

ENDOCRINOLOGY OF INTEGRATED LIPID-PROTEIN METABOLISM IN RUMINANTS¹

by

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Skeletal muscle and adipose tissue make up 90% or more of the carcass weight of market cattle. Both tissues are economically important for efficient production of meat animals, although growth of muscle often is given more importance. Within a genotype, the growth of muscle and adipose occurs in an orderly manner related to body weight. Some of the similarities and differences in the characteristics of the growth of muscle and adipose are listed in Table 1. The postnatal growth of both tissues in cattle takes place by an increase in cell mass rather than by an increase in number of cells. Both tissues are continuously being synthesized and broken down and therefore, remove, or, add, nutrients to the circulatory system. Whether a net gain occurs or loss generally depends upon the nutritional environment of the animal. Growth of skeletal muscle is related to function rather than serving as a storage of protein. Close anatomical harmony between size of skeleton, quantity of muscle and distribution of muscle weight in the body is noted. In contrast, adipose tissue functions as a storage tissue and is more variable both in amount and distribution. When nutrient intake is high, the excess energy is stored as lipids. On the other hand, excess dietary protein is not stored as body protein but is metabolized. The excess nitrogen is excreted, and the carbon stored as lipid or used as a source of energy. The two tissues do not grow independently of each other, but in the young growing animal, muscle has a higher priority than adipose for use of nutrients. If nutrition is limited, growth of adipose will be reduced more

than that of skeletal muscle. Finally, the chemical composition of the two tissues is greatly different. Skeletal muscle contains three to four times more water than adipose. The dry matter of muscle contains predominantly protein, with some mineral and carbohydrate. Adipose tissue is mostly lipid, with small quantities of protein, carbohydrate and minerals.

The metabolism of both tissues is influenced by many aspects of physiology. The main difference between the two is that skeletal muscle uses amino acids to synthesize protein and adipose uses acetate to synthesize fatty acids. The metabolism of both tissues is influenced by genetic factors, environmental influences, or, the interaction of both these factors. Consideration of an integration of factors controlling metabolism should include the influence of the triad of genetics, hormones and nutrition (Figure 1). Genetics influences the number of cells to increase to a certain population and to grow to a given size. The genetic influence is mediated by the endocrine system in addition to other genetic factors. The intracellular supply of nutrients has a major influence on the rate of growth of cells. The supply of nutrients may be limited by the quantity of feed available to the animal, or nutrient utilization by a tissue with high priority may limit the growth of other tissues. The endocrine system functions by integrating the metabolism of different tissues and the partitioning of nutrients to different tissues of the body. Skeletal muscle and adipose are quantitatively important in utilization of nutrients because of their mass. The liver also has a central role because of its high metabolic activity and its anatomical location in having first priority to use absorbed nutrients. The relationships between nutrition and the endocrine system are complex and not too well understood at the molecular level. The purpose of this review is to give consideration to several roles of the endocrine system in regulation of metabolism of protein and lipids in ruminants.

TABLE 1

CONTRASTS OF POSTNATAL GROWTH OF SKELETAL MUSCLE AND ADIPOSE TISSUE IN CATTLE

Similarities	Differences
Increase in cell size	Muscle-related to function
Both are dynamic	Adipose-storage of excess energy
	Muscle has priority over adipose
	Chemical composition

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¹ Journal Paper No. J-9571 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project 2027.

Reciprocal Meat Conference Proceedings, Volume 32, 1979.

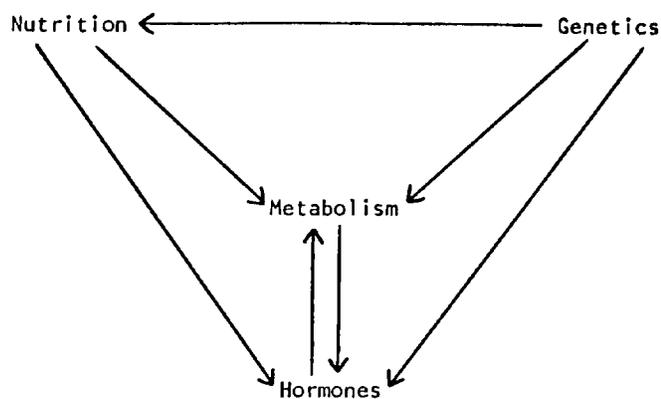


FIGURE 1

Interrelationships of hormones, nutrition and genetics on regulation of metabolism.

Endocrine Control of Metabolism

It is only within recent years that very many data have been collected from ruminant animals on the endocrine control of metabolism. Enough differences have been found in the endocrine systems of ruminants and nonruminants that it is not possible to make generalizations applicable to ruminants from all the basic data available from studies of humans and laboratory animals.

The endocrine complex controlling metabolism includes the glands producing the hormones, the circulatory system transporting the hormones and the hormone-specific receptors at the cellular level. Hormonal responses result from the interaction of a hormone with its specific tissue receptor, which causes subsequent events to occur within the cell. Hormones do not act completely independently, because of hormone-hormone interactions, hormone-metabolite interactions and hormones with multiple sites of action. Therefore, it is necessary to consider the combined action of hormones on body tissues to gain some insight into the influence of the endocrine system on metabolism of muscle and adipose.

An outline of the effects of growth hormone, insulin, glucagon and adrenal glucocorticoids on skeletal muscle and adipose tissue is given in Tables 2 and 3. Other hormones undoubtedly are involved, but the available data suggest that these four hormones are more involved in the longer-term nutritional and genetic regulation of lipid and protein metabolism.

Skeletal muscle. Most of the studies of the action of growth hormone on protein synthesis in skeletal muscle have been done with laboratory rats. The decrease in plasma concentrations of amino acids after administration of exogenous growth hormone to sheep

(1) indicates increased uptake of amino acids by body tissues. The decreased plasma amino acids probably mean increased protein synthesis. Exogenous growth hormone has been shown to increase carcass protein (2) and to increase nitrogen retention (1) in sheep. The increase in calcium and phosphorus retention (3) with injection of growth hormone in sheep is indicative of greater skeletal growth as well as that of soft tissue.

Insulin decreases concentration of amino acids in plasma of ruminants (4) as well as in other species. Infusion of glucose, which causes increased secretion of insulin, also results in increased uptake of amino acids by the tissues of the hind limb of sheep (5). Amino acids are released from the hind limb of sheep during fasting when secretion of insulin is decreased (6). Insulin has no effect on removal of plasma amino acids by the liver of sheep (4), so that its effects are limited to the peripheral tissues, presumably skeletal muscle. The effects of insulin on protein synthesis in skeletal muscle are less clear. A preliminary study with fetal lambs (7) indicated that exogenous

TABLE 2
HORMONES AFFECTING GROWTH OF SKELETAL MUSCLE.

Hormone	Specific effects	Net effect
Growth hormone	Increase uptake of amino acids Increase protein synthesis Increase DNA and RNA synthesis	Increase growth-anabolic
Insulin	Increase uptake of amino acids Increase uptake of glucose Decrease breakdown of proteins	Necessary for action of growth hormone-anabolic
Glucagon	Increase uptake of amino acids by liver	Indirect-catabolic
Glucocorticoids	Decreases protein synthesis May increase breakdown of muscle proteins	Decrease growth-catabolic

TABLE 3
HORMONES AFFECTING ADIPOSE TISSUE.

Hormones	Specific effects	Net effect
Insulin	Increase uptake of glucose Increase utilization of acetate Increase lipogenesis Decrease lipolysis	Anabolic
Glucagon	Increase lipolysis Increase gluconeogenesis in liver	?
Growth hormone	Increase lipolysis	Catabolic
Cortisol	Increase gluconeogenesis in liver Increases insulin secretion	Anabolic

insulin did not increase protein synthesis but decreased breakdown of protein.

The actions of glucagon seem to be directed towards the liver, which then results in indirect effects on protein metabolism in skeletal muscle. Glucagon promotes the uptake of glucogenic amino acids by the liver and their conversion to glucose (4, 8). This decreases the concentration of amino acids in plasma and makes them less available to nonhepatic tissues.

Exogenous cortisol in sheep increases blood glucose concentrations and increases nitrogen excretion during fasting (9). In another study with sheep (10), cortisol increased blood glucose and also increased the conversion of alanine to glucose by the liver. The net effects of glucocorticoids are catabolic on protein metabolism in skeletal muscle, with an increase in gluconeogenesis from amino acids in the liver.

Adipose. The action of growth hormone on adipose tissue of ruminants has been investigated by injection of exogenous hormone in fasting sheep (11, 12, 13). In all these studies, relatively high levels of growth hormone increase the release of free fatty acids and glycerol into plasma 4 to 6 hours later. Concentrations of free fatty acids in plasma are increased during fasting of ruminants when the ratio of growth hormone to insulin in plasma is elevated, mostly because of a decrease in insulin (14, 15).

Injection of insulin or glucose into fasting ruminants reduces plasma free fatty acids (16). Several studies indicate that insulin increases the utilization of acetate, the major substrate for lipogenesis. *In vitro*, the combination of insulin and glucose increased acetate utilization by isolated bovine adipocytes (17). Insulin also restores the uptake of acetate to normal in alloxan diabetic sheep (18).

Glucagon acts primarily on the liver to increase gluconeogenesis. Its action on adipose tissue is lipolytic if insulin concentrations are kept low (19). Injection of glucagon into normal sheep causes an insulinogenic response (20) and no increase in lipolysis. Seemingly, the effects of insulin on adipose tissue are dominant over those of glucagon. In fasting animals, when the ratio of glucagon to insulin increases in plasma because of a decrease in insulin concentrations, glucagon may contribute to the overall lipolytic response.

The action of glucocorticoids on adipose tissue is less clear. Administration of cortisol to sheep results in hyperglycemia and hyperinsulinemia (10, 21). The increased concentration of blood glucose is caused by increased gluconeogenesis from amino acids in liver and decreased glucose space (10). The increased concentration of blood glucose causes increased insu-

lin secretion. Insulin seems to be less active, though, in the cortisol-treated animal. The net effect of these endocrine responses seems to be lipogenesis. Injection of cortisone acetate into steers has been shown to increase lipid deposition. In the fasting state, glucocorticoids may contribute to the lipolytic effects of growth hormone. Cortisone injections decrease plasma free fatty acids in fasting sheep, but there was an increased lipolytic response to exogenous growth hormone in the cortisone-treated animals (Trenkle, unpublished studies).

Hormonal Changes Associated With Nutrition

Pancreatic hormones. In cattle and sheep fed once or twice per day, a daily pattern of increased insulin and glucagon secretion is found during the 2- to 3-hour period after feeding (22, 23). With fasting, the concentrations of both hormones decrease, but insulin decreases to a greater extent than glucagon. Because most of the dietary carbohydrates are fermented in the rumen, a corresponding increase in blood glucose is not noted after feeding. Consequently, the concentration of insulin in the blood of ruminants is not correlated with blood glucose (24). Considerable research has been done on the effect of the volatile fatty acids, the end products of the fermentation in the rumen, on secretion of the pancreatic hormones (14, 22, 23). Intravenous injection of propionate and butyrate stimulates an acute release of insulin and glucagon, but it has not been clearly established that these fatty acids cause the post-prandial rise of either hormone. Propionate and butyrate are rapidly cleared from portal blood by the liver, and their concentration in peripheral circulation does not change much after feeding. Acetate is not completely removed by the liver, but it does not stimulate release of insulin.

Intravenous injections of free amino acids also causes a release of both hormones (23, 25), but normally, no marked increase in concentration of free amino acids in the blood of ruminants after feeding.

Preliminary evidence shows the presence of feed in the intestine initiates a series of reactions that result in secretion of the pancreatic hormones. The stimulatory effects of various peptides produced by the gastrointestinal tract have not been extensively studied in ruminants, but it has been observed in two studies (24, 26) that secretin and pancreozymin stimulate insulin secretion. It seems likely that the end products of digestion, volatile fatty acids and amino acids, initiate these reactions. Positive correlations have been observed between the quantity of organic matter or protein digested in the tract and plasma insulin concentrations (27).

Cattle fed high-grain diets (14, 28) or high-protein diets (29) have significantly higher concentrations of plasma insulin. Concentrations of glucagon in cattle or sheep fed under practical feeding conditions have not been studied.

Growth hormone. Secretion of growth hormone is much less responsive to feeding than are the pancreatic hormones. In ruminants fed once or twice per day, a decrease in concentrations of growth hormone in plasma for the 2 to 4 hours after feeding is noted (27, 30). This is followed by a gradual return to pre-feeding levels. With prolonged fasting, no increase in growth hormone concentrations results unless mobilization of fatty acids from adipose tissue is blocked pharmacologically (31). A more prominent pattern of growth hormone secretion in ruminants is an episodic release of the hormone every 4 to 6 hours (32, 33). This pattern is modified by gonadal steroids (32, 33), but the physiological mechanisms involved are not known.

Even though intravenous infusion of volatile fatty acids, glucose or a mixture of amino acids does not significantly alter growth hormone secretion in cattle (30), the concentrations of growth hormone are lower in plasma of ruminants fed greater amounts of grain (11) and are negatively correlated with the amount of organic matter digested in the alimentary tract (27).

Glucocorticoids. The effects of nutrition on plasma concentrations of glucocorticoids have not been as well studied as those of the pancreatic hormones or growth hormone. Eating has little influence on the concentrations of these hormones in sheep (34) or cattle (35). Fasting cattle for 72 hours increased plasma concentrations of glucocorticoids (35). In another study with cattle (36), higher concentrations of glucocorticoids were observed 16 to 22 hours after feeding in limited-fed animals in comparison with those fed *ad libitum*. Higher concentrations of glucocorticoids were found in cattle fed high-grain diets than in those fed high-roughage diets (35).

Hormonal Differences Associated
With Genotype

Evidence of genetic influence on concentrations of hormones in blood of cattle is increasing. Hart *et al.* (37) have studied the concentrations of hormones in high-yielding (Friesian) and low-yielding (beef x dairy) cows during lactation and the dry period. Some of these data are shown in Table 4. The dairy Friesians had higher concentrations of growth hormone and lower concentrations of insulin than did the beef-cross cows during lactation, as during the

dry period. The concentration of growth hormone was higher during lactation than during the dry period in both genotypes.

In another study (38), the concentration of growth hormone and insulin in small-type (Angus) and large-type (Simmental) steers was compared (Table 5). In this study, the smaller-type cattle had lower concentrations of growth hormone and higher concentrations of insulin. Implanting the cattle with an estrogen, which results in increased muscle growth and decreased adipose tissue, increased the concentration of growth hormone in both types.

Relationship of Plasma Hormone
Concentrations to Sex of the Animal

Entire males are known to be leaner than castrated males or heifers at a specified body weight. Entire males have been found to have higher concentrations of growth hormone than castrated males in both cattle (32, 33, 39) and sheep (33). Bulls have been reported to have higher concentrations of growth hormone than heifers (40). Injecting wethers with either estrogen or androgen increased the concentration of plasma growth hormone similar to that in the rams (33).

No definitive study has been made to compare concentrations of pancreatic hormones or glucocorticoids in the plasma of entire and castrated males or heifers. In studies with cattle, no differences in concentration of insulin in plasma of steers or heifers (41) or bulls and steers was found (39).

Conclusions

Long-term effects. The role of hormones in regulation of metabolism in ruminants has been reviewed

TABLE 4
MEAN CONCENTRATIONS OF INSULIN AND GROWTH HORMONE IN COWS OF DAIRY AND BEEF BREEDING^a.

	Dairy	Beef x Dairy
Lactating		
Growth hormone, ng/ml	6.96	2.25
Insulin, μU/ml	13.00	29.80
Dry period		
Growth hormone, ng/ml	3.05	1.90
Insulin, μU/ml	16.30	22.60

^a Eight cows per group. Samples taken at hourly intervals throughout a 48-hour period.

TABLE 5
MEAN CONCENTRATIONS OF GROWTH HORMONE AND INSULIN IN ANGUS AND SIMMENTAL STEERS^a.

	Angus	Simmental
Control		
Growth hormone, ng/ml	2.53	4.36
Insulin, μ U/ml	49.78	22.94
Implanted ^b		
Growth hormone, ng/ml	3.70	5.56
Insulin, μ U/ml	42.94	38.06

^a Four animals per group. Samples taken at 20-minute intervals throughout a 24-hour period.

^b Subcutaneous estradiol implants. Released 50 μ g of estradiol per day.

recently (42, 43, 44). Insulin, growth hormone and glucocorticoids each seem to be physiologically important for the long-term regulation of body composition. Simple correlation coefficients between plasma concentrations of these three hormones and weight gain or carcass composition of cattle (45) are given in Table 6. These values are in close agreement with the previously discussed functions of these hormones. The different growth hormone parameters were negatively related to carcass lipids and positively related to muscle. No relationship to gain, seemingly because of the offsetting effects of growth hormone on the two main constituents of body gain were noted. Plasma insulin was highly correlated with carcass fat. Plasma glucocorticoids were negatively related to daily gain, as has been observed by others (46).

The larger, leaner breeds of cattle have more growth hormone and less insulin (Table 5), which

TABLE 6
CORRELATION OF ENDOCRINE MEASUREMENTS WITH DAILY GAIN AND BODY LIPIDS AND PROTEINS.

Hormone	Daily gain kg	Carcass	
		Adipose %	Muscle
Plasma growth hormone, ng/ml	-.19	-.46*	.42*
Plasma insulin, ng/ml	.04	.70**	-.59**
Plasma glucocorticoids, ng/ml	-.73**	.32	-.35
Growth hormone secretion, μ g/hr/kg	-.06	-.55**	.47*
Pituitary growth hormone, μ g/kg	-.11	-.82**	.74**

* P<.05 ** P<.01

favors increased and more prolonged growth of skeletal muscle rather than shifting more energy to adipose tissue. The smaller breeds have higher insulin, which tends to increase utilization of acetate for fatty acid synthesis (17). The higher growth hormone and lower insulin found in the large breeds, many of which originated as dual-purpose cattle, are similar to those of lactating cows (Table 4). Bulls that are leaner than steers also have higher concentrations of growth hormone, which increases protein synthesis at the expense of lipids. Administration of exogenous growth hormone causes similar changes in carcass composition (2).

How much the endocrine system can be manipulated to change body composition is not completely known. Administration of estrogens (33) or growth-promoting implants (29) increases growth hormone secretion in ruminants, which is associated with increased protein and less lipids in the carcass. The data in Tables 4 and 5 suggest some genetic variation in the endocrine balance of cattle. Strategic uses of nutrition to alter the endocrine system, which might result in long-term effects on body composition, remain to be more fully explored. Feeding high levels of dietary protein, though, is associated with higher concentrations of insulin in the blood and fatter carcasses (29).

Short-term adjustments. After feeding, the concentration of insulin and glucagon both increase for several hours, which seems contradictory to their well-known effects on metabolism in nonruminants. The increase in insulin stimulates the uptake of amino acids and glucose by nonhepatic tissues of the body. Because ruminants absorb limited quantities of glucose from the digestive tract, they would soon become hypoglycemic if there was not a high rate of gluconeogenesis immediately after feeding. Stimulating hepatic gluconeogenesis in the fed state may be a primary function of glucagon in ruminants. Gluconeogenesis and the metabolism of glucose are greater in ruminants after feeding than during fasting (47). Concentrations of growth hormone are lowest after feeding, but, not severely depressed to the point of being deficient. The balance of metabolic hormones after feeding favors increased utilization of nutrients by nonhepatic tissues. In the fed state, insulin is the dominating hormone. Insulin increases the uptake of essential amino acids by skeletal muscle (4). The liver is the main site for the catabolism of all essential amino acids except the three branched-chain amino acids, so that the diversion of the essential amino acids to muscle by increased insulin after feeding would conserve their use for protein synthesis when adequate energy is available. The stimula-

supply two requirements in fed ruminants, one for synthesis of protein and the other as a source of carbon for gluconeogenesis. The breakdown of dietary proteins, the synthesis of microbial proteins in the rumen and the slower rate of feed passage in ruminants evens out the quantity and quality of amino acids absorbed to meet these requirements.

The insulin-dominated hormone balance after feeding also favors greater utilization of acetate for lipogenesis in adipose tissue. Acetate has a higher net energy value in cattle fed grain (43), a situation that provides more precursors for gluconeogenesis (propionate and amino acids) and a greater secretion of insulin.

Between meals and even more pronounced during fasting, the endocrine balance shifts from insulin to being dominated by growth hormone and glucocorticoids. The predominant target tissue is adipose with increased lipolysis. The higher glucagon to insulin ratio in the fasting state also increases lipolysis as well as breakdown of muscle protein. The elevation of glucocorticoids, during fasting is involved in the lipolysis and proteolysis during fasting or starvation. This fasting endocrine balance would promote greater uptake of mobilized nutrients by the liver. The shift from uptake to loss of amino acids from skeletal muscle occurs in cattle within 20 hours after feeding (49). The decrease in protein synthesis within 20 hours may be caused by a decrease in the energy available to support protein synthesis in muscle. The energy requirement for protein synthesis, 1 or 2 ATP equivalents per amino acid residue for membrane transport and 4 ATP equivalents per peptide bond, is very high and requires active energy metabolism. An important role of insulin may be to increase the uptake of energy precursors as well as of amino acids.

Other hormones, such as epinephrine (50), probably are involved in short-term changes in metabolism of adipose and muscle, but their role in regulation of growth of each tissue remains to be established.

As more information becomes available, other relationships will be shown to be involved in the metabolic adjustments of ruminants to different feeding schedules and the factors regulating body composition.

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