.05$

		Week 3	9	15
Butyrate[1]	SBM	0.5	0.8	0.6
	DBG	0.3	0.6	0.9
Isobutyrate[1]	SBM	12.5	12.0	11.4
	DBG	11.2	10.8	11.6

(1) Significant (diet x week) interactions $p<.05$

TABLE 9

Rumen Ammonia and Blood Urea Nitrogen

	Body Condition		Protein Source	
	Fat	Thin	SBM	DBG
Rumen NH_3 mg/%	6.6	8.0*	8.2	6.4**
Plasma Urea[(1)] mg/%	9.7	10.8	10.0	10.5

	Contrasts			
	FS	FB	TS	TB
Rumen NH_3 mg/%	7.4	5.8	8.9	7.1*
Plasma Urea[(1)] mg/%	10.3	9.1	9.7	11.9#

(1) Body condition x ration $p<.05$
\# $p<.10$
* $p<.05$
** $p<.01$

without correspondingly high rumen ammonia in often interpreted as an indication of poor protein utilization. It is possible that protein source had some effect on protein catabolism in the thin cows, however no data are available to support this hypothesis. Danielson et al. (1981) found significantly higher blood urea in thin cows but no effect of body condition on rumen ammonia. In the present study rumen ammonia was higher in thin cows with a trend toward higher plasma urea.

GROWTH HORMONE, INSULIN AND SECRETORY RESPONSES TO ARGININE

Mean plasma hormone concentrations and response areas are presented by treatment and stage of lactation in Tables 10 and 11. A series of graphs (figures 9-17) show mean growth hormone and insulin concentrations before and after intravenous arginine(-120 to +120 min) comparing the responses of fat vs thin cows and of rations S vs B at 6 and at 15 wk of lactation. Figure 17 shows pre- and post-arginine growth hormone concentrations at 15 wk of lactation, separated by treatment combination i.e. FB, FS, TB and TS. This separation of treatment effects was included because statistical analysis indicated a significant body condition*ration*time interaction, meaning that the shape of the four response curves differed from each other in some way.

Overall, the concentrations of plasma GH found in this study were about half that reported in some other studies (Vasilitos and Wangness, 1981). In the present study, anti-ovine GH was used as first antibody in the assays. This was later found to produce values about half as large as those obtained when anti-bovine GH is used as the first antibody(see appendix). The inter- and intra-assay variations were quite large. The plasma pools which were used to measure inter- and intra-assay variation had very low concentrations of GH and insulin. Therefore an absolute variation between assays of 0.5 ng/ml could translate into a large percent variation. For example, inter-assay variation for insulin was based on a mean of 1.05 ng/ml and a standard deviation of 0.43 for the plasma pool samples.

Stage of Lactation

Plasma GH was higher ($p<.09$) at 6 vs 15 wk of lactation. Several studies have shown that in dairy cattle, plasma GH is highest early in lactation and declines as lactation proceeds (Hart et al., 1980; Aeillo et al., 1982; Vasilitos and Wangness, 1981). These data are consistent with the lipolytic role of GH. Area under the GH response curve was greater at 6 than at 15 wk of lactation. Similar results have been found when thyrotropin releasing hormone was used

to release GH (Bourne et al., 1977). Peak concentration of GH following arginine was greater at 6 than at 15 wk. These findings suggest that a larger pool of releasable GH is present early in lactation as compared to mid-lactation.

Conversely, mean plasma insulin and area under the response curve were greater at 15 than at 6 wk of lactation. Studies have shown that diurnal and postprandial insulin levels increase as lactation proceeds (Bines et al.,1982; Aeillo et al., 1982; Jenny et al., 1973; Vasilitos and Wangness, 1981). Therefore the ratio of plasma GH/insulin is highest early in lactation and declines thereafter. A high GH/insulin ratio favors mobilization of body tissue in support of milk production (Bines and Hart, 1982).

Growth Hormone in Fat and Thin Cows

Effect of body condition on mean plasma GH and response to arginine was less pronounced than the effect of stage of lactation (Table 10). However certain significant differences and trends were evident. Mean plasma GH was higher ($p<.05$) in thin cows than in fat cows at 6 weeks of lactation. At 15 weeks plasma GH tended to be higher in fat cows. This resulted in a significant interaction of body condition and stage of lactation. Plasma GH decreased from week 6 to 15 in thin cows. The same change in plasma GH

TABLE 10

Effect of Body Condition, Ration and Stage of Lactation on Plasma GH , Insulin and Response to Arginine

	Plasma GH[2] ng/ml		GH Response[1,2] area ng/ml x min		Plasma Insulin ng/ml		Insulin Response[1] Area ng/ml x min	
	mean	se	mean	se	mean	se	mean	se
6 Weeks	5.0	.4*	20.7	3.1**	0.7	.1**	36.7	9.0**
15 Weeks	4.1	.4	6.6	3.1	1.1	.1	70.7	9.0
Fat Cows	4.1	.4	13.9	3.1	0.9	.1	61.8	9.1
Thin Cows	5.0	.4	13.4	3.1	0.8	.1	45.6	8.9
Ration S	4.4	.4	16.7	3.1	0.8	.1*	61.9	8.9
Ration B	4.7	.4	10.6	3.1	1.0	.1	45.5	9.1

[1] Area under curve after arginine minus basal area.

[2] Peak GH after arginine greater (13.1 vs 6.0 ng/ml).

* $p < .10$

** $p < .01$

TABLE 11

Effect of Body Condition and Ration on Plasma GH, Insulin and Response to Arginine at 6 and 15 Weeks of Lactation

	Plasma GH[2] ng/ml		GH Response[1] area ng/ml x min		Plasma Insulin ng/ml		Insulin Response[1] Area ng/ml x min	
6 WEEKS	mean	se	mean	se	mean	se	mean	se
Fat Cows	4.0	.7*	23.1	5.6	0.7	.1	37.6	11.7
Thin Cows	6.0	.7*	18.4	5.4	0.6	.1	35.9	11.5
Ration S	5.1	.7	23.0	5.5	0.5	.1▲	36.6	11.8
Ration B	5.0	.7	18.4	5.6	0.8	.1▲	36.9	11.5
15 WEEKS								
Fat Cows	4.2	.4	4.7	2.7	1.1	.2	86.0	13.9
Thin Cows	3.9	.4	8.4	2.7	1.1	.2	55.4	13.6
Ration S	3.6	.4	10.3	2.7▲	1.0	.2	87.3	13.9#
Ration B	4.5	.4	2.8	2.7▲	1.2	.2	54.1	13.6#

[1] Area under curve after arginine minus basal area.

[2] Body condition x stage $p<.05$

* $p<.05$

▲ $p<.07$

\# $p<.10$

usually occurs in high producing dairy cows (Vasilitos and Wangness, 1981). However in fat cows, plasma GH tended to increase slightly from week 6 to 15 of lactation. The area under the GH response curve was not significantly different between fat and thin cows at either stage of lactation; however the response area tended to be greater in fat cows at week 6 but greater in thin cows at week 15. The peak GH concentration after intravenous arginine was higher in fat cows at week six. These data suggest that growth hormone secretion in fat cows was suppressed at 6 weeks of lactation. Statistical analysis revealed that the shape of the response curve at six weeks was different between fat and thin cows (figure 9). Fat cows had a faster and sharper GH secretory response to arginine. This may indicate that fat cows had a larger pool of readily releasable growth hormone at this stage of lactation. In the present study, the area under the GH response curve was inversely related to plasma GH concentration. This suggests that plasma GH levels were to some degree a reflection of secretory rate. Studies of GH deficient and normal children have shown that response to intravenous arginine is closely related to plasma levels of GH. However other factors such as metabolic clearance rate also affect plasma hormone concentrations (Bines et al., 1983).

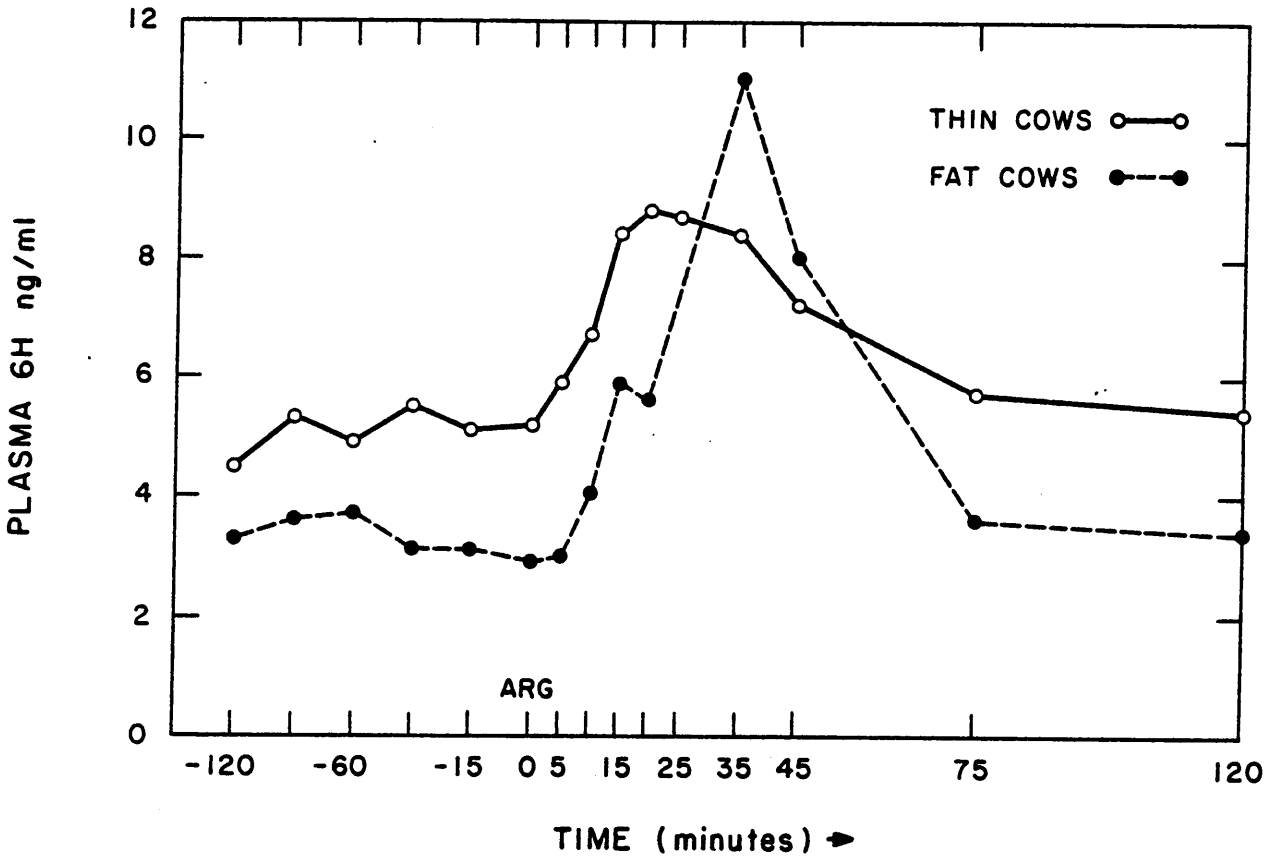

Figure 14: Effect of Body Condition on Response of Plasma GH to Arginine at 6 Weeks of Lactation

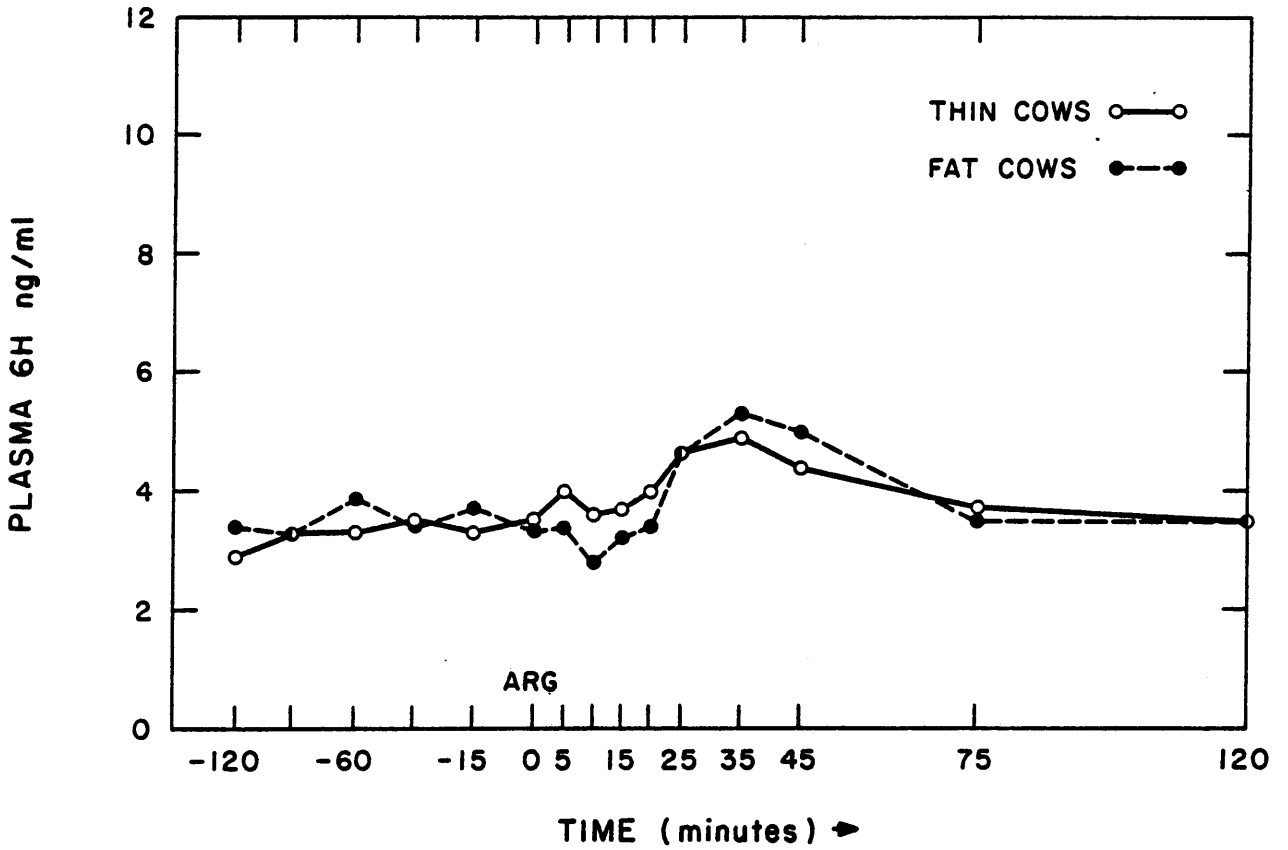

Figure 15: Effect of Body Condition on Response of Plasma GH to Arginine at 15 Weeks of Lactation

Plasma GH concentrations at 6 weeks of lactation were negatively related to body condition. Judging from feed intake and fat corrected milk production, fat cows were mobilizing more body fat at this stage of lactation. Greater release of free fatty acids from adipose tissue into the bloodstream could inhibit the release of growth hormone (Reynaert et al., 1975). The influence of fat tissue on plasma GH would be expected during early lactation when fat is being mobilized and should disappear when the cows pass peak lactation and enter positive energy balance. At 15 weeks of lactation, plasma GH was similar in fat and thin groups.

Ration Effects on Growth Hormone

Basal GH was similar between ration groups at week 6, but tended to be higher ($p<.12$) in cows fed ration B at 15 wk of lactation. Based on their performance during weeks 1-3 of lactation, cows fed ration B seemed to be higher producing cows than those fed ration S. Plasma GH is usually higher in cows of greater producing ability (Bines and Hart, 1982). The area under the GH response curve at 6 weeks of lactation tended to be greater for cows fed ration S and was greater ($p<.07$) at 15 wk for cows fed ration S. Plasma GH was inversely related to the area under the response curve in both

ration groups (Table 10). Thus lower plasma GH was associated with a greater GH response to a secretory stimulus (arginine). Differences in plasma GH and GH response area between cows fed rations S and B may have been due to differences in producing ability. The estimated energy value of ration B was lower than that of ration S. Differences in protein quality were also evident. Fermentation patterns of the two rations appeared to differ as well. Thus rations S and B were likely to have supplied different balances of nutrients to the cows. This could conceivably affect GH secretion over the long term. Consistent with this idea is the fact that ration effects on GH were most pronounced at 15 wk of lactation. The author is unaware of any study testing the long term effects of ration composition on hormone secretion in lactating cows. Such a study would require meticulous characterization of both fiberous and nitrogenous components of the ration plus an in vitro system capable of predicting the effects of chemical components of feeds on VFA production and synthesis and composition of microbial proteins. Very little is known about the actual composition of nutrients absorbed from the gut by dairy cows fed different diets.

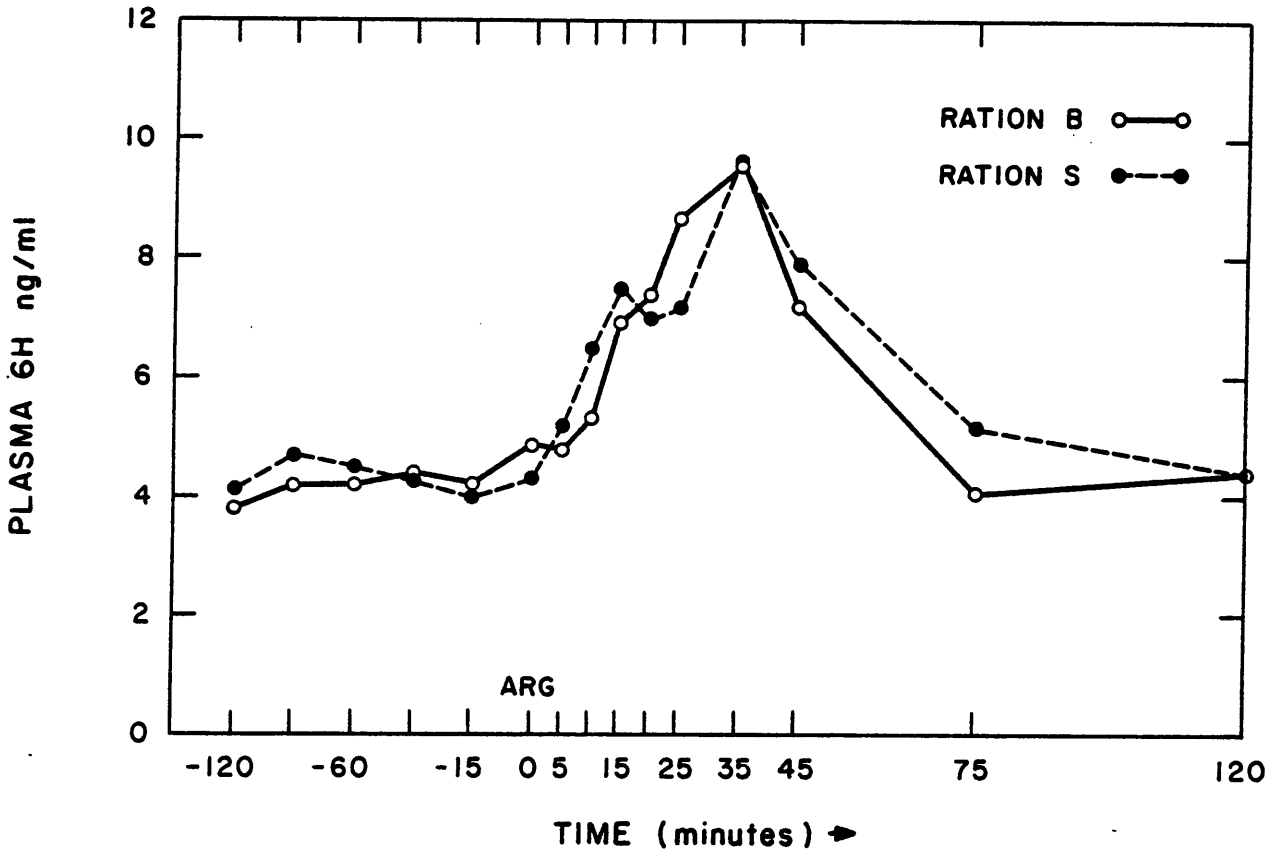

Figure 16: Effect of Ration on Response of Plasma GH to Arginine at 6 Weeks of Lactation

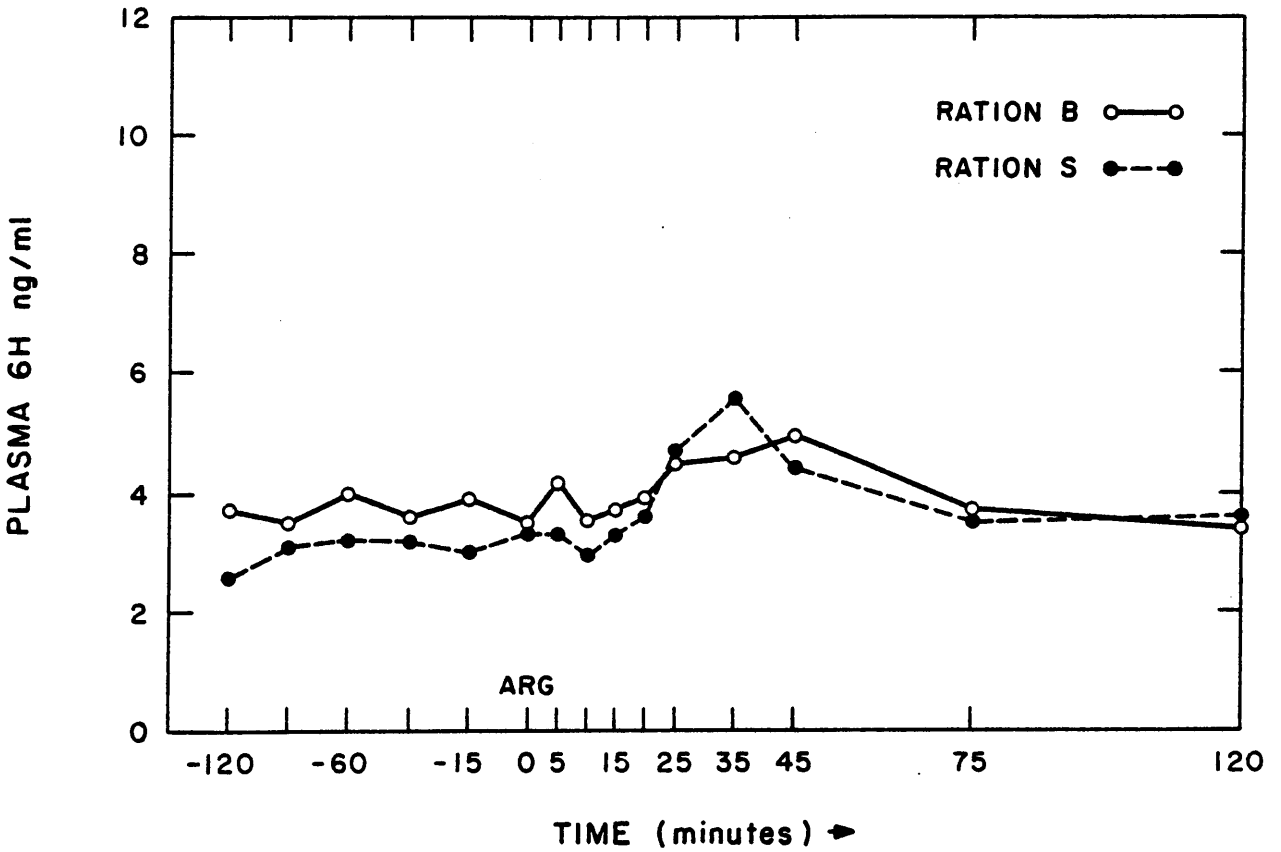

Figure 17: Effect of Ration on Response of Plasma GH to Arginine at 15 Weeks of Lactation

Insulin in Fat and Thin Cows

Plasma insulin and the area under the insulin response curve tended to be greater in fat cows at 6 weeks but the differences were not significant (Table 11). At fifteen weeks of lactation plasma insulin was similar in fat and thin cows while area under the insulin response curve tended to be greater ($p<.12$) in fat cows. The shape of the insulin response curves were not significantly different between fat and thin cows at either stage of lactation and in fact were quite similar. The insulin response to exogenous glucose was greater in obese vs lean Holstein heifers while the glucose clearance rate of the two groups was identical (McCann and Reimers, 1981). This suggests that insulin sensitivity was reduced in the obese heifers. In dairy cows, a high ratio of plasma GH/insulin favors mobilization of body tissue for milk production (Bines and Hart, 1982). In the present study, fat cows mobilized more body tissue than thin cows but had a lower ratio of plasma GH/insulin at 6 weeks of lactation. It is possible that the insulin sensitivity of adipose tissue was reduced in the fat cows. Research in non-ruminant animals and man has shown that plasma insulin is higher and GH lower in obese vs normal subjects (Martin and Gahagan, 1977; Sinha et al., 1975). This is opposite to the high GH/insulin ratio noted in high producing cows dur-

ing peak lactation (Smith et al., 1976), but similar to the fat cows in the present study.

Arginine causes release of insulin, GH, glucagon and prolactin in farm animals (Hertelendy et al., 1969). The response of plasma insulin to arginine differs from the response to glucose. Genetically obese mice fail to produce an insulin response to intraperitoneal glucose, but do respond to arginine or glucagon (Flatt and Baily, 1982). Similarily, non-insulin dependent diabetics (Palmer et al., 1976) and ketonemiic dairy cows (Hove, 1978) have a diminished insulin response to glucose. In the case of diabetics the insulin response to arginine is similar to normal subjects (Palmer et al., 1976). Therefore the insulin response to arginine may reflect the total available pool of insulin. In the present study arginine response area for GH appeared to be inversely related to plasma GH concentration, but this relationship was weaker in the case of insulin. However, insulin secretion is more sensitive than growth hormone to short term stimuli such as feeding (McAtee and Trenkle, 1970).

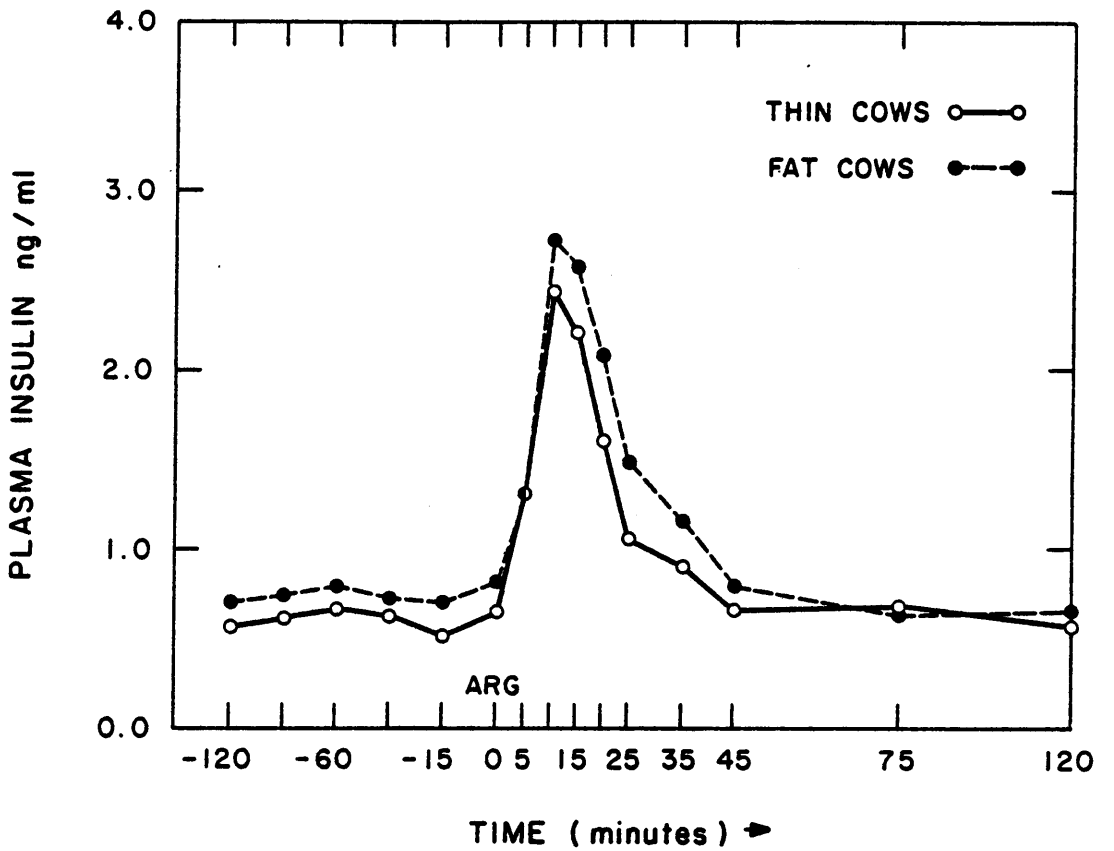

Figure 18: Effect of Body Condition on Response of Plasma Insulin to Arginine at 6 Weeks of Lactation

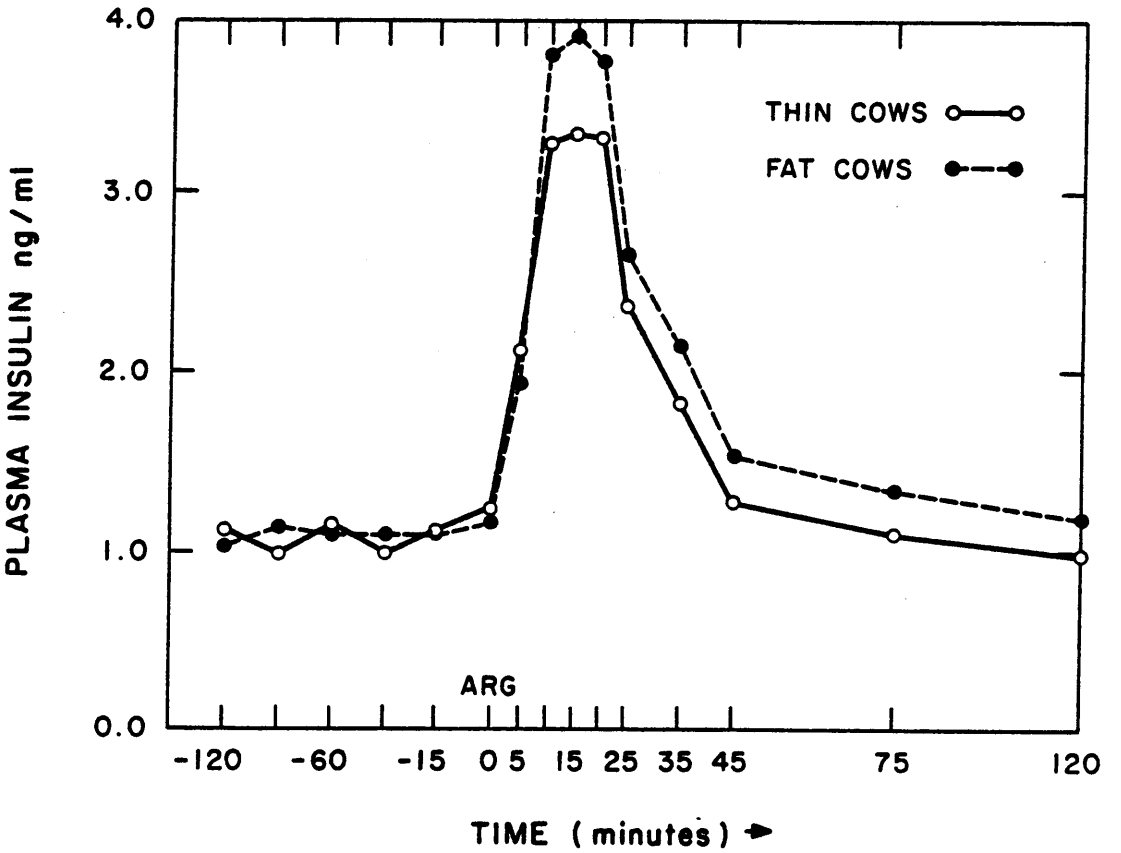

Figure 19: Effect of Body Condition on Response of Plasma Insulin to Arginine at 15 Weeks of Lactation

Ration Effects on Insulin

Plasma insulin was higher in cows fed ration B ($p<.06$) at 6 weeks and numerically higher (not significant) at fifteen weeks. At 6 weeks the area under the insulin response curve was similar in the two ration groups. However at 15 weeks the response area of cows fed ration S was greater ($p<.10$) than for cows fed ration B. The shape of the insulin response curve was different between the ration groups at fifteen weeks. Plasma insulin peaked higher and more suddenly in response to arginine in cows fed ration S. Clearly ration type affected hormone release but the reason for the effect, as discussed in the case of GH, is not clear.

General Discussion

Growth hormone and insulin are involved in nutrient partitioning in lactating dairy cows (Bines et al., 1981). Daily injections of GH increases milk production in lactating cows (Peel et al., 1983) apparently by re-directing fatty acids from adipose tissue to milk synthesis (Bitman et al., 1984). Plasma GH is higher and insulin lower in high producing cows as compared to low producers (Bines et al., 1983). In the present study fat cows tended to have a lower ratio of plasma GH/insulin and yet produced more fat corrected milk on less feed than thin cows. Bauman et al.

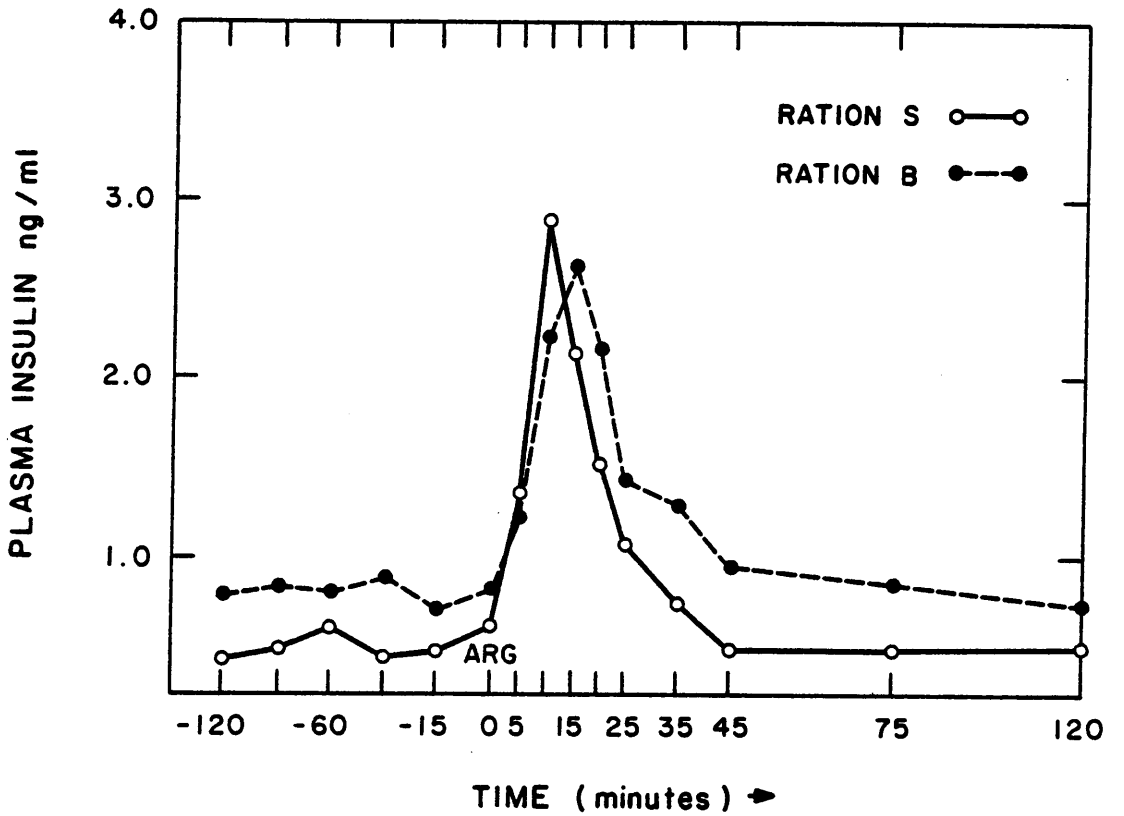

Figure 20: Effect of Ration on Response of Plasma Insulin to Arginine at 6 Weeks of Lactation

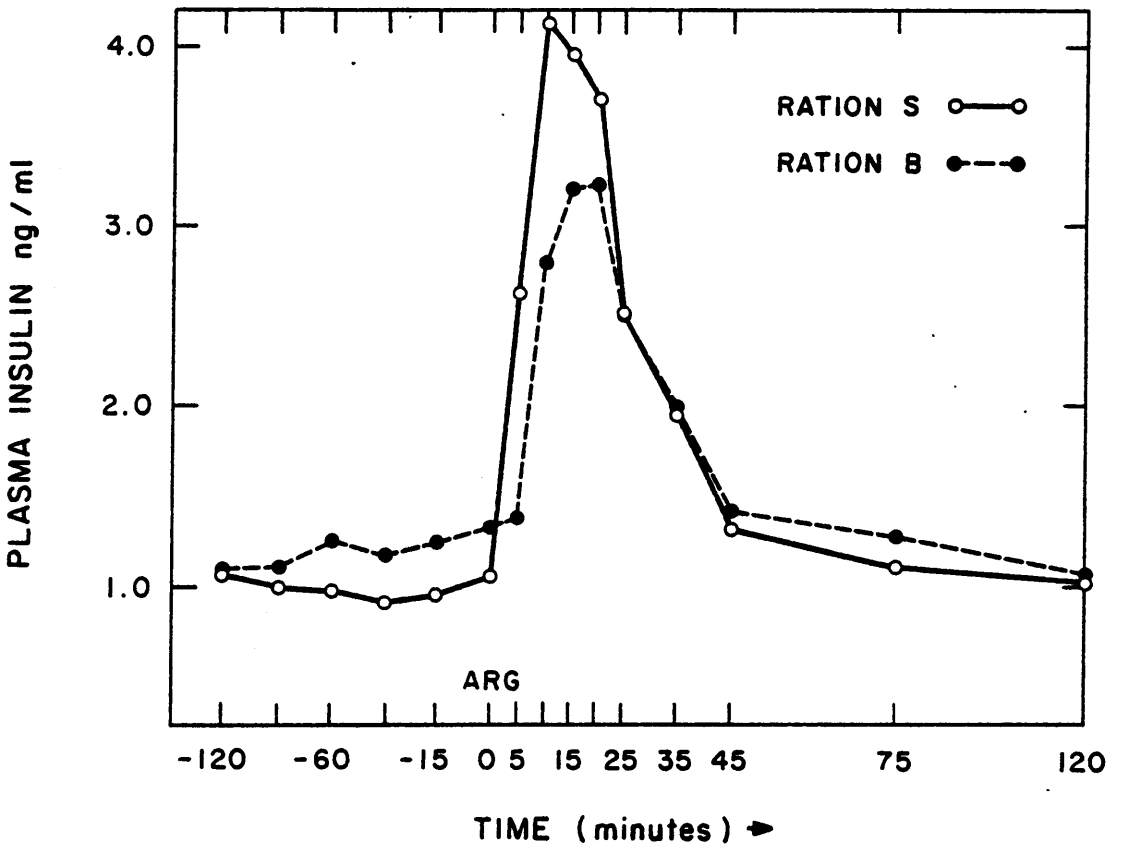

Figure 21: Effect of Ration on Response of Plasma Insulin to Arginine at 15 Weeks of Lactation

(1979) reported that plasma GH and TRH induced response area for GH was greatest in lactating cows which were underfed with respect to energy requirements as compared to cows fed at or above energy requirements. Therefore plasma GH and GH response to TRH was determined by the energy status of the cows. The results of the present study support this hypothesis. The cows which were overfed in the previous lactation had lower plasma GH early in the next lactation. In the present study fat cows tended to have higher plasma insulin at 6 wk of lactation and greater response areas for insulin at both stages of lactation. Plasma insulin and free fatty acids were higher in fat than in thin wether sheep (McNiven, 1984). The response of plasma insulin to changes in ration energy and to fasting was different between fat and thin sheep as well (ibid.) It appears that in sheep insulin secretion responds to energy status.

Insulin secretion may be related to energy status of dairy cows. Therefore the GH/insulin ratio should decrease as the energy status of the cow improves.

The energy status of dairy cows in early lactation may be changed by increasing ration energy density or by fattening the cows prior to calving. Based on the findings of Bauman and co-workers and on the present study plasma GH/insulin ratio is likely to be decreased in both instances. However

the productive responses of the cow differ depending on how energy status has been altered. Feeding very high energy rations during early lactation reduces bodyweight loss (Broster and Broster, 1984), while fattening cows prior to calving resulted in lower feed intake and greater loss of bodyweight during early lactation. An alternative method of increasing energy supply is the feeding of protected fat.

Like body condition, ration affected GH and insulin in cows on this study. Unlike body condition, ration had no significant effect on milk production, feed intake or bodyweight change. Cows fed ration S tended to have lower plasma insulin at 6 wk, lower plasma GH at 15 wk and greater response area for both hormones at week 15. Cows fed ration B weeks 4 to 15 of lactation produced slightly more milk during the period but also produced more milk during weeks 1-3. Therefore some of the differences in GH and insulin secretion attributed to ration may have been due to differences in producing ability of the cows.

The two rations fed to cows in this study differed primarily in protein quality, although the estimated energy value of ration S was greater than ration B. Protein quality for the ruminant animal depends on the degradation of feed protein in the rumen, the quantity of microbial protein synthesized and the effect of these two factors on the quantity

and composition of amino acids absorbed by the animal. The rations fed in this study were predicted to differ in the net quantity and composition of protein reaching the duodenum of the cows. This would result in a different pattern of amino acids being absorbed by the animals fed the two rations. During early lactation when the demand for amino acids is high, different patterns of absorbed amino acids could result in different metabolic responses by the animal as its body attempted to supply the mammary gland with the proper balance of amino acids. Thus dietary amino acids and energy sources would have to be integrated with protein and fat reserves within the animal. This would very likely require changes in hormonal secretion.

Milk production, feed intake and bodyweight changes indicate that the thin cows were regulating bodyweight upwards during the lactation. Recent work with rats (Harris and Martin, 1983) suggests that previously underfed animals will regulate bodyweight according to protein reserves, i.e. animals regain bodyweight until protein reserves are repleted. Lactating cows which had been underfed in the previous lactation may have been deficient in body protein stores and would be especially sensitive to amino acid nutrition during lactation.

Analysis of the GH secretory response at 15 weeks revealed a significant body condition*ration*time interaction. This indicates the shape of the response curve differed between the treatment groups FB,FS,TB and TS. The response of the FB group appeared to lag behind the other three groups while the FS group had the largest response area. The shape of the response curve appears most similar in TS and FB. The TB group (thin cows fed ration B) were unique in having a biphasic GH response to arginine. The insulin response area of the TB group at 15 weeks was smaller than that of the other three groups (FB 78.8, FS 93.2, TB 29.3, TS 81.4). While the differences were not significant ($p<0.3$), it appears that the response of the TB group differed from the other three groups. No such trend was evident in the insulin response area at 6 wk of lactation. While the insulin response area increased from 6 to 15 weeks in FB, FS and TS cows, it actually decreased slightly in the TB group, from 33.6 to 29.3 ng/ml x minute. Milk production of cows in the TB group appeared to be increasing relative to the other three groups during the latter part of the study. This is consistent with the higher levels and response area of GH and the lower levels and response area of insulin observed at 15 weeks of lactation in the TB cows. Plasma urea was highest in TB cows, high enough to cause a significant body

condition*ration interaction. This suggests some difference in the nitrogen metabolism of thin cows fed ration B. This may have affected the response of TB cows to intravenous arginine.

Mobilization of body tissue for milk production is clearly a complex process involving many hormonal and nutritional factors. The role of steroid hormones in the process must be considered. For example, plasma glucocorticoids, which are elevated during early lactation (Koprowski and Tucker, 1973), have been shown to antagonize, in vivo, the effects of insulin at the tissue level (Kahn et al., 1978). Growth hormone has been shown to have the same effect (ibid.). This could be a mechanism of nutrient partitioning in lactating cows. Because lactation is part of the reproductive cycle, it follows that ovarian steriods play a major role in mammary development and function. Recently it was shown that secretion of estradiol 17b and prostaglandin F2 by the mammary gland is associated with lactogenesis in sheep and cows (Maule-Walker et al., 1984). Progesterone has been shown to affect secretion of pancreatic hormones (Bines and Hart, 1982) and its role in nutrient partitioning during lactation has been studied by others (Flint et al., 1984). Nutrient partitioning and body tissue mobilization in cows cannot be understood without further study of the role of steroid hormones.

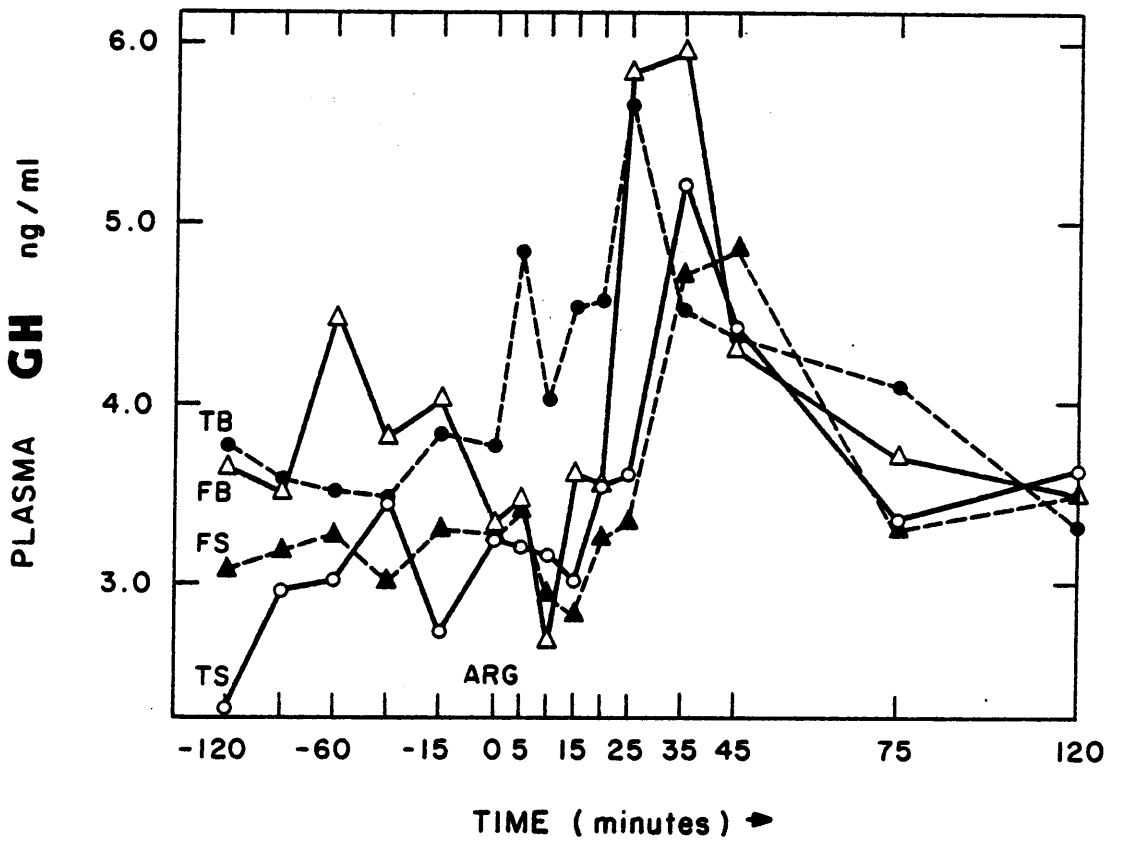

Figure 22: Effect of Body Condition * Ration on Response of Plasma GH to Arginine at 15 Weeks of Lactation

In mammals, deposition of fat during pregnancy insures that adequate energy will be available to support lactation and thereby to nourish the young. Hormonal signals from the fetus may stimulate body fat deposition in the dam, as they do for mammary growth. Milk production tends to decline more in pregnant as compared to non-pregnant cows suggesting a shift in physiological priorities from milk production to tissue deposition. Selection for milk producing ability in dairy cattle has increased the nutrient requirements of cows as well as their dependence on body fat as an energy source during early lactation. Broster and Broster (1984) state " there is an a priori case for adequate body reserves at calving and a need to demonstrate that failure to provide them will result in reduced milk yield". The results of the present study provide such a demonstration. Furthermore it appears that fattening cows in late lactation is a viable means of providing adequate body reserves without impairing performance. The energetic efficiency of milk production from fat accumulated during lactation is comparable to that of milk production directly from feed (Van Soest, 1982). Feeding above NRC requirements during late lactation must be compared to feeding cows at requirements. Furthermore, the effects of overfeeding in late lactation over several lactations must be evaluated.

Excessive mobilization of body fat, resulting from some dietary imbalance or from excessive fattening prior to calving, is associated with metabolic disorders such as ketosis (Baird, 1982). Clearly the process of tissue mobilization depends on a certain balance between dietary nutrients and body reserves. In certain situations, deficiency of amino acids may limit tissue mobilization in lactating cows (Orskov, 1977). The present study did not find a significant interaction between the level of energy intake in the previous lactation and protein source in the ration. However, the large amount of bound protein found in the dried brewers grains along with the lower than normal degradability of the soybean meal would tend to decrease the expected effects of the two protein sources in the rations. The interplay of nutrients absorbed from the gut with body tissue reserves in lactating cows deserves further attention.

Finally it was found that when body energy stores of cows were changed by feeding high or low energy rations during late lactation the changes were compensated for during the early stages of the next lactation. Cows which had been prevented from storing body fat consumed more feed while producing less fat corrected milk and gaining more bodyweight than cows fed to gain body condition in the previous lactation. While lactation had a high metabolic priority in

both groups of cows, the energy status of the animals affected the extent to which nutrients from the diet were partitioned toward milk production.

CONCLUSIONS

1. Feeding a high energy ration ad lib during late lactation is preferable to feeding below energy requirements. Cows fed a low energy ration during late lactation had lower fat corrected milk production in the next lactation, especially at peak lactation, while consuming more feed than cows fed above NRC energy requirements in the previous lactation.
2. The energy balance of cows was altered by feeding high or low energy rations during late lactation and the change in energy balance was compensated for during the early stages of the next lactation. Nutrient partitioning was affected by energy status of the animals.
3. Dried brewers grains, when fed as the main protein source to lactating cows, supported equal or slightly better milk production than soybean meal despite having a high percentage of bound nitrogen.
4. Changes in plasma growth hormone, insulin and the response of each hormone to arginine at week 6 and 15 of lactation are consistent with the proposed role of these hormones in controlling nutrient partitioning in lactating dairy cattle.

5. Milk production, metabolite and hormone data suggest an interaction of body condition and ration protein source in the case of thin cows fed dried brewers grains.
6. Both body condition and ration affected hormonal responses of lactating dairy cows. Differences in hormonal responses between ration groups may reflect metabolic adjustments of cows to a particular ration in order to maintain peak milk production. Differences in hormonal responses of between body condition groups may reflect adjustment of metabolism to maintain energy/nutrient balance.

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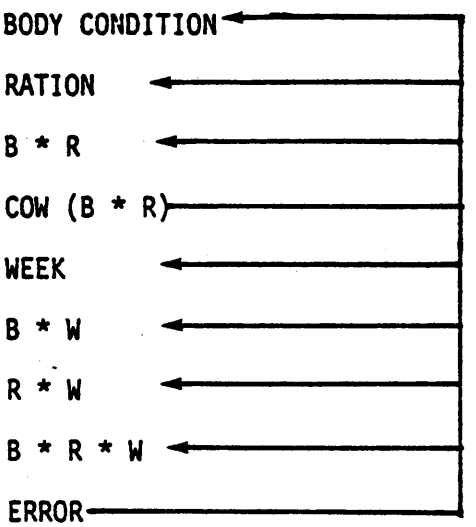
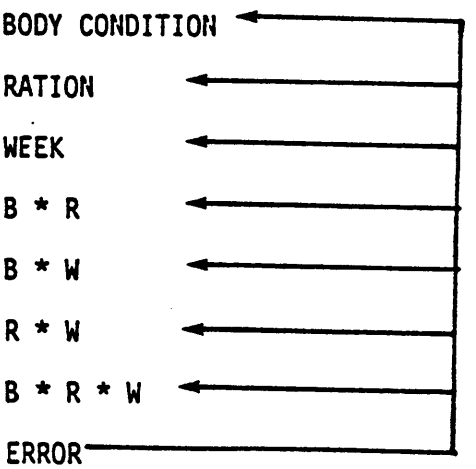
APPENDIX

STATISTICAL MODELS

Model A



Model B



USE OF ANTI-OVINE GROWTH HORMONE IN RADIOIMMUNOASSAY

Reported values for plasma growth hormone in dairy cattle in early lactation vary. In the present study plasma GH concentrations were low as compared to the finding of others (Vasilitos and Wangness,1981). Although use of anit-ovine growth hormone as the first antibody in the GH radioimmunoassay has been validated (Eisenmann and Chew,1982), the values for GH obtained from the same plasma pool were slightly more than two times greater when anti-bovine GH was used as first antibody as compared to when anti-ovine GH was used (Akers, R.M. unpublished). If the values for plasma GH from the present study are adjusted accordingly, values match those reported by those using anti-bovine GH as first antibody (Aeillo et al.1982). The values obtained in the present study are similar to those found by Chew et al. (1984) using anti-ovine growth hormone as the first antibody.

Health Records of Cows

Treatment Group	Fat	Thin	S	B
Discharge	4	2	3	3
Cleaned	1	1	1	1
Ketosis-off feed	1	2	1	2
Milk Fever	2	1	1	2
No heat	7	7	8	6
Mastitis	6	6	6	6
Sold-Cull	6	8	9	5
Other[1]	3	5	3	5

Treatments are fat and thin cows, soybean meal and dried brewers grains.
[1] Includes foot and leg problems, abcesses, pinkeye, abortion, cystic.

Health and Reproductive Records of Cows

Treatment Group	Fat	Thin		S	B	
Body Condition	-1.3	-1.1		-1.0	-1.3	(.1)
Bodyweight	-2.7	0.9		-2.1	-1.9	(5.5)
Days Open	106	115	(12)	109	111	(15)
Services	2.2	2.4	(0.3)	2.3	2.3	(0.4)

Treatments are fat and thin cows, soybean meal and dried brewers grains.
Data represent changes in body condition and bodyweight.

Degradation constants for SBM, DBG and rations.

	Fraction[1]				
Feed	B	Kd	C	A	Net
DBG-Dry Matter	.361	.053	.358	.280	41.5
DBG-Nitrogen	.445	.039	.218	.337	47.2
DBG-Ration DM	.513	.066	.179	.308	52.5
DBG-Ration N	.521	.060	.138	.341	55.0
SBM-Dry Matter	.434	.071	.017	.549	74.1
SBM-Nitrogen	.443	.053	.100	.457	62.1
SBM-Ration DM	.527	.082	.113	.360	61.1
SBM-Ration N	.567	.102	.040	.394	69.5

[1] fraction B is slowly degraded in the rumen,
fraction C is the residual after 72 h incubation,
fraction A is instantaneously degraded,
Net is degradation assuming rumen turnover of .09 h.

Bodyweight Means

Bodyweight[1]	1	2	3	4
High Energy	588 15	679 33	641 39	603 20
Low Energy	586 12	660 36	591 30	612 17

[1] Mean bodyweights of treatment groups at day 190 of lactation, end of lactation, at calving, at day 105 of next lactation.
Cows at 190 d lactation were fed high or low energy ration until dry.

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