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EVALUATION OF THE ENERGY AND PROTEIN OF CORN GRAIN ON NUTRIENT PARTITIONING IN GROWING STEERS

Iowa State University

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Evaluation of the energy and protein of corn grain on nutrient partitioning in growing steers

by

Eric James Hentges

A Dissertation Submitted to the Graduate Faculty in Partial Fulfillment of the Requirements for the Degree of DOCTOR OF PHILOSOPHY

Major: Animal Nutrition

Approved:

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In Charge of Major Work

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For the Graduate College

Iowa State University
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1984
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INTRODUCTION

In the endeavor to improve beef production and increase profit, the genetic limits of rate of gain may be approaching limits. Likewise, feeding to increase rate of gain may be reaching a limit. If this is true, and the maximums are being obtained, then improvement will come mostly through improving the efficiency of maintaining these rates of gain. This study examined where, when and how the protein and energy components of a feedstuff affected performance and were partitioned into the various tissues of growing cattle. Through this kind of knowledge, the efficiency of feed usage may be increased and a more desirable product produced.

Modern consumer demands are dictating a leaner meat product. A better understanding of nutrient partitioning should allow such a product to be produced efficiently in the feedlot. Producing the product by dietary control would be much preferred to cutting off waste fat at the packing plant, especially when the high cost of labor is considered. Greater efficiency of feed grain use may be more important in the future as the use of feed grains for livestock production, as opposed to human consumption, becomes more of a concern to the animal industry. It will be advantageous to
know what components or nutrients in the grain give which results at what time. This knowledge may have to be applied to other feedstuffs to mimic the advantage of grain, or to show that the grain itself may be processed to provide products for both human and livestock use.

In this study, the feed grain under study was corn. The energy-yielding components (starch and oil) and the protein component (corn gluten meal) were examined to determine their contributions to feedlot performance and to the composition of live weight gain in cattle. In addition, several plasma endocrine profiles were examined to determine a metabolic basis for diet-induced differences in performance.
REVIEW OF LITERATURE

Animal Growth Models

Munro (1978), in a review of nutrition and muscle protein metabolism, discussed the changes of skeletal muscle throughout life. "First, changes occur in the proportion of muscle in the body at various stages of life. Second, the structure and chemical composition of muscle undergo alterations during development. Finally, the proportion of muscle to viscera varies systematically in mammals of different body size." Skeletal muscle in general makes up approximately 25% of body weight at birth and increases to about 40-45% at maturity. It is generally accepted that this growth is through hypertrophy of existing fibers at birth, and not through hyperplasia. The muscle of a mature animal has increased concentrations of myofibrillar and sarcoplasmic proteins and decreased collagen content when compared to the muscle of a newborn. Furthermore, with increasing age, there is a change in nucleic acid content of muscle indicative of decreased protein synthesis activity. Both DNA and RNA concentrations decrease per gram of tissue.

Hammond (1955) reported that different tissues reach their maximum rate of growth in a definite order with age as
follows: (1) nervous tissue, (2) bone, (3) muscle and (4) fat. He also discussed the different rates of accumulation of fat in various depots during growth. In order of deposition, fat accumulates initially as mesenteric fat, secondly as kidney fat, and then as intermuscular fat and subcutaneous fat.

Berg and Butterfield (1976) suggested a model incorporating the following principles: "(1) Vital organs will have first claim on available nutrients for both maintenance and growth. The more vital the organ, the higher the priority and more minimal the retardation by inadequate nutrition; (2) During positive growth, muscle and bone growth proceed at the same relative rates to each other, irrespective of the rate of growth; (3) The proportion of muscle to bone is altered during body weight loss. The relative rate of depletion may be affected by intake of protein as well as energy; (4) Fat growth, relative to muscle and bone growth, is dependent on the level of energy intake; (5) The loss of body weight depletes fat, muscle and bone. There is not a selective depletion of fat."

"The different organs and organ groups also exhibit marked heterogenic growth," according to Hammond (1955), "with the thoracic organs as a whole maturing earlier than the digestive tract." Latimer (1929), in studying developmental changes of chicks, found that the viscera as a
whole accounts for a higher percentage of the body weight at hatching than in adults, which indicates that these parts mature early when compared with the muscular and fatty tissues. Palsson and Verges (1952) found similar results with sheep in that with increasing age and weight, the dressed carcass made up an increasing proportion of the live weight because of the greater growth rate of the carcass muscle and fat when compared with the organs and offal.

Plane of Nutrition

Of the two major nutrients under consideration, the effects of energy on compositional growth in ruminants have been studied most extensively. In growing cattle, as in other species, energy use by the animal is partitioned into maintenance and production. Maintenance energy is, just as the word implies, energy needed to maintain vital functions and sustain body tissues. Production energy is energy used for new tissue growth in the case of beef cattle. This relationship has been described well and has been set forth as a feeding system, the California Net Energy System (Lofgreen and Garrett, 1968). It is the production energy that is of interest now, and how this energy is partitioned into body tissues during growth.
Recent studies show that there are occasions when maintenance needs do not necessarily conform with metabolic body weight (body weight, in kg, raised to the three-fourths power). These situations need to be considered when evaluating the results from multi-level energy studies. Work by Knox and Handley (1973) and recent work by Koong et al. (1983) indicates that maintenance requirements increase with increasing production. If indeed this is the case, then calculated energy levels may be inaccurate in terms of energy available for production. The heat production of a growing ruminant has been shown to be influenced markedly by the nature of its diet (Elaxter and Boyne, 1978). This is of particular importance in ruminants, because roughage level in the ration almost always is confounded with energy level. Both of these considerations are tied directly to the relative size of the splanchnic tissues in comparison with the whole animal.

Haecker (1920) and Moulton et al. (1922) published extensive studies on the effects of dietary energy levels on compositional growth in cattle. These studies were the foundation for many subsequent studies, right up to the present, to examine partitioning of production energy during growth. From these subsequent studies, two basic theories have been put forth. The first, a diet-dependent theory, suggests that nutritional level can influence body
composition in growing cattle. According to this theory, higher energy levels in the diet should result in greater fat deposition at similar live weights. The second theory, a gene-dependent theory, suggests that growing animals exhibit the same body composition at a given live weight, regardless of nutritional level.

The work of Haecker (1920), Moulton et al. (1922), Geay et al. (1976) and Byers and Parker (1979) showed changes in the body composition of growing cattle in response to alterations in either the energy density of the diet or the level of intake of the diet. Increasing the dietary energy density or level of intake resulted in more fat production relative to protein and bone production. It was also shown in these studies that fattening increased with increased rates of gain. Work by Guenther et al. (1965), Reid et al. (1968), Trenkle and Topel (1978) and Loveday and Dikeman (1980) showed similar body compositions of cattle slaughtered at similar live weight, regardless of dietary energy density or rate of gain. These observations were in cattle of similar genetic backgrounds within each study.

Interest in the effect of plane of nutrition on the growth of genetically dissimilar cattle has recently increased. The reason for this interest is the rapid growth in popularity of the large-frame exotic breeds from Europe. Both similarities and differences between breeds and types
have been reported, depending on the growth characteristics observed. Butterfield (1963) reported that, after approximately five months of age, cattle show no differences in muscle weight distribution that are attributable to breed differences. Berg and Butterfield (1976) reported that the concept of uniformity of muscle weight distribution within a species, irrespective of breed, is as equally true in pigs as it is in cattle. They did observe differences in distribution of fat in depots as a consequence of breed differences, but remarked that all depots filled at uniform rates.

Trenkle et al. (1978) found a higher quantity of lipid in the M. longissimus of Angus-sired calves at each of four slaughter weights when compared with Charolais-sired calves. No differences were noted in muscle cellularity characteristics of RNA, DNA content or protein/DNA ratio.

Geay and Robelin (1979) found large differences in dry matter intake (DM/kg W.75) between young Charolais and Friesian bulls compared on a percentage of mature weight basis, i.e., at the same physiological age. Friesian bulls consumed 5-30% more food and energy than Charolais bulls when allowed feed ad libitum. Friesian bulls also gained more fat and less protein than Charolais bulls at each point between 30 and 50% of mature weight. Comparing Charolais and Saler bulls, they reported a genotype by feeding level interaction. A 17%
metabolizable energy restriction caused a 31% decrease in carcass fat without significant change of empty body weight gain in Saler bulls. The same energy restriction in Charolais bulls showed no change in carcass fat content, but resulted in an 8.1% decrease in growth rate. They concluded that the effect of restriction at the same chronological age depends on the rate of maturity of the animal.

Webster (1980) noted that it is not yet possible to precisely describe how breeds differ in the way they partition ME between protein, heat and fat. He stated that it is clearly recognized that the main difference between breeds is in mature size. Recent performance tests by the U.K. Meat and Livestock Commission showed an interaction between breed and plane of nutrition for food conversion efficiency. Breeds which are characterized as smaller frame, earlier maturing and fatter have a more favorable feed efficiency at slow rates of growth and vice versa.

Protein Level

The relative importance of protein synthesis rates versus protein degradation rates in the regulation of growth during various nutritional states is poorly understood. Millward and Waterlow (1978), in their review of nutritional effects on muscle protein turnover, stated that the most
rational explanation for the changes in the fractional breakdown rate in muscle is that protein breakdown in this tissue is not a process that is normally involved in the regulation of protein balance, and rates of protein breakdown in muscle do not rise except in what is called the terminal catabolic phase. These conclusions were based on previous work using rats (Millward et al., 1975, 1976) and are supported by work with humans recovering from malnutrition or surgical injury (Waterlow et al. 1977 and Golden et al. 1977), but Maruyama et al. (1978) used young broiler and leghorn chicks and reported the opposite effect. They reported that nutritional regimes had relatively little effect on protein synthesis rates in young chicks and that decreases in protein degradation rates accounted for much of the increase in protein content in rapidly growing chicks. The inherent problem lies in the fact that protein degradation rates could not be measured directly.

The role of amino acids has received much attention in other nutritional work involving growth and protein turnover. In vitro work with rat diaphragms by Fulks et al. (1975) showed that the addition of amino acids at plasma concentrations both promoted protein synthesis and inhibited degradation in the diaphragm. Higher concentrations of amino acids had greater effects and the three branched-chain amino acids together stimulated synthesis and reduced degradation,
whereas the remaining amino acids had no significant effect. Glucose by itself inhibited protein degradation, but in the absence of insulin it did not significantly affect protein synthesis.

Hedden and Buse (1979) further explored the effect of branched-chain amino acids in vitro on protein synthesis in diaphragms. They found that leucine, isoleucine and valine stimulated synthesis of soluble and myofibrillar protein fractions equally. They noted that this lack of selectivity of the stimulatory effect by the branched-chained amino acids was compatible with an effect on translation.

In reviewing the role of amino acid metabolism in skeletal muscle, Goldberg and Chang (1978) explained that muscle does not degrade most amino acids, but is probably the primary site in mammals for the catabolism of branched-chain amino acids. Skeletal muscle oxidizes leucine to CO2 and can convert the carbon skeleton of aspartate, asparagine, glutamate, isoleucine and valine into intermediates of the tricarboxylic acid cycle. The ability of leucine alone to stimulate protein synthesis and retard protein degradation makes these pathways of special interest. Greater amounts of alanine and glutamine are synthesized by muscle using amino groups from the degradation of branched-chain amino acids. Thus, in fasting or the postabsorptive state, muscle releases most amino acids generated by net protein breakdown but
converts isoleucine, valine, glutamate, aspartate and asparagine into glutamine and alanine which is then released for use by other tissues.

Protein metabolism in ruminants is much more complex than in monogastrics. The rumen microorganisms have the ability to degrade amino acids and make use of ammonia nitrogen to synthesize their own proteins. The host animal then receives its protein either from microbial protein passing out of the rumen or from dietary protein that escapes degradation and is passed on to the lower tract. Several new protein feeding systems have been developed as rumen metabolism has become better understood and as the use of non-protein nitrogen sources, such as urea, has increased (Owens, 1980). Use of one of these protein feeding systems allows for a more definitive calculation of the true protein level being fed to cattle.

One of the new protein systems, the metabolizable protein (MP) system (Burroughs et al., 1974), was used to calculate the amount of protein supplied by corn grain, corn gluten meal and urea in the rations fed in this study. Corn has been the preferred feed grain for growing and finishing cattle in the United States. This status generally has been attributed to the high metabolizable energy (ME) value of corn. Recent studies, however, by Trenkle et al. (1981, 1982) indicated that corn protein may have unique
characteristics which contribute to the excellent performance of corn grain as a cattle feed. In these studies, diets containing protein from corn gluten meal or corn silage produced cattle with leaner carcasses, improved feed efficiencies and similar rates of gain when compared with diets containing soybean protein.

Corn protein has the highest percentage of branched-chain amino acids of any commonly used feedstuff. In corn 20.2% of the amino acids are branched, and leucine alone constitutes 11.0% (Atlas of Nutr. Data on U.S. and Can. Feeds. 1971). Evaluation of corn protein by the criteria of the MP system shows that approximately 45% of the protein escapes rumen degradation and passes down to the lower gastrointestinal tract. In light of the previous discussion regarding the role of branched-chain amino acids in skeletal muscle, these characteristics of corn protein suggest that serious consideration be given to the potentially unique quality of corn protein in cattle rations.

Most of the studies on the effect of dietary protein content on composition of growing animals have not been done with ruminants. Work with chickens and pigs is more plentiful than studies with other meat animals. Holsheimer (1975) increased crude protein content from 16 to 24% in isoenergetic broiler rations and found that increasing the crude protein intake increased protein production in birds
with decreased efficiency of dietary protein utilization. In other words, with higher protein levels, the degree of additional gain lessened. Hartel (1970) obtained similar results, again feeding isoenergetic broiler rations containing either 18, 20, 22, 24 or 26% crude protein. Here, too, increasing crude protein intake resulted in increased protein growth and, as protein level increased, the additional gain decreased.

Just (1977) stated that protein deposition in pigs increased linearly with increasing protein intake, provided that the energy requirement was met and the protein intake was less than the daily requirement. An excess of protein above the physiological requirement affected protein deposition only slightly, but decreased the energy value of the diet, whereas increased energy caused a linear increase in fat deposition. The work of Homb (1962), investigating the relationship between daily protein intake and daily protein deposition in growing pigs, found a linear relationship between intake and deposition ($r = .99$). Protein levels in this experiment did not exceed optimum requirement. Garrett (1977) summarized the literature on rats, chickens and pigs by stating that protein utilization ($^\wedge$ protein retention/$^\wedge$ protein intake) was shown to be constant for intakes of zero to those commensurate with maximal weight gains.
Altering the dietary protein content of ruminant rations is not as easily accomplished as in monogastric rations. This is related to ruminant protein metabolism and microbial degradation of amino acids. Orskov (1977) pointed out the differences in ruminant protein requirements and the effect of protein levels in ruminant rations. He stated that, "even if the contribution of protein from the rumen exceeds the needs of the host animal, the nitrogen needs of the rumen organisms must be satisfied to ensure optimum energy utilization." If too much protein bypasses the rumen, or if too little protein is fed, the energy supplied to the animal by microbial-produced volatile fatty acids will be decreased because of poor microbial growth. Conversely, protein levels are limited in rations that are extensively degraded in the rumen. With these rations, the ammonia nitrogen requirement of the microbes is met, and excess ammonia is lost. In any study observing the effect of dietary protein on growth in ruminants, failure to take into consideration the previous discussion, or failure to make use of the new protein feeding systems, may result in errors in determining the actual protein levels fed.

Studies with ruminants on the effects of dietary protein levels on compositional growth are few, as mentioned before, and none of these studies use the new protein feeding systems. Andrews and Orskov (1970) and Orskov et al. (1976)
fed diets varying in protein content to growing lambs and observed greater fat deposition in the empty bodies of those receiving the low-protein diet. Similar results were obtained by Waldo and Tyrrell (1980) in Holstein steers; increased intake of insoluble feed protein increased protein gain. Rohr et al. (1982) observed a decrease in live weight gain and in empty body gain of Friesian bulls fed diets containing a protein level below that needed for optimum growth, but observed no change in carcass composition.

Garrett (1977) drew two conclusions regarding the influence of dietary protein level and protein production in ruminants: "1) Protein intakes below those which promote growth to a genetic potential can have a measurable influence on the composition of the animal when compared to similar weight, adequately fed animals. The differences in body composition are, however, small and do not appear to affect the commercial value of the carcass; and 2) Dietary protein levels considerably above those promoting protein deposition to some genetic potential do not have a stimulatory influence on protein deposition."
Endocrinology

Hormones have a major role in the regulation of growth and development. In controlling the metabolism associated with these functions, the endocrine system regulates partitioning of nutrients to various tissues. The process of endocrine control of metabolism and growth involves two major phases, homeostasis and homeorhesis (Bauman et al., 1982). These phases may be thought of as being similar to maintenance and production phases associated with nutrition. Homeostasis is defined as "the operation of multiplex compensatory mechanisms to preserve relative steady state of variables with vital function, despite challenges from the external environment." Homeorhesis can then be viewed as "the coordination of metabolism of body tissues in support of a dominant developmental or physiological process."

Many advances have been made in understanding endocrine control of metabolism and growth in the last two decades. The use of radioimmunoassay techniques for measuring hormone concentrations in the blood has greatly aided in these advancements. In a review of endocrine regulation of ruminant energy metabolism, Trenkle (1981) pointed out that most of the current knowledge is derived from studies of factors affecting concentrations of hormones in blood plasma.
The accuracy of plasma hormone concentrations as indicators of physiological response has been questioned. Preliminary evidence from studies of metabolic clearance and hormone receptors suggests that the concentrations of hormones in blood are meaningful values and are related to biological responses to hormones. Furthermore, changes in concentrations of hormones in plasma were influenced more by secretion than by clearance.

Many hormones are involved in the regulation of growth and nutrient partitioning. The actions of the hormones in controlling these functions are interrelated, and usually are not the result of a single hormone. In this review, and in the studies reported later, only growth hormone from the pituitary gland, insulin and glucagon from the pancreas and thyroxine and triiodothyronine from the thyroid gland will be considered. These hormones have been shown previously to exert major control over protein and energy metabolism related to growth (Trenkle, 1980, 1981; Bauman et al., 1982; Martin et al., 1984; Etherton and Kensinger, 1984).

Growth hormone (GH) is a peptide secreted by the anterior pituitary gland. It is necessary for normal skeletal and muscular growth. Hypophysectomy of a growing animal halts growth of these tissues, but growth is restored by GH injections (Trenkle, 1974). The secretion of GH is episodic, with secretory spikes, or peaks, that are 5- to
10-fold greater than the basal concentration (McAtee and Trenkle, 1971; Anfinson et al., 1975). When this type of secretory pattern exists, frequent blood samples over an extended period of time are necessary to properly assess GH status because an increase in the frequency or amplitude of the secretory spikes may be more important than the basal concentration.

Much attention is currently focused on the role of GH as a possible anabolic agent for commercial use. Exogenous administration of GH will increase nitrogen retention and decrease plasma concentrations of amino acids, and it appears to have positive effects on lipolysis and negative effects on lipogenesis (Davis et al., 1970; Machlin, 1972; Moseley et al., 1982). Bauman and coworkers (1982) observed an increase of 10-15% in the milk yields from high-producing dairy cows when the cows were treated with exogenous GH. These cows showed an increase of 17-18% in milk energy secretion without changes in feed intake, or in energy and protein digestibility. In that short-duration study, the response was confined to postabsorbptive events. In the meat animal studies of Machlin (1972) and Wagner and Veenhuizen (1978), chronic GH administration increased feed efficiency, as well as increased growth rate. The specific action by which GH causes these effects is unclear. The most prevalent concept expounded is that GH action is mediated indirectly by
somatomedins. Evidence in support of this concept comes from observations that GH did not increase amino acid uptake, cell proliferation or actin synthesis in cultured myoblast and satellite cells but somatomedins did have an effect (Ewton and Florini, 1981; Allen et al. 1983). When the influence of pituitary GH was removed by fetal decapitation, general body or muscle development was not affected in pigs (Campion et al., 1980; Hausman et al., 1982). In their review of the role of somatomedins, or insulin-like growth factors (IGF), in fetal development, Etherton and Kensinger (1984) stated that the concentration of somatomedins in fetal blood appears to be regulated by placental hormones rather than by pituitary GH as in the postnatal animal. Not all effects of GH, however, are ascribed to somatomedins. Isaksson (1982) reported stimulation of bone growth in vivo by administration of hGH to the proximal cartilage plate of rat tibia.

Insulin is a protein hormone secreted by the islets of Langerhans in the pancreas. Insulin enhances glucose transport into muscle and fat cells and increases utilization of glucose for oxidation, fatty acid synthesis, glyceride-glycerol synthesis and glycogen synthesis (Mersmann, 1979). These effects of insulin seem to be mediated by interaction of the hormone with a specific cell membrane receptor.
In ruminants, the major carbon source for fatty acid synthesis is acetate, a rumen fermentation product. Glucose is not readily incorporated into fatty acids by ruminants, but is used in glyceride-glycerol synthesis. The incorporation of acetate into fatty acids in vitro is increased by the addition of insulin and glucose into the medium (Mersmann, 1979). The insulin-stimulated increase of incorporation of substrate into fatty acids in ruminants is modest when compared with many monogastric species. An explanation of the low response of ruminant adipose tissue to insulin may be that it is an evolutionary adaptation to the essentially continuous eating patterns of these animals, and to the continuous supply of nutrients from the rumen (Mersmann, 1979).

In their review of the growth and development of meat animals, Trenkle and Marple (1983) discussed the ability of insulin to stimulate protein synthesis. This action is assumed to be the result of an increase in intracellular amino acid uptake and an increase in the activity of the initiation factor of protein synthesis. Czech (1984) has shown that the receptors for IGF-1, IGF-2 and insulin form a similar family, with varying degrees of cross-reactivity. The receptors and hormones have different affinities and abilities to stimulate, but all will cross-react. The addition of insulin does not stimulate myogenic activity in
vitro at physiological concentrations, but at concentrations several fold above physiological levels, it can stimulate myoblast proliferation (Florini et al., 1977; Florini and Ewton, 1981). The insulin-like growth factors will stimulate this activity at physiological concentrations, so it can be assumed that insulin is reacting with the IGF receptor when it is present in elevated amounts.

Concentrations of insulin in plasma show little relationship to growth rates in normal animals (Trenkle and Topel, 1978; Martin et al., 1979; Etherton, 1982). Steel and Etherton (1983) fed swine isocaloric diets with either a high or low protein level and gave insulin injections to half of each group for six weeks. Growth rate, feed efficiency, and muscle and adipose tissue mass were not affected by insulin administration within respective protein levels. They concluded that insulin concentration in swine is not normally rate limiting to animal growth. The removal of insulin, as in diabetes, shows a marked effect on growth rate in postnatal animals, and on both growth rate and composition in fetuses. These effects are well-documented in the reviews of Martin et al. (1984) and Etherton and Kensinger (1984). Neonates from diabetic mothers are hyperinsulinemic, very large and excessively fat (Martin et al., 1984). It is proposed that increased fetal glucose originating from the maternal blood stimulates B-cell development and insulin
secretion. Fetal decapitation did not change body growth or muscle cell development, but stimulated adipose cell development. In these decapitated fetuses, pancreatic insulin output increased and plasma insulin concentrations increased, suggesting insulin involvement in adipose tissue development (Martin et al., 1984). Postnatal growth is severely limited or halted by insulin deficiency, but can be restored to near normal rates by insulin administration (Martin et al., 1984; Etherton and Kensinger, 1984).

The biological effects of insulin, as of other hormones, are not solely a function of their plasma concentration, but also are influenced by hormone-receptor concentration, receptor concentration and receptor affinity for the hormone (Etherton, 1982). Much is left to be discovered in this area before it is fully understood. In addition, recent studies indicate that insulin is internalized by the target cell and bound by many organells (Izzo et al., 1979; Suzuki and Kono, 1979; Posner et al., 1980). Martin et al. (1984) found the data supportive of the presence of insulin-sensitive neurons in the hypothalamus and of a role of insulin in controlling energy intake. A humoral mechanism of the control of insulin secretion has also been suggested (Bobbioni and Jeanrenaud, 1982). A purified bovine hypothalamic extract stimulated insulin release when added to islets or administered in vivo.
to rats. The purified extract that had activity was of low molecular weight and was trypsin-sensitive.

Glucagon is also a protein hormone secreted by the pancreas. Glucagon acts on the liver to increase gluconeogenesis. Its action on adipose tissue is lipolytic when insulin concentrations are low. Glucagon participates in protein metabolism by increasing the uptake of glucogenic amino acids by the liver. This action results in an overall decrease in plasma amino acid concentrations, with less amino acids available for other metabolic processes. These functions of glucagon, and its relationship to other hormones, are discussed in a review of endocrine regulation of energy metabolism in ruminants by Trenkle (1981).

The role of glucagon in energy metabolism might best be considered in the context of the ratio of insulin concentration to glucagon concentration (I/G) (Bassett, 1975). In ruminants, this may be even more relevant, because little or no glucose is derived directly from the diet, but instead is produced by gluconeogenesis in the liver. Stimulatory substances, such as VFA's, glucose and amino acids, each affect secretion of both insulin and glucagon (Bassett, 1980). The two hormones, insulin and glucagon, work together in energy metabolism, with insulin regulating metabolism of peripheral tissues and glucagon dominating hepatic regulation. Unger (1971) has proposed that the I/G
ratio in plasma can be used as an index for the relative balance of these two hormones in maintaining homeostasis.

Considerable difficulties in measuring plasma glucagon by radioimmunoassay are incurred, because extensive cross-reaction between most antibodies to pancreatic glucagon and a glucagon-like peptide secreted by the mucosa of the intestine occurs (Bassett, 1975). In studies by Bassett (1975) using a specific pancreatic glucagon antiserum and feeding a lucerne chaff:oat grain diet once daily to sheep, a subsequent increase in glucagon concentration similar to that of insulin concentration was noted. The I/G ratio in that study ranged from 1.9 to 3.3 and prolonged fasting produced an I/G ratio averaging 1.0. These observations were consistent with Unger's (1971) proposal that low I/G ratios are associated with low carbohydrate diets. Ruminant diets, because of the conversion of carbohydrates to short chain fatty acids in the rumen, can be considered to be low carbohydrate diets in terms of digestion.

Brockman (1978) showed that glucagon stimulates gluconeogenesis in sheep from propionate in vivo. He examined the conversion of propionate to glucose under conditions of reduced or enhanced glucagon availability. Glucagon infusion increased the incorporation of propionate into glucose by 30%, whereas total glucose production rose 36% over control values. In studies with ad libitum-fed
dairy cows in early lactation, Elliot (1980) observed a positive correlation between serum insulin and plasma acetate concentrations, a positive correlation between serum glucagon and plasma propionate concentrations and a negative correlation between serum glucagon and liver vitamin B12 concentrations. Recognizing the pitfalls of correlation studies, the investigator hypothesized that lower liver B12 concentrations allowed more propionate to pass to the peripheral circulation where it stimulates glucagon release, which in turn acted on the liver to enhance propionate clearance.

Thyroid hormone plays an important role in growth and development and acts on the peripheral tissues of the adult to regulate the metabolic rate. The main secretory products of the thyroid gland are thyroxine (T4) and triiodothyronine (T3). Both compounds are metabolically active. Thyroxine concentrations in plasma are typically 10-fold or more greater than T3 concentrations, and much of the T3 is derived from the monodeiodination of T4. On a molar basis, however, T3 is 3 to 4 times more potent than T4.

Thyroid hormone deprivation during antenatal or early neonatal life causes severe mental and physical growth retardation, known as cretinism. Continuous thyroid hormone deprivation almost completely halts linear growth. In adult homeotherms, thyroid hormone administration increases oxygen-
consumption and heat production, and accelerates the metabolism of carbohydrates, proteins and fats. Not all tissues, however, respond to thyroid hormone with an increase in energy metabolism. Brain, gonads, lymph nodes, spleen and dermis are not affected by thyroid hormone. In addition, the action of thyroid hormone may be biphasic, that is, the enhancement of protein synthesis by thyroid hormone may subsequently increase the metabolic rate, causing an obligatory wastage of protein. A review of these functions of thyroid hormone, and of more in-depth studies, was presented by Bernal and Refetoff (1977).

During starvation, there was a drastic decline in plasma T3 concentrations, whether the subject was lean or obese at the start, and the plasma T4 concentration remained essentially the same (Williams, 1981). The low T3 concentration appeared to be the result of a decrease in the conversion of T4 to T3. Refeeding small quantities of pure carbohydrate restored the T3 concentration to normal, but similar quantities of protein or fat were ineffective. Overfeeding, particularly with carbohydrates, increased T3 production rates, as well as increasing plasma T3 concentrations.

In thyroidectomized rats, moderate doses of T4 increased protein synthesis and nitrogen retention, but larger doses inhibited protein synthesis and increased the free amino acid
concentration in plasma, liver and muscle (Williams, 1981). In sheep, the infusion of thyrotropin-releasing hormone (TRH) for eight weeks decreased rate of gain 21% and increased feed conversion 26% (Muir and Wien, 1983). Davis et al. (1976) reported an increase in rate of gain and increased nitrogen retention in sheep injected twice daily with TRH. These improvements in performance were not statistically significant. The dose levels, mode of administration or length of the studies may have contributed to the discrepancies between the two trials. However, both trials showed marked increases in plasma prolactin and thyrotropin concentrations and decreases in plasma GH concentrations as a result of TRH treatment. Wagner and Veenhuizen (1978) showed even greater net protein accretion rates in sheep when exogenous GH and thyroid hormone were administered together, as compared with GH alone. The same relationship is true for rats, in which optimal doses of thyroid hormone are needed for maximal responses to GH (Williams, 1981).

In carbohydrate metabolism, thyroid hormone can enhance the rate of glucose absorption from the intestines. Thyroid hormones also increase the uptake of glucose by adipose tissue and muscle, and potentiate the effect of insulin in this respect (Williams, 1981). It must be remembered, though, that much of the information concerning the effects
of thyroid hormone on carbohydrate metabolism comes from data on monogastrics, and ruminants may have altered responses.
EXPLANATION OF DISSERTATION FORMAT

This dissertation is presented in the alternate format, as outlined in the Iowa State University Graduate College Thesis Manual. Use of the alternate format allows for the preparation of independent sections in a scientific journal.

Three separate papers have been prepared from the data collected from research performed to partly fulfill requirements for the Ph.D. degree. Each paper is complete in itself and has an introduction, materials and methods, results and discussion, and bibliography. The closeness of the subject matter of the three papers allowed a general summary to be prepared.
REFERENCES


PART I. EVALUATION OF CORN ENERGY AND PROTEIN ON FEEDLOT PERFORMANCE AND BODY COMPOSITION OF STEERS
INTRODUCTION

In the endeavor to improve beef production and increase profit, the genetic limits of rate of gain may be reaching limits. Likewise, feeding to increase rate of gain may be reaching a limit. If this is true, and the maximums are being attained, then future improvements are more likely to be through increased efficiency in maintaining these performance levels. A better understanding of the growth process may provide ways to increase the efficiency of production.

Growth is often measured as live weight gain per unit of time, but live weight is a commercially useful measure of growth only if it relates to increased amounts of edible product (Berg and Butterfield, 1976). This becomes more important in light of the greater demand by consumers for a leaner product, and the increase in the costs for removal of fat which has a lower value than the lean. A better understanding of the partitioning of dietary protein and energy to the tissues of growing animals may allow greater efficiency of production, as well as production of a more desirable product.

Corn has traditionally been the preferred feed grain for finishing cattle and other livestock. The characteristics of
corn grain which give it this status in cattle feeding include its high metabolizable energy value and the physical characteristics of the kernel that are advantageous in mechanical processing. In addition, corn is an excellent source of protein for cattle because, unlike the protein in legumes and hays, corn protein is not as extensively degraded in the rumen. Work by Trenkle et al. (1981, 1982) indicated that the extent to which corn protein is responsible for this preferred status for corn grain may be underestimated.

The objectives of this study were to examine the contributions of the energy-yielding component of corn grain, in the form of starch and oil, and the protein component in the form of corn gluten meal, to improvement of feedlot performance and to alteration of body composition of steers fed a low energy, low protein diet.
MATERIALS AND METHODS

Two feeding experiments were conducted in successive years (1982 and 1983) using weanling steers from the Iowa State University beef nutrition herd. In the first experiment, 24 Angus x Charolais steers from the same sire were randomly assigned to one of 6 diets, with 4 steers assigned to each diet. The steers had an average initial body weight of 250 kg. They were fed individually in covered stalls, and feed intake was monitored daily to provide as closely as possible ad libitum feed intake. Under these conditions, steers had access to feed for approximately 11-12 hours daily, with restriction from water for never more than 6 hours. Feed offered and orts were recorded weekly, and live weights were recorded biweekly. In the second experiment, 16 Angus x Charolais steers were used. Two sires were represented in this group, with 8 steers from each sire. Two steers from each sire were assigned to each of 4 diets, with a total of 4 animals assigned to each diet. Steers were individually fed using electronic broadbent headgates (American Calan Inc., Northwood, NH) to allow ad libitum feed intake. Feed offered and orts were recorded weekly and live weights were recorded biweekly, as in the first experiment.
The design of the diets, illustrating the levels of metabolizable energy (ME) and metabolizable protein (MP), is shown in Table 1. The compositions of the diets are shown in Table 2. In experiment 1, all six diets were fed, but in experiment 2, only 4 diets were fed: low protein-low energy (LL), low protein-high energy (LH), high protein-low energy (HL) and high protein-high energy (HH). Dietary roughage was provided by corn cobs ground through a 1.4 cm screen. Energy level was increased independently of protein level by the addition of corn starch and corn oil, whereas protein level was increased independently of energy level by the addition of corn gluten meal. Molasses was added to all diets at 15% of the dry matter, and vitamins and minerals were added to meet recommendations (National Research Council, 1976). Enough urea was added to each diet to make use of available positive urea fermentation potential. The ranges of protein and energy levels were chosen to allow growth above maintenance, but not to exceed the requirement for maximal growth (National Research Council, 1976).

Steers were allowed two weeks to adapt to the diets before initiation of the experiments. Apparent dry matter digestibility (DMD) was determined at the start of each experiment and at every 90 kg of gain. For each 90 kg gain period, fecal samples were collected twice daily from each steer for 6 days, and a composite sample was prepared. Dry
Table 1. Experimental Design

<table>
<thead>
<tr>
<th>PROTEIN LEVEL (gMP/kg)</th>
<th>Low 49.7</th>
<th>Medium 55.7</th>
<th>High 63.0</th>
</tr>
</thead>
<tbody>
<tr>
<td>ENERGY LEVEL (Mcal ME/kg)</td>
<td>Low 2.19</td>
<td>Medium 2.50</td>
<td>High 2.80</td>
</tr>
<tr>
<td></td>
<td>L/L</td>
<td>L/H</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M/L</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>H/L</td>
<td>H/M</td>
<td>H/H</td>
</tr>
</tbody>
</table>
Table 2. Diet Composition

<table>
<thead>
<tr>
<th>INGREDIENT</th>
<th>L/L</th>
<th>L/H</th>
<th>M/L</th>
<th>H/L</th>
<th>H/M</th>
<th>H/H</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ground corn cob (IFN 1-02-782)</td>
<td>62</td>
<td>38</td>
<td>63</td>
<td>63</td>
<td>44</td>
<td>28</td>
</tr>
<tr>
<td>Corn (IFN 4-02-931)</td>
<td>20</td>
<td>20</td>
<td>17</td>
<td>14</td>
<td>37</td>
<td>55</td>
</tr>
<tr>
<td>Corn gluten meal (IFN 5-02-900)</td>
<td>--</td>
<td>1.0</td>
<td>3.0</td>
<td>6.5</td>
<td>2.1</td>
<td>1.2</td>
</tr>
<tr>
<td>Corn starch (IFN 4-02-889)</td>
<td>--</td>
<td>18</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Corn oil (IFN 4-07-882)</td>
<td>--</td>
<td>4.0</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Urea (IFN 4-04=696)</td>
<td>1.1</td>
<td>1.1</td>
<td>0.8</td>
<td>0.5</td>
<td>0.9</td>
<td>0.5</td>
</tr>
<tr>
<td>Molasses (IFN 4-04=696)</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>15</td>
</tr>
</tbody>
</table>

1 Sodium chloride (IFN 6-04-151), dicalcium phosphate (IFN 6-01-080), trace minerals, vitamin A and sulfur were added to each diet so that levels of minerals and vitamins met National Research Council recommendations. Rumensin, at the level of 30 mg/ton, was also added to each diet.
matter digestibility was estimated by using acid-insoluble ash as an endogenous marker. Acid-insoluble ash of the composite samples was determined by using the 2N HCl procedure described by Van Keulen and Young (1977).

Empty body composition (live weight - gut fill) was measured at the beginning of each experiment and at 3 other times, as each group attained average increments of live weight gain of 90 kg. Deuterium oxide (D2O) dilution was used to obtain these serial measurements of body composition. A one-pool model of D2O dilution, as described by Arnold et al. (1984)(Appendix C), was used to calculate the empty body weight and the percentages of fat, protein, ash and water in the empty body. Feedlot performance was also determined for each 90 kg gain period. Parameters measured included average daily gain (ADG), feed efficiency, expressed as unit of feed per unit of gain (F/G) and average days on feed (DOF).

In the second experiment, volatile fatty acid (VFA) ratios were determined in rumen ingesta after the steers had consumed the diets for 100 days. Duplicate samples of rumen fluid, collected one week apart, were obtained from each steer. Samples were taken approximately 6 hours after feeding by passing a tube through the esophagus into the reticulo-rumen and then by using a vacuum to draw up 50 ml of the fluid through a stainless steel sieve. Samples were
placed in plastic bottles that contained 1 ml of 50% H2SO4, and frozen until analyzed by gas chromatography (Baumgardt, 1964).

The steers were slaughtered at a commercial slaughter facility as each diet group attained an average total gain of 270 kg. Hot carcass weights, rib eye area and backfat thickness at the 12th rib were recorded, and the following carcass characteristics were determined by a USDA grader: yield grade, quality grade and % kidney, heart and pelvic fat (KHP).

The experiments were analyzed as a split-plot design in which dietary treatments represented the whole plots and 90 kg gain periods represented the split-plots (Steel and Torrie, 1960) (Appendix A). Data were analyzed by using the General Linear Model procedure of the Statistical Analysis System (SAS, 1979) and the least significant difference procedure was used to make specific comparisons where significant differences were determined to exist (Steel and Torrie, 1960). Because of the differences in feeding facilities and in the weather between the two experiments, data from the experiments were not combined. In the first experiment three animals were removed from the experiment due to health problems. Two of these animals were from the LH diet group and one from the ML diet group. Data collected from these animals was dropped from analysis. One
replacement steer was added to the LH diet group eight weeks past the start of the experiment. This animal was of similar initial weight to the other steers, adapted previously to the diet and data measurements were obtained for each 90 kg of individual live weight gain.
RESULTS AND DISCUSSION

Feedlot performance, i.e., average daily gain, feed efficiency (kg feed dry matter/kg live weight gain), days on feed, apparent dry matter digestibility and apparent protein digestibility, are shown in Tables 3 and 4 for the first and second experiments, respectively. Addition of either energy or protein to the LL diet increased ADG. In the first experiment, the addition of the high level of ME to the LL diet increased ADG by 13.2% (P>.05), whereas the addition of the high MP level increased ADG by 27.0% (P<.01). Addition of either ME or MP at the high level doubled the ADG in the second experiment (P<.01). In both experiments, the simultaneous addition of ME and MP (the HH diet) had an additive effect on ADG. Live weight gains for the steers in each diet group equalled the gains predicted from intake of ME (National Research Council, 1976) and MP (Burroughs et al., 1974) for each diet. Average daily gains of the steers consuming the highest energy levels declined in the final 90 kg gain period. Steers on all the other diets maintained similar rates of gain for all the gain periods.

The relationship between average daily gain and age follows a bell-shaped curve. When a typical production
Table 3. Feedlot Performance and Diet Digestibility (Experiment 1)\textsuperscript{1}

<table>
<thead>
<tr>
<th>DIET (Protein/energy)</th>
<th>L/L</th>
<th>L/H</th>
<th>M/L</th>
<th>H/L</th>
<th>H/M</th>
<th>H/H</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average daily gain, kg</td>
<td>.58a</td>
<td>.67ab</td>
<td>.68ab</td>
<td>.84bc</td>
<td>.85bc</td>
<td>.96c</td>
<td>.058</td>
</tr>
<tr>
<td>Feed/gain</td>
<td>14.2a</td>
<td>12.5b</td>
<td>13.0ab</td>
<td>10.5c</td>
<td>10.9c</td>
<td>9.8c</td>
<td>.50</td>
</tr>
<tr>
<td>Days on feed</td>
<td>124a</td>
<td>117a</td>
<td>124a</td>
<td>118a</td>
<td>95b</td>
<td>81c</td>
<td>4.3</td>
</tr>
<tr>
<td>Dry matter digestibility, %</td>
<td>66.7ab</td>
<td>65.6ab</td>
<td>59.7a</td>
<td>70.4b</td>
<td>71.9b</td>
<td>84.9c</td>
<td>2.7</td>
</tr>
<tr>
<td>Protein digestibility, %</td>
<td>60.4ab</td>
<td>59.3ab</td>
<td>55.3a</td>
<td>72.7cd</td>
<td>65.5bc</td>
<td>78.5d</td>
<td>2.7</td>
</tr>
</tbody>
</table>

\textsuperscript{1}Values with different letters, but in the same line, are different, $P<.05.$
Table 4. Feedlot Performance and Diet Digestibility $^{1,2}$
(Experiment 2)

<table>
<thead>
<tr>
<th>DIET (Protein/energy)</th>
<th>L/L</th>
<th>L/H</th>
<th>H/L</th>
<th>H/H</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average daily gain, kg</td>
<td>.42a</td>
<td>.80b</td>
<td>.81b</td>
<td>1.15c</td>
<td>.067</td>
</tr>
<tr>
<td>Feed/gain</td>
<td>15.2a</td>
<td>12.1b</td>
<td>10.9b</td>
<td>10.5b</td>
<td>.68</td>
</tr>
<tr>
<td>Days on feed</td>
<td>141a</td>
<td>95b</td>
<td>101b</td>
<td>84c</td>
<td>3.2</td>
</tr>
<tr>
<td>Dry matter digestibility, %</td>
<td>61.4d</td>
<td>64.6de</td>
<td>60.1d</td>
<td>72.8e</td>
<td>2.9</td>
</tr>
<tr>
<td>Protein digestibility, %</td>
<td>57.8</td>
<td>58.5</td>
<td>59.2</td>
<td>65.4</td>
<td>3.7</td>
</tr>
</tbody>
</table>

$^1$Values with different letters, but in the same line, are different, $P<.001$.

$^2$Values with different letters, but in the same line, are different, $P<.04$. 
scheme is followed, weanling calves have rates of gain that fall on the ascending slope of this curve, whereas long yearling cattle have rates of gain that fall on the descending slope. The declining gains during the final period of the steers consuming the high level of ME suggest that the degree of fatness of the animal, as well as chronological age, may play a role in the reduced rate of gain. Whereas steers on all the diets gained fat at all times, steers receiving the higher levels of ME had a greater proportion of their gain as fat. Gain of fat contributes less to live weight gain than does protein gain, because protein gain is accompanied by water in order to form muscle. Thus, gains beyond the stage where protein accretion has plateaued would be expected to occur at a slower rate.

Feed efficiency improved with increasing levels of either nutrient. The addition of the high level of ME to the LL diet improved feed efficiency by 12.0% and 20.4% (P<.01) in the first and second experiment, respectively. When added to the LL diet, the high MP level improved feed efficiency by 26.0% in the first experiment (P<.01) and by 28.3% in the second experiment (P<.01). The greater improvement in feed efficiency obtained with the HL diet as compared with the LH diet was significant only in the first experiment. Steers consuming the HH diet had the lowest F/G in both experiments, but this F/G was not statistically different from the F/G
observed with cattle fed the HL diet. The ratio of feed to gain increased in successive gain periods, regardless of which diet was fed ($P < .02$).

Feed efficiency improved as energy or protein density of a diet increased because a greater proportion of the nutrients were available for production processes after the maintenance needs of the animal were satisfied. The efficiency of ME utilization by monogastrics for fat gain is approximately 75%, and of protein gain, 45% (Pullar and Webster, 1977). These values would be much lower for ruminants, but as stated earlier, the protein gain is accompanied by water. Thus, when efficiency is measured as unit of feed per unit of live weight gain, animals gaining a greater proportion of muscle will be more efficient than animals with similar live weight gains that are gaining more fat. This would explain the poorer feed utilization that was observed for steers consuming the LH diet when compared with those consuming the HL diet, in spite of similar live weight gains by the two groups.

Maintenance requirements increase as live weight increases. This is not a direct relationship, but a function of the "metabolic" body weight (live weight raised to the 0.75 power). Because of this relationship, F/G increased in successive gain periods for all diet groups.
Dry matter digestibility was improved, when compared with the LL diet, only by the HH diet (P<.04). Dry matter digestibility was usually highest for all diets in the second gain period, and declined slightly in the final gain period (P<.03). In the first experiment, protein digestibility was highest in the diets containing the high MP level. Protein digestibility increased from the first to the second gain period (P<.01), and then remained constant until the end of the experiment. There was no statistical difference between the protein digestibility of the diets in the second experiment, however the digestibility of protein in the diets with high MP levels tended to be greater than in the other diets. In this experiment, protein digestibility of all diets except the HH diet decreased with successive gain periods (P<.01). Protein digestibility of the HH diet remained constant throughout the experiment.

Dry matter digestibility of the LH diet did not improve in spite of the replacement of 22% of the dry matter as ground corn cobs by 18% corn starch and 4% corn oil. The improved gain of steers consuming the LH diet indicates increased absorption of ME when the starch and the oil diet was fed. The lack of improvement in DMD of this diet may reflect a decrease in the digestion of fiber resulting from a
decrease in rumen pH and in rumen turnover time caused by the rapid fermentation of the highly digestible corn starch (Sutton, 1980).

The protein of corn grain is not degraded as extensively in the rumen as the proteins of other commonly used feeds. Approximately 45% of the protein in corn will bypass the rumen and pass into the abomasum and intestines for digestion. Protein digestibility could be influenced by an effect of the ratio of protein to energy in the diet on rumen microbial activity and on rate of passage of digesta through the gastrointestinal tract. Neither of these factors, however, can account for the differences in protein digestibility between the two experiments, or for the generally low protein digestibility of all the diets. The differences in feeding regimes between the two experiments may have had some effect on protein digestibility, because animals in the first experiment had access to feed for 10-14 hours each day, whereas animals in the second experiment had access to feed for 24 hours each day.

Molar ratios of acetate, propionate, and butyrate in strained rumen fluid are presented in Table 5. Values represent the average of each diet group in the second experiment. The relative amounts of propionate increased and acetate decreased when the level of ME was increased (P<.05). Higher levels of MP in the diet resulted in relatively more
Table 5. Rumen VFA Ratios (Experiment 2)\(^1\)

<table>
<thead>
<tr>
<th>PROTEIN</th>
<th>Low</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>75a:17ab:8</td>
<td>68b:24c:8</td>
</tr>
<tr>
<td>High</td>
<td>77a:14a:9</td>
<td>70b:20b:9</td>
</tr>
<tr>
<td>SEM</td>
<td>1.5:1.3:0.4</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\)Values with different letters are different, \(P<.05\).
acetate and relatively less propionate, but the differences were not significant. The relative proportion of butyrate was not affected by nutrient density.

In ruminants, the 2-carbon yielding compounds (acetate and butyrate) can be used readily for fat synthesis, whereas the 3-carbon compounds (propionate) and amino acids are used to meet the demand for gluconeogenic precursors. The requirement for energy from glucose stems from the need for 3-carbon compounds for oxidation, synthesis of nonessential amino acids and generation of NADPH and glycerol for synthesis of lipids. Work by Orskov et al. (1979a, b) showed no consistent difference in the efficiency of utilization of widely-varying VFA ratios for maintenance, growth and energy retention. The authors concluded that there was little likelihood that glucose could ever be the limiting factor in growth. Thus, it appears that the increased fat in the steers receiving the high ME levels is associated more strongly with an excess of available energy (beyond the needs for maintenance and protein synthesis) than it is with any effect of altered VFA ratios.

The average empty body composition of steers in each diet group that were calculated from the dilution of D2O in the live animals is summarized in Tables 6 and 7. In the first experiment (Table 6), the steers consuming the medium and high levels of MP at the low ME level had the lowest
Table 6. Empty Body Composition (Experiment 1) ¹

<table>
<thead>
<tr>
<th>DIET (Protein/energy)</th>
<th>L/L</th>
<th>L/H</th>
<th>M/L</th>
<th>H/L</th>
<th>H/M</th>
<th>H/H</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protein, %</td>
<td>18.1ab</td>
<td>17.6a</td>
<td>18.6b</td>
<td>18.7b</td>
<td>17.6a</td>
<td>17.5a</td>
<td>.24</td>
</tr>
<tr>
<td>Fat, %</td>
<td>17.8ab</td>
<td>20.7a</td>
<td>14.5b</td>
<td>14.1b</td>
<td>20.2a</td>
<td>21.0a</td>
<td>1.39</td>
</tr>
<tr>
<td>Ash, %</td>
<td>4.0a</td>
<td>3.9a</td>
<td>4.2b</td>
<td>4.2b</td>
<td>3.9a</td>
<td>3.9a</td>
<td>.05</td>
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</table>

¹Values with different letters, but in the same line, are different, P<.05.
Table 7. Empty Body Composition (Experiment 2)\textsuperscript{1}

<table>
<thead>
<tr>
<th></th>
<th>L/L</th>
<th>L/H</th>
<th>H/L</th>
<th>H/H</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protein, %</td>
<td>18.4a</td>
<td>17.4b</td>
<td>18.8a</td>
<td>17.5b</td>
<td>.30</td>
</tr>
<tr>
<td>Fat, %</td>
<td>15.7a</td>
<td>21.5b</td>
<td>13.5a</td>
<td>21.3b</td>
<td>1.7</td>
</tr>
<tr>
<td>Ash, %</td>
<td>4.1ab</td>
<td>3.9b</td>
<td>4.2a</td>
<td>3.9b</td>
<td>.07</td>
</tr>
</tbody>
</table>

\textsuperscript{1}Values with different letters, but in the same line, are different, P<.05.
percentage of fat and the highest percentages of protein and ash (P<.05). The steers receiving the medium and high levels of ME, regardless of MP level, had the highest percentage of fat and the lowest percentages of protein and ash (P<.05). The LL diet produced steers with empty body compositions that were intermediate. A similar relationship between diet group and empty body composition was observed in the second experiment (Table 7). Percentages of fat, protein and ash were similar to those obtained in experiment 1, except that the steers on the LL diet in experiment 2 were leaner than in the previous experiment, and were closer in composition to steers consuming the HL diet.

The patterns of fat accretion by each diet group as they increased in live weight are shown in Figures 1 and 2. By the first 90 kg of gain, the steers consuming the medium and high ME levels already exhibited greater fat accretion. This pattern of a greater percentage of fat in the live weight gain was maintained throughout the remainder of the experiment. All steers in all diet groups increased in percentage fat as they increased in live weight.

Carcass measurements and grading scores, as determined by USDA graders, are presented in Table 8. Carcass characteristics and grading scores directly reflected empty body composition estimated by dilution of deuterium oxide. The leaner steers, diet groups LL, ML and HL, had lower
Figure 1. Average percent empty body fat of diet groups initially (I) and subsequent live weight gain periods of 90 kg (Experiment 1) Diet effect $P < .01$ Period effect $P < .01$ SEM = 1.39
% Empty Body Fat

Diet Group
- LH
- LL
- HM
- HH
- HL
- ML

90 kg Gain Period
Figure 2. Average percent empty body fat of diet groups initially (I) and subsequent live weight gain periods of 90 kg (Experiment 2) Diet effect $P<.05$ Period effect $P<.01$ SEM = 1.58
% Empty Body Fat

LL

LH

HL

HH

% Empty Body Fat vs 90 kg Gain Period
Table 8. Carcass Characteristics (Experiments 1 and 2)

<table>
<thead>
<tr>
<th>DIET (Protein/Energy)</th>
<th>DRESSING PERCENTAGE (%)</th>
<th>LOIN EYE AREA (sq in)</th>
<th>QUALITY GRADE</th>
<th>YIELD GRADE</th>
<th>BACKFAT THICKNESS (in)</th>
<th>KHP FAT (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L/L</td>
<td>56.9</td>
<td>11.8</td>
<td>CH-1</td>
<td>1.75</td>
<td>0.20</td>
<td>2.6</td>
</tr>
<tr>
<td>L/H</td>
<td>60.3</td>
<td>12.2</td>
<td>CH-</td>
<td>2.00</td>
<td>0.27</td>
<td>2.5</td>
</tr>
<tr>
<td>M/L</td>
<td>58.3</td>
<td>11.5</td>
<td>G+2</td>
<td>2.00</td>
<td>0.15</td>
<td>2.3</td>
</tr>
<tr>
<td>H/L</td>
<td>55.0</td>
<td>11.5</td>
<td>G</td>
<td>1.50</td>
<td>0.22</td>
<td>2.4</td>
</tr>
<tr>
<td>H/M</td>
<td>60.6</td>
<td>12.3</td>
<td>CH-</td>
<td>2.50</td>
<td>0.36</td>
<td>3.0</td>
</tr>
<tr>
<td>H/H</td>
<td>61.5</td>
<td>13.3</td>
<td>CH</td>
<td>2.25</td>
<td>0.35</td>
<td>3.0</td>
</tr>
<tr>
<td>Experiment 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L/L</td>
<td>57.1</td>
<td>11.0</td>
<td>G</td>
<td>1.25</td>
<td>0.19</td>
<td>1.8</td>
</tr>
<tr>
<td>L/H</td>
<td>61.8</td>
<td>12.8</td>
<td>CH-</td>
<td>2.25</td>
<td>0.33</td>
<td>2.8</td>
</tr>
<tr>
<td>H/L</td>
<td>56.6</td>
<td>12.5</td>
<td>G+</td>
<td>1.25</td>
<td>0.19</td>
<td>1.9</td>
</tr>
<tr>
<td>H/H</td>
<td>62.1</td>
<td>13.4</td>
<td>CH-</td>
<td>2.25</td>
<td>0.48</td>
<td>2.9</td>
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</tbody>
</table>

1CH = choice.
2G = good.
dressing percentages in both experiments. Muscling, as indicated by loin eye area, was greater in steers consuming the HH diet and was similar in the other diet groups. Steers receiving medium and high ME levels had thicker backfat, higher yield grades, quality grades of choice minus or better and a higher percentage of kidney, heart and pelvic fat than the other diet groups.

During the growth period observed in these studies, empty body composition was significantly different between steers consuming diets varying in ME density. The indication of greater muscling in steers receiving the HH diet was probably because these steers were slaughtered at live weights that were higher than planned. Steers receiving the LL diet had the slowest rate of growth and consequently had the longest time on feed. This caused the final 90 kg gain period of these steers to extend into early winter. In the second experiment, the ambient temperatures during this period were unusually cold, and this may partially account for the lower percentages of body fat observed in this experiment when compared with experiment 1, because during extreme cold more dietary energy would be required to maintain body temperature instead of being deposited as body fat.

Accurate determination of body composition in live animals has proven to be difficult. Many studies have used
serial slaughter techniques to estimate body composition, because more precise, non-terminal techniques were not available. The use of dilution of deuterium oxide in the body water to predict changes in body water and then relating body water to protein and fat content allows for repeated measurements on the same animals. A unique modification of this technique using a two-component kinetic model has recently been proposed (Byers, 1979), but further evaluation by Arnold et al. (1984) indicated that this two-compartment approach is less desirable than the one-compartment model that was used in the present studies.

Differences in compositional growth as a result of nutritional manipulation have been reported by other workers (Orskov and McDonald, 1970; Byers and Parker, 1979). Previous studies of the effects of nutritional manipulation on compositional gain have dealt largely with the effects of level of energy or level of intake. Results obtained in the present studies agree well with the results of these studies. As shown by comparing the LL and HH groups in this study, increased level of feeding resulted in an increase in the percentage of fat in the live weight gain. Similar results are obtained when only the energy level of the diet was increased, regardless of the MP level, as can be seen by comparing the LL group with the LH group, and the HL group with the HH group. In both of these comparisons, similar
additions of energy resulted in similar improvements in gain, regardless of MP level. In addition, at all MP levels, increased rates of gain in response to the increase in energy level were accompanied by an increase in fat accretion by the steers.

The changes in composition that were observed in this experiment were not necessarily dependent on rate of gain. Steers receiving the LH and HL diets had similar ADG, but differed widely in the composition of those gains. These results are consistent with the concept of partitioning dietary energy to meet the priority energy needs that were described by Berg and Butterfield (1976). Energy is first partitioned for maintenance of vital functions and metabolic needs of organs and structural tissues. Next, energy is partitioned for growth of new tissues until the genetic potential for growth is reached, or until other available nutrients, such as amino acids and minerals, become limiting. Finally, excess energy is then partitioned for storage in the form of fat. All fat accretion is not simply energy storage, however, and some partitioning of energy for essential fat accretion does occur at all stages of growth.

The higher protein levels at the low energy level decreased the relative amount of fat gain in the steers, and increased the protein gain. At the high energy level, increasing the protein content of the diets did not alter
empty body composition, but did increase average daily gain. This increased gain included muscle gain, as well as fat gain. Increasing the protein level did allow for increased muscle deposition.

Much more research into the effects of protein level on body composition has been done with nonruminants animals than with ruminants. Recently, several new protein feeding systems have been introduced that define more exactly the useable protein content of rations fed to ruminants. Previous studies that did not have these systems available for use may have been in error as to the actual protein level fed. The problem is demonstrated in the work of Waldo and Tyrrell (1980), in which cattle were fed either untreated or formaldehyde-treated silages. The treated silage supplied more by-pass protein, but had the same crude protein content as the untreated silage. Empty body weight gain was substantially higher in cattle consuming the formaldehyde-treated silage.

In nonruminants, increasing the crude protein level in a diet increases the percentage of muscle in the carcass, and decreases the percentage of fat (Just, 1982). This relationship is true for levels from zero to the level that is optimal for growth. Levels of protein in excess of that for optimal growth have no stimulatory effect on growth, but do tend to decrease the ration's energy value. In one of the
few studies with ruminants, increasing the protein levels fed to lambs resulted in empty body compositions that were lower in fat and higher in protein (Orskov et al., 1976). Waldo and Tyrrell (1980) observed similar results when Holstein steers were fed increasing levels of insoluble protein. Rohr et al. (1982) found a decrease in live weight gain and in empty body gain, but no change in carcass composition of Friesian bulls fed protein levels below those associated with optimal growth.

In summary, the addition of either energy or protein improved daily gain, and the two components showed an additive effect when increased together. While both components improved feed efficiency, the addition of protein resulted in the greatest improvement, presumably because of the greater weight of increased muscle deposition relative to fat deposition. Varying the relative amounts of protein and energy, and the ratio of protein to energy, in diets fed to steers resulted in different empty body composition at similar live weights.
REFERENCES


PART II. EFFICIENCY OF UTILIZATION OF CORN ENERGY AND PROTEIN FOR FINISHING BEEF CATTLE
INTRODUCTION

The efficiency with which beef cattle convert feedstuffs into edible meat for human consumption is quite low when compared with other meat animals. A better understanding of the partitioning and utilization of energy and protein in various tissues during growth may allow for an improvement in the efficiency of production.

Recent studies have demonstrated the ability to alter empty body composition in growing cattle by nutritional manipulation (Rohr and Daenicke, 1978; Geay and Robelin, 1979; Byers and Parker, 1979; ARC, 1980; Waldo and Tyrrell, 1980; Hentges and Trenkle, 1983). These studies show a relationship in ruminants similar to that in nonruminants that daily body fat accretion increases with increasing feeding intensity (Just, 1984), and low protein intake reduces daily gain and feed efficiency. In contrast, excess protein, above an optimum for muscle growth, has little or no stimulatory effect on growth (Just, 1977). Not all researchers agree, however, that tissue growth can be modified by nutritional factors (Reid et al., 1968; Jesse et al., 1976; Loveday and Dikeman, 1980).
Studies of nutritional modification of body composition in ruminants usually have involved energy level, and few studies have dealt with the effects of protein level on body composition. The metabolizable protein system described by Burroughs et al. (1974), one of several new protein feeding systems, allows for a more precise calculation of the useable protein levels in diets for ruminants. The objective of this study was to observe the efficiency of utilization of digestible energy and protein by feedlot steers fed diets varying both in the levels of and in the ratios of protein and energy. These observations were made for fixed increments of live weight gain.
MATERIALS AND METHODS

Two experiments were conducted in successive years (1981 and 1982). The first experiment used 24 Angus x Charolais weanling steers from a single sire. The second experiment used 16 Angus x Charolais weanling steers, 8 from each of two sires. The average initial body weight of the steers was 240 and 254 kg, respectively, for the first and second experiments.

Four steers were randomly assigned by sire group to each dietary treatment and were allowed two weeks to adjust to the diets before the experiments were begun. Six diets were fed in the first experiment, and four were fed in the second. In the first experiment, three levels of metabolizable energy (ME) and three metabolizable protein (MP) levels were fed. Experimental design and MP and ME levels are shown in Table 1. The four diets fed in the second experiment utilized only the low and high levels of protein and energy used in the first experiment. The steers were fed individually once daily to allow ad libitum feed intake. Composition of the diets is shown in Table 2. Corn gluten meal was used to increase protein levels, and corn starch and corn oil were used to increase energy levels. A more detailed discussion
### Table 1. Experimental Design

<table>
<thead>
<tr>
<th>PROTEIN LEVEL (gMP/kg)</th>
<th>ENERGY LEVEL (Mcal ME/kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low</td>
</tr>
<tr>
<td>Low 49.7</td>
<td>L/L</td>
</tr>
<tr>
<td>Medium 55.7</td>
<td>L/H</td>
</tr>
<tr>
<td>High 63.0</td>
<td></td>
</tr>
<tr>
<td>INGREDIENT</td>
<td>L/L</td>
</tr>
<tr>
<td>---------------------------</td>
<td>-----</td>
</tr>
<tr>
<td>Ground corn cob</td>
<td>62</td>
</tr>
<tr>
<td>(IFN 1-02-782)</td>
<td></td>
</tr>
<tr>
<td>Corn</td>
<td>20</td>
</tr>
<tr>
<td>(IFN 4-02-931)</td>
<td></td>
</tr>
<tr>
<td>Corn gluten meal</td>
<td>--</td>
</tr>
<tr>
<td>(IFN 5-02-900)</td>
<td></td>
</tr>
<tr>
<td>Corn starch</td>
<td>--</td>
</tr>
<tr>
<td>(IFN 4-02-889)</td>
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</tr>
<tr>
<td>Corn oil</td>
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</tr>
<tr>
<td>(IFN 4-07-882)</td>
<td></td>
</tr>
<tr>
<td>Urea</td>
<td>1.1</td>
</tr>
<tr>
<td>Molasses</td>
<td>15</td>
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<tr>
<td>(IFN 4-04696)</td>
<td></td>
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</tbody>
</table>

1Sodium chlorite (IFN 6-04-151), dicalcium phosphate (IFN 6-01-080), trace minerals, vitamin A and sulfur were added to each diet so that levels of minerals and vitamins met National Research Council recommendations. Rumensin, at the level of 30 mg/ton, was also added to each diet.
of the experimental design and the dietary treatments is presented in the Materials and Methods section of Part I. of this dissertation.

The same experimental parameters were recorded in both experiments. Live weight gain was recorded biweekly, and dry matter intake was recorded weekly. Dry matter digestibility (DMD) and empty body composition were determined initially and at three subsequent times, for each average live weight gain of 90 kg within a diet group. Dry matter digestibility was determined using acid-insoluble ash as an endogenous marker in the feed. The 2N HCl method described by Van Kuezen and Young (1977) was used to measure acid-insoluble ash. Empty body composition of protein, fat, water and ash was determined by using the deuterium oxide dilution technique in a one-pool model as described by Arnold et al. (1984) (Appendix C).

The caloric content of feed and feces was determined by bomb calorimetry (Parr Oxygen Bomb Calorimeter, Model 1241, Moline Ill.), and then used to calculate digestible calorie intake. Kjeldahl nitrogen content of feed and feces was determined for subsequent calculation of apparent protein digestibility and digestible protein intake.

The data were analyzed in a split-plot design in which dietary treatments represented the whole plots, and 90 kg gain periods represented the split-plots (Steel and Torrie,
Statistical analyses were conducted by using the General Linear Model procedure of the Statistical Analysis System (SAS, 1979) and the least significant difference procedure was used to make specific comparisons where significant differences were determined to exist (Steel and Torrie, 1960). Because differences existed in the feeding facilities and in the weather conditions between the two experiments, data from the experiments were not combined. In the second experiment performance data for the final growth period from steers consuming the low protein:low energy diet are not included in the statistical analysis but are recorded in tables and figures presented. This action was deemed necessary because of unusually severe cold environmental conditions which greatly affected normal growth of steers on this low plane of nutrition. In the first experiment three animals were removed from the experiment due to health problems. Two of these animals were from the LH diet group and one from the ML diet group. Data collected from these animals were dropped from analysis. One replacement steer was added to the LH diet group eight weeks past the start of the experiment. This animal was of similar initial weight to the other steers, adapted previously to the diet and data measurements were obtained for each 90 kg of individual live weight gain.
The average empty body composition and feedlot performance of the dietary treatment groups over the entire feeding period are shown in Tables 3 and 4. In both experiments, the steers receiving either the medium or high energy levels were fatter at similar live body weights than those receiving the low energy level. This pattern was established by the first 90 kg gain period and continued throughout the experiment (Figures 1 and 2). Steers were leanest when fed the medium and high protein levels at the low energy level. All treatment groups increased in empty body fat as they increased in live weight. A more detailed discussion of feedlot performance and body composition is found in the Results and Discussion section of Part I of this dissertation.

The intake of digestible energy (DE) and digestible protein (DP) increased in all dietary groups as live weight increased (Figures 3 to 6). The rate and magnitude of this increase were similar for all diet groups at similar live weights, and were related to increases in intake of dry matter. Although diets were formulated to provide the same concentration of DE, steers receiving the LH diet had lower calculated DE intakes than those receiving the HH diet. This
Table 3. Feedlot Performance and Body Composition (Experiment 1)¹

<table>
<thead>
<tr>
<th></th>
<th>L/L</th>
<th>L/H</th>
<th>M/L</th>
<th>H/L</th>
<th>H/M</th>
<th>H/H</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Average daily gain, kg</strong></td>
<td>.58a</td>
<td>.67ab</td>
<td>.68ab</td>
<td>.84bc</td>
<td>.85bc</td>
<td>.96c</td>
<td>.58</td>
</tr>
<tr>
<td><strong>Feed/gain</strong></td>
<td>14.2a</td>
<td>12.5b</td>
<td>13.0ab</td>
<td>10.5c</td>
<td>10.9c</td>
<td>9.8c</td>
<td>0.50</td>
</tr>
<tr>
<td><strong>Dry matter digestibility, %</strong></td>
<td>66.7ab</td>
<td>65.6ab</td>
<td>59.7a</td>
<td>70.4b</td>
<td>71.9b</td>
<td>84.9c</td>
<td>2.7</td>
</tr>
<tr>
<td><strong>Protein digestibility, %</strong></td>
<td>60.4ab</td>
<td>59.3ab</td>
<td>55.3a</td>
<td>72.7cd</td>
<td>65.5bc</td>
<td>78.5d</td>
<td>2.7</td>
</tr>
<tr>
<td><strong>Protein, %</strong></td>
<td>18.1ab</td>
<td>17.6a</td>
<td>18.6a</td>
<td>18.7b</td>
<td>17.6a</td>
<td>17.5a</td>
<td>0.24</td>
</tr>
<tr>
<td><strong>Fat, %</strong></td>
<td>17.8ab</td>
<td>20.7a</td>
<td>14.5b</td>
<td>14.1b</td>
<td>20.2a</td>
<td>21.0a</td>
<td>1.39</td>
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</table>

¹Values with different letters, but in the same line, are different, \( P<.05 \).
<table>
<thead>
<tr>
<th>DIET (Protein/energy)</th>
<th>L/L</th>
<th>L/H</th>
<th>H/L</th>
<th>H/H</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average daily gain, kg</td>
<td>0.42a</td>
<td>0.80b</td>
<td>0.81b</td>
<td>1.15c</td>
<td>0.07</td>
</tr>
<tr>
<td>Feed/gain</td>
<td>15.2a</td>
<td>12.1b</td>
<td>10.9b</td>
<td>10.5b</td>
<td>0.68</td>
</tr>
<tr>
<td>Dry matter digestibility, %</td>
<td>61.4d</td>
<td>64.6de</td>
<td>60.1d</td>
<td>72.8e</td>
<td>2.9</td>
</tr>
<tr>
<td>Protein digestibility, %</td>
<td>57.8</td>
<td>58.5</td>
<td>59.2</td>
<td>65.4</td>
<td>3.7</td>
</tr>
<tr>
<td>Protein, %</td>
<td>18.4d</td>
<td>17.4e</td>
<td>18.8d</td>
<td>17.5e</td>
<td>0.30</td>
</tr>
<tr>
<td>Fat, %</td>
<td>15.7d</td>
<td>21.5e</td>
<td>13.5d</td>
<td>21.3e</td>
<td>1.7</td>
</tr>
</tbody>
</table>

1 Values with different letters, but in the same line, are different, P<.001.

2 Values with different letters, but in the same line, are different, P<.05.
Figure 1. Average percent empty body fat of diet groups initially (I) and subsequent live weight gain periods of 90 kg (Experiment 1). Diet effect P<.01. Period effect P<.01. SEM = 1.39.
Figure 2. Average percent empty body fat of diet groups initially (I) and subsequent live weight gain periods of 90 kg (Experiment 2). Diet effect P < .05. Period effect P < .01. SEM = 1.58.
% Empty Body Fat

90 kg Gain Period

LL  LH  HL  HH
Figure 3. Average daily intake of digestible calories by diet groups for subsequent live weight gain periods of 90 kg (Experiment 1) Diet effect $P<.02$ Period effect $P<.001$ SEM = .72
Figure 4. Average daily intake of digestible calories by diet groups for subsequent live weight gain periods of 90 kg (Experiment 2) Diet effect $P < .002$ Period effect $P < .24$ SEM = .56
Figure 5. Average daily intake of digestible protein by diet groups for subsequent live weight gain periods of 90 kg (Experiment 1). Diet effect $P < .001$, Period effect $P < .001$, SEM = .044
Daily Protein Intake

kg/day

0.7

Diet Group

HH

HL

HM

LH

ML

LL

90 kg Gain Period
Figure 6. Average daily intake of digestible protein by diet groups for subsequent live weight gain periods of 90 kg (Experiment 2) Diet effect P < 0.01 Period effect P < 0.10 SEM = 0.035
difference was greater than could be explained by DM intake differences, and was related directly to the low DMD value of the LH diet and high DMD value of the HH diet, which were used to calculate DE intake. The high DMD value for steers fed the HH diet, during the first experiment, can not be explained, but existed for all steers fed that diet and for all periods. The low DMD value of the LH diet most likely was a reflection of a decrease in fiber digestion. A lower rumen pH and faster rumen turnover time caused by the presence of the readily-fermentable starch in the diet was probably the reason for this depression of fiber digestion. However, based on steer performance, the net energy value of this diet must have been quite high, off-setting the low calculated daily DE intake.

Apparent protein digestibility was higher in steers fed the high protein levels during the first experiment, but was similar between diets in the second experiment. Protein digestibility was generally low for all diets in both experiments, averaging 65.3% in experiment 1 and 60.2% in experiment 2. Low digestibility of the HL diet during the fourth period of the second experiment (37.0%) resulted in the calculation of a greatly reduced DP intake which was less than that of the HH diet, although both were formulated to provide similar quantities of metabolizable protein.
When averaged over all periods, DE and DP intakes were similar to those planned for in the experimental design. The estimates of DMD that are assumed to be aberrant caused deviations from the experimental design for certain diet groups during several gain periods. DE intake was affected more by the apparent DMD values than by DM intake, whereas DP intake estimates were affected more by DM intake than by apparent protein digestibility.

Caloric efficiency for experiments 1 and 2 is shown in Figures 7 and 8, respectively. Caloric efficiency is expressed, for each 90 kg gain period, as the ratio of calories retained in the empty body and the digestible calorie intake. Values of 9.50 kcal/g of fat and 4.98 kcal/g of protein were used in the calculations (Kleiber, 1961). In the first experiment, caloric efficiency increased in consecutive gain periods. Steers receiving the HH diet showed the only major deviation, as they had a substantial decrease in caloric efficiency in the final gain period. There were no overall statistical differences between dietary treatment effects. Numerically, the leanest steers (diet groups LL, ML and HL) had the lowest efficiency of retained DE during the first gain period, and the highest during the last gain period.

In both experiments, steers that received the high energy level, regardless of protein level, exhibited
Figure 7. Efficiency ratio of retained energy gain, in calories, to digestible calorie intake by diet group for live weight gain periods of 90 kg (Experiment 1) Diet effect $P < .33$ Period effect $P < .001$ SEM $= .018$
Caloric Efficiency

Diet Group

LH
HH
HM
ML
HL
LL

90 kg Gain Period
Figure 8. Efficiency ratio of retained energy gain, in calories, to digestible calorie intake by diet group for live weight gain periods of 90 kg (Experiment 2). Diet effect P< .04 Period effect P< .92 SEM= .020
Caloric Efficiency

90 kg Gain Period
decreases in caloric efficiency during the third and final gain periods. In the second experiment, steers consuming the HL and LL diets again had low caloric efficiencies during the first gain period, and the HL group had the highest efficiency during the third period. Those steers assigned to the LL diet remained low in caloric efficiency in the third period, presumably because of the severely cold weather that was mentioned previously in the Materials and Methods section.

As shown in Figures 1 and 2, the percentage of live weight gain that is fat increased in subsequent gain periods. The increase in caloric efficiency with increasing live weight thus would be expected, because fat provides 9.4 Mcal/kg of tissue gain and its deposition cost is 3.4 Mcal of heat lost/kg of fat, whereas tissue protein contains 5.6 Mcal/kg of tissue gain and has a deposition cost of 7.0 Mcal of heat lost/kg of protein (Pullar and Webster, 1977). This relationship also suggests that the leanest steers should have the lowest caloric efficiencies in the early periods when more muscle deposition is taking place. These steers rapidly changed the composition of their gain between 410 and 500 kg live weight.

It is known that efficiency of feed conversion and average daily gain decrease as live weight and degree of fatness increase. It seems that steers receiving the HH diet
in the first experiment, and the LH and HH diets in the second experiment, reached a point during the third period of gain when the efficiency of calorie utilization decreased, even though the major portion of the tissue gain at this time was fat.

Protein efficiency is expressed, for each 90 kg gain period, as the ratio of protein retained in the empty body to DP intake. Figures 9 and 10 illustrate the protein efficiencies calculated for experiments 1 and 2, respectively. A general decrease in protein efficiency in subsequent gain periods was observed in the first experiment. No statistical differences were found for dietary effects, and no clear pattern was exhibited among dietary groups in subsequent gain periods. Steers in both the HL and LH diet groups had surprisingly low protein efficiency ratios in the first gain period. In the second experiment, there also was a tendency toward a decrease in protein efficiency as live weight increased. This trend was not statistically significant, however, most likely because the steers on the HL diet had a sharp rise in protein efficiency in the third gain period. This rise in protein efficiency was caused by the low value calculated for DP intake for this group, as discussed previously, and thus is believed to be aberrant. As in the first experiment, no differences were seen between
Figure 9. Efficiency ratio of retained protein gain, in calories, to digestible protein intake by diet group for live weight gain periods of 90 kg (Experiment 1) Diet effect $P < .24$ Period effect $P < .01$ SEM = .025
Figure 10. Efficiency ratio of retained protein gain, in calories, to digestible protein intake by diet group for live weight gain periods of 90 kg (Experiment 2). Diet effect $P < .35$ Period effect $P < .28$ SEM = .025
Protein Efficiency

90 kg Gain Period

0.4

0.3

0.2

0.1
diet groups, and no consistent pattern was exhibited among diet groups in subsequent gain periods.

Growth curves have shown that protein accretion starts to plateau soon after the rate of increase in live weight begins to decline (the inflection point of the growth curve). This plateau phase of protein accretion coincides with gain periods 2 and 3 in the present experiments. The rates of protein synthesis and degradation in tissues are approaching each other, resulting in less accumulation of muscle mass and the attainment of a mature musculature. At this time, DM intake capacity is reaching its maximum, allowing for an increase in DP intake. This situation (less new tissue protein accretion with an increase in DP intake) resulted in the decrease in the efficiency of protein utilization that was seen in cattle during the stages of growth represented in these experiments. This relationship also was reported by Rohr et al. (1982).

The percentage of the total retained energy gain partitioned to fat gain or protein gain during the various gain periods is shown in Figures 11, 12, 13 and 14. In the first experiment (Figure 11), steers receiving the high energy diets, regardless of protein level, retained over 80% of their total caloric gain as fat during the first two gain periods. The HH diet group had a decrease in the percentage of total caloric gain as fat during the third period, and was
Figure 11. Percent of total retained energy, in calories, retained as fat by diet groups for live weight gain periods of 90 kg (Experiment 1). Diet effect P < .08, Period effect P < .11, SEM = 6.5.
Calories Retained as Fat

Diet Group

LL
LH
HH
HM
ML
HL

90 kg Gain Period

40 50 60 70 80 90 100
Figure 12. Percent of total retained energy, in calories, retained as fat by diet groups for live weight gain periods of 90 kg (Experiment 2) Diet effect $P<.07$ Period effect $P<.42$ SEM = 2.6
Calories Retained as Fat

90 kg Gain Period

LL  LH  HL  HH

90
80
70

(%)
Figure 13. Percent of total retained energy, in calories, retained as protein by diet groups for live weight gain periods of 90 kg (Experiment 1)
Diet effect $P< .88$  Period effect $P< .11$
SEM = 6.5
Calories Retained as Protein

Diet Group

ML
HM
HH
LH
LL

90 kg Gain Period

0 10 20 30

0 10 20 30 40 50 60

(%)
Figure 14. Percent of total retained energy, in calories, retained as protein by diet groups for live weight gain periods of 90 kg (Experiment 2)
Diet effect $P<.07$  Period effect $P<.42$
SEM= 2.6
the only diet group to have such a decline. The steers receiving the higher levels of protein with lower levels of energy retained less than 75% of their total calories as fat. In the final gain period, all diet groups, except the HH group, increased the percentage of retained calories in fat gain to over 85%.

The pattern of partitioning of total caloric gain between fat and protein was similar in experiment 2 (Figure 12). Notable exceptions did exist; steers in the LL diet group had a lower caloric retention as fat in the first gain period than in the first experiment (72% vs 85%), and caloric retention as fat for the HH group remained high (35%) in the third gain period. Only steers in the HL diet group sharply increased their caloric retention as fat in the third gain period in the second experiment, whereas all other groups maintained their previously high percentages.

Tyrrell et al. (1974) and Robelin and Daenicke (1980) reported a decrease in the percentage of retained energy that is retained as protein as daily caloric gain increased. A comparison of the energy retention as protein of the HL, ML and LL diet groups with the HH and HM groups (experiment 1) also shows a decrease in energy retention as protein with increasing daily gain during the first gain period. However, steers consuming the HL and LH diets had similar average daily gains, but showed large differences in the ability to
retain energy as protein. Differences of 10 and 36 percentage units were measured in the percentage of retained calories retained as protein during the first period of experiments 1 and 2, respectively. Variations in the ability to retain energy as protein have been reported between early and late maturing cattle. Hereford steers fed on a high plane of nutrition retained approximately 15% of their energy as protein (Jesse et al., 1976), compared with 35 to 45% for Charolais x Saler bulls (Geay and Robelin, 1979). A range as wide as that reported for intensively-fed cattle of breeds with widely different maturation rates was observed in these trials as a consequence of dietary treatments alone in the first gain period.

In summary, caloric efficiency increased, and protein efficiency decreased, in subsequent gain periods in the first experiment. The second experiment did not show as clear a pattern as the first experiment, but showed the same trends for efficiency of energy and protein utilization. Steers receiving diets with higher energy levels, regardless of protein level, were generally more calorically efficient in the first gain period, whereas dietary treatment resulted in large variations between the two experiments in protein efficiency during the first gain period. Large differences in calorie retention as protein or fat were observed in the first gain period, but these differences disappeared in the
third gain period. Retention of energy as fat or protein was independent of rate of gain, and was directly related to dietary energy level in the early gain periods. Differences in energy retention as fat or protein disappeared in the third gain period with all diet groups retaining a high percentage of energy as fat.

Further studies, utilizing a wider range of energy and protein levels, are needed to describe fully the relationships observed in the present experiments. A wider range in the levels of both dietary components would allow an estimation to be made of the linearity of the results within a gain period, as well as across gain periods. These studies also should utilize breeds of cattle that differ in maturation rates, in order to determine the influence of maturation rate on the partitioning of dietary energy and protein.
REFERENCES


PART III. PARTITIONING OF ENERGY AND PROTEIN OF CORN GRAIN INTO TISSUE OF BEEF CATTLE AS CONTROLLED BY GROWTH REGULATING HORMONES
INTRODUCTION

Previous studies have demonstrated the ability to alter empty body composition of cattle by nutritional means. For this to take place, nutrient partitioning into the various tissues of the body would have to change such that the metabolism associated with the specific tissues being deposited would predominate. Hormonal regulation of metabolism has been well-documented, and several hormones have been shown to be major regulators of the metabolism associated with growth. Growth hormone from the anterior pituitary, insulin and glucagon from the pancreas and thyroid hormones (triiodothyronine, T3, and thyroxine, T4) from the thyroid gland have been determined to be such regulatory hormones. Identification of any changes in plasma concentrations of these hormones in association with dietary-induced changes in body composition may give a better understanding of how the metabolism of these animals is being altered. This knowledge, in turn, could lead to more efficient production of a desirable meat product.

The objective of this study was to measure plasma concentrations of growth hormone (GH), insulin (I), glucagon (G), T3 and T4 every 60 days in feedlot steers fed diets
varying in energy and protein content that had been demonstrated to influence body composition and rate of gain.
MATERIALS AND METHODS

Sixteen Angus x Charolais weanling steers from the Iowa State Beef Nutrition Research herd, representing two sires, were randomly allotted to four dietary treatments by sire group. The steers were started on feed January 1, 1983 and had an average initial weight of 254 kg. The four diets varied in both the level of energy and protein, and in the ratio of energy to protein. These diets were denoted as low protein:low energy (LL), low protein:high energy (LH), high protein:low energy (HL) and high protein:high energy (HH). The two energy levels were 2.2 and 2.8 Mcal of metabolizable energy (ME)/kg of dry matter (DM) and the two levels of metabolizable protein (MP) were 49.7 and 63.0 g/kg DM. All diets were formulated to allow positive gain, but not to exceed optimal growth requirements (National Research Council, 1976; Burroughs et al., 1974). Diet composition is shown in Table 1. The energy level of the diets was increased independently of the protein level by the addition of corn starch, and the protein level was increased independently of the energy level by the addition of corn gluten meal.

Steers were fed individually using electronic broadbent headgates (American Calan, Northwood, N. H.). Feeding level
Table 1. Diet Composition

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<tr>
<th>INGREDIENT</th>
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<th>L/H</th>
<th>H/L</th>
<th>H/H</th>
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<tr>
<td>Ground corn cob (IFN 1-02-782)</td>
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<td>38</td>
<td>63</td>
<td>28</td>
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<td>Corn (IFN 4-02-931)</td>
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<td>20</td>
<td>14</td>
<td>55</td>
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<tr>
<td>Corn gluten meal (IFN 5-02-900)</td>
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<td>1.0</td>
<td>6.5</td>
<td>1.2</td>
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<tr>
<td>Corn starch (IFN 4-02-889)</td>
<td>--</td>
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<td>---</td>
<td>---</td>
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<td>Corn oil (IFN 4-07-882)</td>
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<td>---</td>
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<tr>
<td>Urea (IFN 4-07-882)</td>
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<td>1.1</td>
<td>0.5</td>
<td>0.5</td>
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<td>Molasses (IFN 4-04-696)</td>
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<td>15</td>
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</table>

Sodium chloride (6-04-151), dicalcium phosphate (6-01-080), trace minerals, vitamin A and sulfur were added to each diet so that levels of minerals and vitamins met National Research Council recommendations. Rumensin, at the level of 30 mg/ton, was also added to each diet.
was monitored daily to allow ad libitum intake, and orts were collected weekly. Live weight gain was recorded biweekly. Care and feeding regime has been described in greater detail previously (Materials and Methods section, Part I.).

Plasma samples were taken initially after the steers had been allowed two weeks to adapt to the diets, and every 60 days thereafter until slaughter. Blood samples were collected by way of polyethylene jugular catheters that were inserted one day prior to sampling. Ten-ml samples were taken hourly for nine hours. The steers were not fed after inserting the catheters, resulting in a feed restriction period of approximately 16 hours before sampling was begun. The steers were fed after the fourth hourly sample was drawn. Heparin was used as an anticoagulant. Blood samples were cooled in ice and plasma was separated by centrifugation. The plasma was frozen and stored until analyzed by radioimmunoassay for growth hormone (Trenkle, 1972), insulin (Trenkle, 1972), and glucagon (Harris et al., 1979) and by solid phase radioimmunoassay for T3 and T4 (Coat-a-Count kit, Diagnostic Products Corporation, Los Angeles, CA).

Body composition of the steers was determined initially, and three times thereafter, as each dietary group achieved average increments of live weight gain of 90 kg. Empty body composition was measured by using the deuterium oxide dilution technique in a one-pool model, as described by
Arnold et al. (1984) (Appendix C). Composition and feedlot performance of the steers has been discussed previously (Results and Discussion section, Part I).

Data were analyzed as a split-plot design in which dietary treatments represented whole plots and 60-day sampling periods represented split-plots (Steel and Torrie, 1960) (Appendix B). Analysis of statistical significance was performed by using the General Linear Model procedure of the Statistical Analysis System (SAS, 1979) and the least significant difference procedure was used to make specific comparisons where significant differences were determined to exist (Steel and Torrie, 1960).
RESULTS AND DISCUSSION

Feedlot performance of the steers is shown in Table 2 and is presented as means for each diet group. The change in empty body composition, expressed as percentage of fat after each 90 kg gain period, is shown in Figure 1. Steer performance improved as the level of each nutrient (energy or protein) increased, and had an additional additive increase when both ME and MP were at the high level. Groups LL and HH had similar ratios of protein:energy in their diets, but achieved different body compositions. In this comparison, plane of nutrition, or rate of gain, affected body composition. The HL and LH diet groups, however, had similar rates of gain, but different body compositions. In this comparison, differences in the relative proportion of protein to energy in these diets resulted in different body composition at a similar live weight. The relationship between feedlot performance and empty body composition has been presented in greater detail in Part I. The efficiency of nutrient utilization in achieving the composition of gain has been presented in Part II.

The mean concentration of GH for each group during the growing period is shown in Figure 2. The concentration of GH was elevated in the LL group within 60 days on trial. This
Table 2. Feedlot Performance and Body Composition (Experiment 2)$^{1,2}$

<table>
<thead>
<tr>
<th>DIET (Protein/energy)</th>
<th>L/L</th>
<th>L/H</th>
<th>H/L</th>
<th>H/H</th>
<th>SEM</th>
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<td>Average daily gain, kg</td>
<td>0.42a</td>
<td>0.80b</td>
<td>0.81b</td>
<td>1.15c</td>
<td>0.07</td>
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<td>Feed/gain</td>
<td>15.2a</td>
<td>12.1b</td>
<td>10.9b</td>
<td>10.5b</td>
<td>0.68</td>
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<tr>
<td>Dry matter digestibility, %</td>
<td>61.4d</td>
<td>64.6de</td>
<td>60.1d</td>
<td>72.8e</td>
<td>2.9</td>
</tr>
<tr>
<td>Protein digestibility, %</td>
<td>57.8</td>
<td>58.5</td>
<td>59.2</td>
<td>65.4</td>
<td>3.7</td>
</tr>
<tr>
<td>Protein, %</td>
<td>18.4d</td>
<td>17.4e</td>
<td>18.8d</td>
<td>17.5e</td>
<td>0.30</td>
</tr>
<tr>
<td>Fat, %</td>
<td>15.7d</td>
<td>21.5e</td>
<td>13.5d</td>
<td>21.3e</td>
<td>1.7</td>
</tr>
</tbody>
</table>

$^1$Values with different letters, but in the same line, are different, P<.001.

$^2$Values with different letters, but in the same line, are different, P<.05.
Figure 1. Average percent empty body fat of diet groups initially (I) and subsequent live weight gain periods of 90 kg. Diet effect P < .05, Period effect P < .01, SEM = 1.58.
Figure 2. Mean concentration of plasma growth hormone by diet group for repeated sampling periods. Diet effect $P < .001$, Period effect $P < .03$, SEM = .66.
Concentration of Growth Hormone (ng/ml)

Period (each 60 days on trial)

* different P<.01
elevation persisted throughout the remainder of the experiment at a level that was at least two-fold greater than all other diet groups. The other three groups had similar plasma GH concentrations throughout the experiment. Plasma concentrations of GH decreased in all diet groups with increasing time on trial.

Much attention has been focused recently on GH as an anabolic agent with potential to increase growth rate, much like the steroid implants now in use. In this experiment, however, plasma GH concentrations were highest in the steers that were the slowest growing, and on the lowest plane of nutrition. Under these conditions, growth hormone is probably assuming the same role that has given it its anabolic status, that is, to increase nitrogen retention, or to improve utilization of the limited amount of protein intake. These steers, while still exhibiting positive growth, were much nearer to maintenance levels of energy and protein intake than any of the other diet groups. Thus, the body has responded metabolically to this physiological condition by increasing GH concentrations and presumably, increasing the efficiency of protein utilization. In this experiment, however, an increase in protein efficiency was not observed (Part II). Prewitt et al. (1982) have reported a decrease of serum somatomedian-C concentration in growing rats related to low protein and energy intake. These
observations were recorded at 6 to 12 weeks of age and occurred 2 weeks after the rats started the dietary treatments. It may be that GH and the somatomedins, which mediate its action on muscle growth, are controlled independently under conditions of food restriction. A low serum somatomedin concentration could possibly explain the lack of change in protein efficiency with increased GH concentration observed in he cattle fed the LL diet.

Growth hormone secretion into plasma has been shown to be episodic (McAtee and Trenkle, 1971) and effective measurement of GH requires repeated sampling over an extended period of time at frequent intervals. The frequency of GH spikes may be of more physiological importance than the basal concentrations (Anfinson et al., 1975). The sampling scheme used in this study provided a profile of basal concentration that was consistent over periods, but it may not be the best scheme to employ if GH is the only hormone of interest.

The ratio of plasma insulin concentration to plasma glucagon concentration is shown in Figure 3. Ruminants receive very little of their glucose supply by direct absorption from the gastrointestinal tract but instead, produce it by hepatic gluconeogenesis. It is therefore, more informative to examine the amount of insulin relative to glucagon when studying aspects of metabolism controlled by these hormones (Unger, 1971; Bassett, 1975).
Figure 3. Ratio of plasma insulin concentration to plasma glucagon concentration by diet group for repeated sampling periods. Diet effect \( P < .78 \) Period effect \( P < .72 \) SEM = .123
There was no statistical difference in the ratio of insulin to glucagon (I/G). The I/G did not change over time among diet groups, however, dietary protein level tended to influence I/G more than did energy level. The lowest ratios measured for either group fed the high level of protein was similar in magnitude to the highest ratio for either low protein group. Both high energy diets induced a marked increase in I/G in the final period before the animals were slaughtered. Individual plasma I and plasma G concentrations increased in all diet groups with increasing time on trial.

The lack of change in the I/G in response to dietary treatment and growth (time) seems to indicate that these hormones are concerned with maintaining homeostasis, rather than performing any homeorhetic function. Concentration of I in plasma has been shown to have little relationship to growth rate in normal animals (Trenkle and Topel, 1978; Martin et al., 1979; Etherton, 1982). Increases in plasma I concentrations with increasing body weight and age have been reported in cattle by Trenkle and Topel (1978), and Bassett (1975) observed similar increases of both I and G in sheep after feeding. These reports are consistent with the observations in this study that the individual hormones increased with time, but the ratio of insulin to glucagon remained constant over time.
Plasma I concentrations have been shown to be positively related to body fat percentage (Trenkle and Topel, 1978; Martin et al., 1984). A marked increase in the I/G occurred in steers receiving the high energy level diets, and these steers also had the greatest percentage of empty body fat. This increase in I/G was not significant as an overall time effect, but the trend may have continued if the animals had been allowed to obtain a greater degree of fatness.

The concentrations of plasma T3 and T4 are shown in Figures 4 and 5, respectively. Plasma T3 concentrations were greater in steers receiving the high level of energy, regardless of protein level. An inverse pattern to that of T3 was exhibited by plasma T4 concentrations; as steers receiving the low level of energy had greater concentrations of T4 ($P < .09$) than did steers receiving the high level of energy. No differences were seen in the plasma concentrations of either hormone as a function of time.

The majority of circulating plasma T3 is derived extrathyroidally by the monodeiodination of T4 (Bernal and Refetoff, 1977). This possibly could account for the inverse relationship between T3 and T4 concentrations, because the increase in plasma T3 could be the result of increased conversion of T4 to T3. The potency of T3 is three to four times that of T4, and hyperthyroidism is associated with
Figure 4. Mean concentration of plasma triiodothyronine (T3) for dietary treatment groups. Diet effect $P < .01$; Period effect $P < .96$. SEM = 16.0.
Figure 5. Mean concentration of plasma thyroxine (T4) for dietary treatment groups. Diet effect P < .09
Period effect P < .42  SEM = .87
leanness in animals (Bernard and Refetoff, 1977). Steers fed the high energy level diets were fatterest, but they also had the highest plasma T3 concentrations, which seems to be a contradiction.

In summary, plasma hormone profiles suggested that the pancreatic hormones played a homeostatic role, rather than a homeorhetic role. Plasma growth hormone concentrations were changed only when the intake of protein and energy was low. Based on the amount of protein retained, the higher concentration of growth hormone did not result in an improvement in protein utilization. Increased daily fat deposition was associated with increased concentrations of T3, and lower concentrations of T4.
REFERENCES


GENERAL DISCUSSION AND CONCLUSIONS

These studies were designed to evaluate the utilization of corn grain energy and protein in growing cattle with respect to effects of dietary manipulation on nutrient partitioning. Most previous studies had examined the effect of energy or feed intake alone on composition of live weight gain. Corn grain was chosen because of its preferred status in cattle feeding, and also on the speculation from other work that this status is not solely because of its high digestible energy value, but may be related to unique properties of the corn protein.

The benefit of understanding energy and protein interaction in nutrient partitioning in ruminants may be an improvement in the efficiency of utilization of dietary energy and protein. This increased efficiency can then in turn be translated into a greater economic return. In these studies the addition of protein to the LL diet consistently improved feed efficiency more than addition of energy, however, both provided similar increases in live weight gain. The economic advantage of less feed cost for similar gain is easily appreciated but, as a rule, protein feedstuffs are more costly than energy feedstuffs. A greater advantage is realized from steers grown on the HL diet in the form of more
lean muscle and less fat waste. As of yet, the industry has not been willing to adopt a grading system that recognizes this advantage. The current system may in fact penalize a producer more for too little fat than too much fat.

These studies have shown the necessity of adequate MP to improve feed efficiency at all energy levels examined. The importance of the MP:ME ratio to produce a more desirable composition of gain was shown by the varying amount of fat to protein in total energy gain. The steers receiving the HL diet had a ratio of 75% fat to 25% protein in total energy gain versus 80% fat to 20% protein for steers on the higher energy levels, regardless of protein level. These effects were seen in the first and second gain periods. During the final gain period, all diet groups were retaining approximately 85% of their energy gain as fat. From these data, the importance of adequate MP in the early stages of a feedlot program becomes apparent. It would be expected that a starting ration high in MP with a minimum of excess energy would provide a carcass with a high percentage of muscle and low fat at an acceptable weight. While this type of feeding scheme is not economically feasible today, it may have application if grading standards change in the future.

Future work on practical application of this work to feeding programs might first involve feeding a combination of MP:ME ratios during the feeding period. Because all diet
groups had similar composition of gain in the final period, a feeding regime using the HL diet in the early period to maximize muscling and the HH diet in the later period to maximize gain should be investigated. If the effects on composition seen in the HL diet group are accomplished in the first two gain periods, maybe the diet used in the third period will not alter composition from that seen in continuous feeding of the HL diet.

Future studies of a more basic nature should involve an expanded range of MP and ME levels. This design would allow more measurement points for definition of the composition of gain in mathematical terms for predictive or modeling purposes. Tissue biopsy should be incorporated into future studies for determination of activity of enzymes associated with protein and fat deposition. This type of information may provide a better understanding of the biochemistry of nutrient partitioning.

The following general conclusions were derived from these studies. During the observed growth period, empty body composition was significantly different for steers fed different diets, and this change in composition was independent of rate of gain. Feedlot performance (daily gain and feed efficiency) was improved by an increase in concentration of either nutrient.
Addition of dietary protein, within the range of this trial, allowed for the expression of additional muscle growth. This additional growth of muscle occurred with a reduction in the amount of fat gain and was accomplished with the same efficiency of protein utilization as in the animals with a lower growth rate.

Addition of dietary energy allowed for additional daily gain. When the protein level was low in the high energy diet, the gain was largely composed of fat. When the protein level was high in the high energy diet, gain was increased and was composed of more muscle, as well as fat, with the relative percentage of gain as fat remaining the same in both high energy groups.

Plasma hormone profiles suggested that the pancreatic hormones may have had a homeostatic role, rather than a homeorhetic role, as no changes were observed in insulin/glucagon ratios for diet or time. Growth hormone concentrations were changed only when the intake of protein and energy was quite low. Based on retained protein, the higher concentration of growth hormone did not result in an improvement in protein utilization. Increased daily fat deposition was associated with increased concentrations of triiodothyronine and lower concentrations of thyroxine.
ACKNOWLEDGEMENTS

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### Statistical Model For Least Squares Analysis of Variance

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<td>Calf(Diet) X Period</td>
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### APPENDIX B

**Statistical Model For Least Squares Analysis of Variance**

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</tr>
</tbody>
</table>
APPENDIX C

Procedure Used To Evaluate Body Composition
Of Steers By Deuterium Oxide Dilution,
One Pool Model

Deuterium oxide (99.8 atom %) was injected into the jugular vein via a 60 cm polyethylene catheter inserted one day prior to sampling. A 50 ml disposable syringe was used for the injection. The dose, approximately .2 g/kg of body weight, was administered within one minute. The exact dose was determined by weighing the syringe to the nearest .1 g before and after injection. The catheter was flushed with 10 ml of normal saline after the deuterium oxide injection. Ten ml blood samples were drawn at 4, 6, 8, 24, 48 and 72 hours after deuterium oxide injection. The exact time the sample was drawn was recorded. Blood samples were placed in heparinized glass culture tubes with screw top caps and refrigerated. The steers were allowed free access to water prior to the start of the injection and after the four hour sampling. The steers were weighed on each of three days before the injection of deuterium oxide and each of two days after to obtain an average live weight. Water from the whole blood samples was separated and purified by lyophilization. The deuterium oxide concentration was determined by infrared spectrophotometry as described by Byers (1979). An automated
sampling system was used with the infrared analyzer (Ferrell and Philip, 1980). Chemical composition of the steers was calculated using a one pool model as described by Loy (1983).
Table Al. Calculations Used In The One Pool Model

<table>
<thead>
<tr>
<th>Robelin, 1982</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) Concentration of deuterium oxide at time zero, i.e. time of injection of dose, is equal to the Y-intercept of the regression of deuterium oxide concentration vs time.</td>
</tr>
<tr>
<td>2) Deuterium oxide space = Dose (mg)/ deuterium oxide concentration at time zero</td>
</tr>
<tr>
<td>3) Total body water = 0.986 X deuterium oxide space</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Simpendorfer, 1974</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) Empty body weight = 0.949 X shrunk live weight - 11.987</td>
</tr>
<tr>
<td>2) Gut water = shrunk live weight - empty body weight X 0.847</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Garrett and Hinman, 1969</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) % Empty body fat = 94.32 - (1.266)(% Empty body water)</td>
</tr>
<tr>
<td>2) % Protein = (Empty body weight - kg fat - kg water)(83.1)</td>
</tr>
<tr>
<td>3) % Ash = (Empty body weight - kg fat - kg water)(18.6)</td>
</tr>
</tbody>
</table>

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 superscript 1 Adapted from Loy, 1983.
REFERENCES FOR APPENDIX C


