ENERGY METABOLITES IN BLOOD, LUTEINIZING HORMONE SECRETION AND REPRODUCTIVE PERFORMANCE OF BEEF COWS

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CHAPTER I

INTRODUCTION

Infertility in cattle is a major problem in livestock production worldwide. It is essential for maximum production that beef cows become pregnant within 85 days after calving. Many known and unknown variables influence the interval from calving to conception. The length of the postpartum anestrous interval of cows is a very important factor in the regulation of reproductive efficiency, and has often been called the single most economically important trait in beef cows.

The cow must produce a calf every year to maximize production and potential profits. The length of gestation is 280-285 days and 40-60 days are required after calving before well managed beef cows exhibit estrus and resume normal estrous cycles. Thus, only a few weeks remain in a year for the cow to become pregnant so as to maintain the economically important yearly calving interval. In addition, cows that do not exhibit estrus before 90 days after calving and cows calving later in the calving season are more likely to have reduced conception rates since ovarian activity may not be initiated before the end of the breeding season.

Approximately 70% of the 33 million beef cows in the U.S. exposed to bulls wean a calf the subsequent year. Bellows et al. (1979) determined that seventeen percent of the cows failed to wean a calf because they were not pregnant at the end of the breeding season. The

total yearly cost for the maintenance of an open cow is estimated to be about $350 a year (Thorpe and Beall, 1982). Thus, approximately $1.96 billion are used every year for the maintenance of open cows. Reducing the interval from parturition to conception is an integral key for more efficient and profitable beef production.

Research is needed to determine nutritional impacts on reproduction in beef cows. Several endocrine, metabolic, and physiological changes are associated with fetal growth, mammogenesis, parturition, lactogenesis and restoration of reproductive function post partum. Energy is one of the most important nutrients in a cow-calf nutrition program and also comprises a major feed expense.

The influence of dietary energy on reproductive performance, calf weaning weights and overall productivity of cows has been well documented. During the postpartum period, uterine involution must occur and estrous cycles must be reinitiated. Also, the cow reaches peak lactation at a time corresonding with the normal breeding season. Obviously, proper nutrition is critical during the postpartum period; however, during this period producers may fail to feed their cows adequately.

Energy requirements of cows are maximal during lactation. If nutrient requirements are not met during this period, milk production, calf growth, conception rates and the percentage of the cows cycling during the breeding season may be reduced. For these reasons, the subsequent experiments were designed to study the effects of glucose infusion, insulin administration, extra energy supplementation, suckling and exogenous hormone treatment on metabolic parameters, endocrine changes and reproductive performance of postpartum beef cows.

CHAPTER II

REVIEW OF LITERATURE

Nutrition and Reproductive Function

All nutrients have specific functions in cellular metabolism. Obviously, to maximize production, there must be an adequate supply of these compounds to the cell, specially dietary protein and energy. Requirements for these nutrients are set by the amounts necessary for the maintenance and for production of the animal.

Ruminants have developed the capacity to use feeds that cannot be used directly for human consumption or by non ruminant livestock. These feedstuffs, however, generally have a low energy content which is not adequate to meet the requirements of a productive animal. Diets high in protein and carbohydrates are used less efficiently due to fermentative processes in the rumen. Therefore, for maximum production, ruminants should be fed adequately to avoid problems like reduced feed intake and lesser mobilization of body reserves.

Infertility has been frequently associated with nutritional deficiencies. Dunn and Kaltenbach (1980) indicated that malnutrition during the last trimester of gestation can be particularly detrimental. During late gestation, fetal growth is maximal and severe nutritional deficiencies may increase mortality of calves, reduce calf growth rate and reproductive activity of the cow may be reduced after calving.

Bauman and Currie (1980) observed that initiation of lactation alters metabolism in many maternal organs in order that the mammary gland can be supplied with nutrients necessary for synthesis of milk. A tissue utilizing a substantial portion of maternal nutrients during gestation is the developing fetus. During the last two months of gestation fetal demands for specific nutrients (glucose and amino acids) are equal to mammary use of nutrients for milk synthesis. The metabolic cost of maintaining the fetus is great. Undernutrition during the last trimester of gestation may produce differences in concentration of hormones in plasma (i.e. extracellular signals), in cellular stimulation by hormones (i.e. number or affinity of receptors) and/or responses to hormonal stimulation (i.e. synthesis and/or degradation of products).

Effect of Nutrient Intake on Concentrations of Energy Metabolites in Plasma

Generally, energy content of a diet is the most important factor regulating food intake. Ruminants eat to reach the body energy balance which is determined by the difference between energy input (feed) and energy output in the form of energy expended for maintenance, milk production, reproduction and activity (Baumgardt, 1970).

Cows attempt to meet demands for nutrients by increasing their feed intake. However, the increase in feed intake usually does not satisfy the requirements at the peak of lactation.

Glucose Availability and Utilization in Ruminants

After ruminal fermentation of carbohydrates, only a small portion of glucose remains for absorption and the cow is almost totally dependant on liver gluconeogenesis for provision of glucose. The precursors for gluconeogenesis are propionate, amino acids and recycled lactate and glycerol, whereas glucose cannot be synthesized from acetate and butyrate.

Carbohydrate insufficiency for tissues requiring glucose arises because of the metabolic and hormonal changes of the cow at onset of lactation, which give first priority to glucose needed by the mammary gland at the expense of other body tissues (Baird et al., 1983). Gluconeogenesis cannot keep up with the demands for glucose because the supply of precursors is insufficient.

The major proportion of glucose available to the ruminant has to be supplied by gluconeogenesis, since little glucose is absorbed from the gut (Bergman, 1974). The provision of glucose is an energetically expensive process which is particularly important in situations where glucose demand is great (late pregnancy and early lactation), and it is during these periods that ruminants are highly susceptible to hypoglycemia.

In dairy cows, energy intake influenced food intake and metabolite concentrations during the last 70 days of pregnancy and during the first 125 days after parturition (Kunz and Blum, 1985). Compared with animals fed ad libitum before parturition, cows fed to meet NRC requirements during the same time had no decrease in feed intake at calving. Cows fed at a restricted energy intake had a greater increase in food intake,

a smaller energy deficiency at the onset of lactation and a smaller weight loss after parturition compared to cows fed ad libitum. Cows on the restricted energy had a longer peak of lactation and during the first 2 months of lactation they had greater concentrations of glucose and lactic acid in plasma with reduced concentrations of non-esterified fatty acids (NEFA) and ketone bodies in blood.

Reduced supply of energy during the dry period may improve glucose homeostasis during early lactation by diminishing fat mobilization. Kellog and Miller (1977) observed that as the supply of energy from the ration was reduced, blood concentrations of glucose declined as the demand on energy increases dramatically. Reduced concentrations of glucose in blood is a typical response to energy restriction of lactating ruminants because of the demand for glucose for lactose production and the minimal supply of glucogenic substrates in the body (Linzell, 1967; Kronfeld et al., 1968; Baird et al., 1972). When lactating dairy cows were allocated to either a high or a low plane of nutrition post partum, the cows on the greater supplemental diet had increased concentrations of glucose in plasma when compared to those on the diet with reduced supplement between 21 and 91 days after calving (Easdon et al., 1985). In cows that received the reduced energy diet, the nutrient deficiency caused a reduction in glucose in plasma.

Hormonal control of gluconeogenesis in the ruminant is similar to that in the non-ruminant (Gow et al., 1981). Lactating ewes (3-4 wk post-partum) that were subjected to food restriction for 4 d had decreased concentrations of glucose in plasma, glucose pool size, and plasma insulin. Glucose in plasma was decreased significantly in ewes that were fed ad libitum before the experimental period and glucose

tended to be reduced in ewes that were fed to meet energy requirements before the experiment.

Restricting food intake of lactating dairy cows caused a loss of 101 kg of body weight during the first 6 wk postpartum (de Boer et al., 1985). Weight loss was associated with a significant increase in plasma concentrations of B-OH butyrate and acetoacetate and a decrease in glucose in plasma. In addition, there was a greater rate of gluconeogenesis or increased demand for gluconeogenic precursors. This was associated with reduction in amino acids in plasma.

One function of the endocrine system is for homeostasis of blood glucose (Horino et al., 1968; Manns and Boda, 1977). When glucose was infused in cows (500 ml of 50% dextrose during 20 min), plasma concentrations averaged 175 mg/% at 1 h after injection (de Boer et al., 1984). After 3 h, plasma glucose had returned to preinjection concentrations. Insulin concentrations were increased at 1 h after injection of glucose and paralleled concentrations of glucose. Insulin concentrations at 3 to 6 h postinfusion were numerically doubled (3 ng/ml) but not significantly higher than the preinjection concentration. Similarly, concentrations of B-OH butyrate were decreased to approximately one half of preinjection concentrations by 2 h after initiation of glucose infusion. Exogenous glucose delivered into the blood increased the transfer of glucose to milk components with a decrease in endogenous glucose production (Bartley and Black, 1966). The mammary gland appears to have the first priority for blood glucose and may be responsible for the relatively low oxidation of glucose in lactating cows.

Judson and Leng (1973) studied the effect of glucose infusions on the rate of gluconeogenesis in sheep, as indicated by changes in the irreversible loss of plasma glucose, synthesis of glucose from ruminal propionate or fixation of blood bicarbonate into glucose. Glucose infusion suppressed endogenous production by 50 to 60%. Transfer rates of labelled carbon from blood bicarbonate or ruminal propionate to plasma glucose were also reduced during glucose infusion (gluconeogenesis). Only a small portion (usually less than 10%) of the glucose administered to sheep was apparently retained in extracellular fluid, as indicated by the change in plasma glucose concentrations.

Infusion of lactating cows with a 50% glucose solution during 48 h resulted in concentrations of glucose in plasma that were significantly increased at 4 h and 24 h after the beginning of the infusion. In non-lactating cows, the increase in glucose in plasma was constant during the total infusion period (Lomax et al., 1978). Glucose infusion decreased hepatic glucose output and decreased the uptake of the gluconeogenic precursor, lactate (Lomax et al., 1977).

Glucose uptake per unit of weight of tissue in the ewe was almost double the value found in the cow and goat (Davis and Bickerstaffe, 1978). The ratio of mammary gland uptake to lactose output was also greater in the ewe than that found in the cow and goat. During lactation, there is a large net uptake by the mammary gland of both glucose and lactate for lactose synthesis and milk production (Gardner and Hogue, 1964). In this way, a large proportion of glucose would be excluded from participation in whole-body metabolic interconversions.

Glucose supplies approximately 90% of the carbon in lactose (Bruckenthal et al., 1980). If the extent of feed restriction is

significant, gluconeogenesis declines and less glucose is available for maintenance and productive function. Feed restriction resulted in substantial and rapid decreases in milk output, losses of body weight and significant decreases in the rates of glucose loss and glucose pool size. When sheep were fasted, concentrations of glucose in plasma averaged 39 mg/% and the glucose concentration was significantly correlated with dry organic matter intake (Basset et al., 1971). Mean insulin concentrations were correlated with glucose entry rate or infusion. However, plasma insulin concentrations were not related to the plasma glucose concentration. Prepartum cows had greater basal plasma insulin concentrations during the last 3 wk of gestation than during lactation (Blum et al., 1972). Concentrations of insulin in the plasma of cows can be increased by treatment with glucose. Brockman (1983) observed that in sheep, insulin infusion affects rates of production and metabolic clearance rates of glucose. Metabolic clearance rates of glucose doubled with increased insulin.

The mean fasting concentration of glucose in blood of women during pregnancy was significantly less than after parturition (Landgraf-Leurs et al., 1983) and concentrations of glucose after oral glucose ingestion were less antepartum than postpartum. This suggests that the decrease in glucose utilization observed by Fisher et al. (1980) in women during gestation may not occur.

The homeostatic mechanisms in cattle regulate concentrations of glucose in blood within narrow limits under very different conditions of input and output, and blood glucose concentrations are of little value as an index of energy status in these circumstances (Parker, 1977; McClure, 1977). Also, diurnal variations in concentrations of glucose

in blood may be greater than the variations due to energy status (Hartman and Lacelles, 1965; Radloff et al., 1966; Coggins and Field, 1976).

Non-Esterified Fatty Acids

Non-esterified fatty acids (NEFA) have been identified as a major transport form of lipids under conditions of fat mobilization (Engel and White, 1960). Adipose tissue is the major source of NEFA, which, in turn, are available for utilization by other tissues.

Concentration of Free Fatty Acids (FFA) may provide an indicator of the long term energy status or nutritional status of humans and they tend to be negatively correlated with arteriovenous differences in blood glucose.

Dairy cattle and goats responded to nutritional stress (e.g. to high milk production) with increased concentrations of NEFA (Radloff et al., 1966). Nutrient intake along with the ability to mobilize and utilize body stores, are the major factors which may limit milk production in early lactation. Increases in FFA in plasma during a negative energy balance may stimulate feed intake.

Concentrations of NEFA in plasma of the cow usually reflects the rate of release of NEFA from adipose tissue as it does in other species (Fritz, 1961). Kronfeld (1965) observed concentrations of NEFA in plasma from 356 to 1805 uEq/l. Cows fasting during 1 to 5 d had mean concentrations of NEFA of 1400 uEq/l, while non fasted cows had 286 uEq/l. After 24 h of fasting, concentrations of NEFA increased to at least twice the prefasting concentration, indicating that concentrations

of NEFA in plasma may be taken as a sensitive clinically useful index of fat mobilization.

Restricting feed intake for 4 d in lactating ewes (Gow et al., 1981) decreased body weight and increased plasma NEFA. When food intake was restored, concentrations of NEFA returned to normal. The changes in concentration of NEFA in plasma during feed deprivation were consistent with increased mobilization of body tissues as a supply of energy. Although adipose tissue is mobilized during feed restriction to supply energy in the form of NEFA (Patterson, 1963), the concomitant release of glycerol, a glucose precursor, may make a significant contribution to the glucose supply.

Radloff et al. (1966) conducted experiments with cows and goats to determine the normal concentrations of NEFA and their relationship to blood sugars. Upon fasting, concentrations of NEFA in plasma increased, whereas blood sugars were depressed and blood ketones increased. In milking goats, 24 h of fasting increased concentration of NEFA threefold whereas, glucose declined 15 mg/%. Upon fasting of nonlactating goats, concentrations of NEFA in plasma increased and glucose decreased, but the changes were of lesser magnitude and occurred more gradually. Concentrations of glucose in blood and NEFA in plasma were correlated (-0.75).

Holmes and Lambourne (1970) observed that concentrations of NEFA were correlated with DE intake in heifers. During hypoglycemia, concentrations of NEFA were increased (Annison, 1960), whereas glucose injections reduced concentrations of NEFA (Fritz, 1961).

Factors that directly or indirectly increase carbohydrate utilization inhibit the net release of fatty acids from tissue stores

(Fredrickson and Gordon, 1958; Dole, 1958), while conversely, conditions associated with impaired glucose utilization accelerate the release of fatty acids. There is a simple reciprocal relationship between glucose utilization and fatty acid release from adipose tissue.

Thye et al. (1970) found that NEFA concentrations 7 h after a meal were the best single predictor of subsequent feed intake of ewes. Animals receiving a restricted meal had NEFA values similar to prefeeding levels, whereas, ewes receiving a normal meal were at minimum values. During lactation, cows attempt to meet the increased demand for nutrients by increasing their feed intake. Cows adapt to the increased energy demands by increasing the rate of lipolysis and decreasing the rate of lipogenesis (Sidhu and Emery, 1972). Chilliard et al. (1977) observed that a reduction in lipogenesis in goats is achieved by reduced uptake of fatty acids and less de novo fatty acids synthesis, since the activity of lipoprotein lipase and acetyl CoA carboxylase were reduced during lactation.

Beta-Hydroxy Butryate

Ketosis and hypoglycemia occur most frequently in high-producing dairy cows and in pregnant ewes. However, ketosis of varying intensity may occur in all animal species due to starvation, reduced amounts of carbohydrates in diets specially during lactation or pregnancy, inadequate feed intake or unusually large withdrawals of metabolites. All these alterations in energy overwhelm the body's ability to mobilize its metabolic fuels (Bergman, 1974). The major ketone in plasma of ruminants is beta-hydroxy butyric acid. It comprises about two-thirds to three-fourths of the total ketones under usual circumstances and just

over half of the total when concentrations of ketones in blood are greatly increased (Fritz, 1961). An increased supply of fatty acids to the liver together with low glucose availability, results in a physiological ketosis with the resultant elevated beta-hydroxy butyrate (BHB) in plasma which further inhibits lipolysis (Bines and Hart, 1982). Increased ketogenesis and ketosis in starved animals can be inhibited by the administration of carbohydrates (Fritz, 1961).

A reduction in feed intake results in increased concentrations of BHB in plasma (about 25 to 50%; Roberts et al., 1978). Greater demands for glucose in the dairy cows producing great amounts of milk resulted in increased plasma concentration of BHB (Bines and Hart, 1982). There were greater concentrations of BHB at all stages of lactation in high producing cows. Throughout lactation, concentrations of BHB were greater in high-yielding cows compared with low producing cows (Hart et al., 1978). Concentrations of BHB in plasma after parturition are usually increased for about two months, compared to values during the dry period. Cows restricted to 75% of the energy required for maintenance and production had the greater concentrations of BHB from 5 to 60 d after parturition compared with cows fed to meet requirements (Kunz et al., 1985).

Onset of lactation caused concentrations of BHB to increase (de Boer et al., 1985). Mean concentrations of BHB were not increased significantly in early lactation; however, there was a significant difference when ketonemia was induced by feed restriction. Concentrations of BHB returned to those of the dry period after a 4-wk recovery period.

In general, BHB is mobilized under conditions of prolonged and severe underfeeding. Lomax et al. (1977) observed that during infusion of glucose to dairy cows the hepatic output of BHB was decreased, and there was a corresponding decrease in hepatic uptake of the ketogenic precursor, butyrate. Concentrations of glucose in the blood of ewes were greater during lactation than during pregnancy, and concentrations of BHB were reduced during lactation compared to pregnancy. In contrast to the response in ewes, the concentrations of glucose, lactate and pyruvate in cows were less during lactation than during pregnancy, while concentrations of BHB tended to be greater.

The use of energy reserved for milk fat production represents a severe energy loss by a cow. Depot fat is used very inefficiently to meet the energy needs or milk production.

Effect of Body Energy Reserves on Concentrations of Energy Metabolites in Plasma

Intense selection of dairy cattle for high milk yield has resulted in a situation in which the genetic ability to produce milk during early lactation exceeds the ability of the animal to consume sufficient feed to meet the requirements for energy (Moe et al., 1971). In mammals, nutrients are utilized by tissues involved in maintenance and growth. Excess nutrients are stored in the body as lipids (energy), glycogen (glucose) and labile protein (amino acids). Bauman and Currie (1980), suggested that changes in the partitioning of metabolites associated with energy are very important at the onset of lactation. If the animal is unable to alter energy metabolism rapidly or to the extent needed to meet demands for milk synthesis, either the cow produces below her

capability or she is susceptible to various metabolic disorders and, even, infertility. Because production of milk during early lactation has a high priority in the dairy cow, production of large quantities of milk may continue despite insufficient dietary energy intake. In such a case, cows must mobilize body tissue reserves to provide the energy which is lacking in the diet (Moe et al., 1971). During early lactation, daily feed intake of cows usually increases and the resulting increase in rumen fill may mask decreases in empty body weight. Roberts et al. (1978) suggested that changes in body weight are unreliable indicators of changes in condition or of energy status. Milk yield attains a maximum at 3 to 4 weeks of lactation, whereas energy intake usually does not reach a maximum until several weeks later. During the first one-third of lactation, most dairy cows are in a negative energy balance and use body reserves to meet requirements. As a consequence, a net energy balance (i.e., intake sufficient to meet requirements) is not achieved until later lactation when milk production decreases to less than 80% of maximum production.

Metz and Van der Bergh (1977) proposed that fat mobilization in early lactation may be caused by a negative energetic balance. It has been suggested (Schultz, 1968) that cows could be considered under much fat mobilization if concentrations of glucose in blood are less than 40 mg/% and total ketone body concentrations are greater than 10 mg/%. Due to inability of the cow to meet the energy requirements early in lactation, fatty acids, protein and glycogen must be mobilized from storage sites (Kellog and Miller, 1977). Adipose tissue, the primary source of reserve of energy, provides fatty acids for mobilization and transport in plasma. Bailey and Matty (1971) suggested that fat depots

of the body may be the basis of energy balance regulation. A marked lipid mobilization is accompanied by depletion of triglycerides in adipose cells and elevated plasma concentration of NEFA in early and mid-lactation (Radloff et al., 1968), and decreased concentration of NEFA in blood at peak lactation (Radloff et al., 1966). Bauman and Currie (1980) reported that during the first 10 weeks of lactation, the net energy deficit of lactating dairy cows was equivalent to approximately 50 kg of pure lipid or an average daily production of 9 kg of milk. Even more impressive, during the first month of lactation the body reserves that were utilized (i.e., net energy deficit) were equivalent to about 33% of the milk produced.

The concentration of NEFA in plasma is an important determinant to the rate of both fatty acid oxidation and synthesis (Fritz, 1961). The rate of release of NEFA from adipose tissue is usually responsible for changes in plasma NEFA concentrations. Fredrickson and Gordon (1958) reported that the major NEFA in the plasma are palmitic, oleic and linoleic acids, with small amounts of stearic, myristic and arachidonic. These NEFA are similar to those present in depot fat. A negative energetic balance leads to increased concentrations of NEFA in plasma and increased peripheral utilization of NEFA (Bines and Hart, 1982). Moreover, NEFA release from adipose tissue is in balance with NEFA uptake by other tissues. The rate of NEFA production from adipose tissue, as well as the rate of NEFA utilization, is closely correlated with the plasma NEFA levels (Reid and Hinks, 1962).

Glucose in plasma is frequently associated with energy metabolism in the animal. Glucose reserves in the body are limited, and at fasting when dietary precursors to gluconeogenesis cease to be absorbed, the

body attempts to spare glucose in several ways: a) concentrations of insulin decrease, which reduces peripheral uptake of glucose; b) reesterification of adipose tissue is depressed, thus decreasing requirements for glucose; c) mobilization of NEFA from adipose tissue is increased, and since NEFA is the preferred substrated, it will spare glucose. Thin ruminants have a typical decrease in glucose and insulin concentrations and an increase in NEFA during fasting (McNiven, 1984).

Amount of milk produced by cows affects plasma metabolites. Hart et al. (1978) observed differences in changes of body weight between high- and low-yielding cows, indicating that, in early lactation, animals were in different metabolic states. The loss in body weight in high-yielding cows is coupled with significant greater concentrations of NEFA in plasma, suggesting the mobilization of body tissues for milk production. The low-yielding cows maintained a positive energy balance throughout most of lactation, as indicated by a steady increase in body weight without alterations in NEFA. De Boer et al. (1985) observed decreased concentrations of NEFA during a recovery period after weight losses, suggesting that the cows were at energy equilibrium or in a positive energy balance.

Concentrations of glucose in plasma are usually negatively correlated with concentrations of NEFA, indicating that fat mobilization occurs with reduced energy intake and reduced glucose in plasma. Reid et al. (1979) observed that cows mobilizing more adipose tissue during the 8 weeks after calving, had reduced concentration of glucose in plasma compared to cows with milk fat mobilization. Similarly, de Boer et al. (1985) reported that intense fat mobilization during the first 3

weeks postpartum was associated with significant decrease in concentration of glucose in plasma.

Concentrations of energy metabolite in plasma are affected by the body condition (energy stores) of the animal. Bines and Morant (1983) found greater concentrations of NEFA in fat cows, especially before feeding, which implies a greater rate of lipolysis in response to an energy deficit. Garmendia et al. (1984) reported that body condition was correlated with concentrations of NEFA in plasma during the prepartum period in beef cows. After calving, concentrations of NEFA were negatively correlated with changes in body weight and body condition score from 120 days before calving.

Restriction of feed intake around parturition also affects concentrations of plasma metabolite. Easdon et al. (1985) compared the average liveweight of cows with feed restricted or a normal diet during the postpartum period. Restricted cows lost 21% of their initial weight during the first 63 days postpartum, whereas normal cows maintained weight. Concentrations of NEFA in plasma were significantly greater in cows losing weight during the postpartum period, suggesting mobilization of body reserves. Concentrations of glucose in plasma were significantly greater in cows maintaining weight during the postpartum period compared with cows losing weight. McNiven (1984) examined differences in blood concentrations of glucose and NEFA in sheep at two levels of fatness. Fat sheep had greater concentrations of NEFA in plasma than the thin sheep. However, there was no difference in concentrations of glucose in plasma. Concentrations of glucose and NEFA were significantly correlated in both the thin and fat sheep; however, the correlation coefficients were larger in the thin sheep.

Body energy reserves are associated with body condition scoring systems. Dunn et al. (1983) reported that body condition score of the live beef cow was correlated with carcass energy content and carcass fatness (r = .77, .86, respectively). A larger correlation (r = .92) was found between body condition score and total energy in the carcass (Wagner et al., 1985).

Relationship of Body Energy Reserves with Reproduction

Variations in reproductive performance are related to the supply of nutrients before and after parturition and, consequently, to changes in weight and body condition of the cow. Beef cows in thin body condition have reduced pregnancy rates. The least fertile cows are cows with their first calves that are in thin body condition (Lamond, 1970).

Body condition of cows at calving is highly correlated with length of the interval from calving to first estrus (Whiteman, 1975; Bellows and Short, 1978; Bellows et al., 1982; Selk, 1986). Cows in good body condition had more normal luteal cells, fewer early degenerative cells and a greater corpora lutea weight than cows in thin or poor body condition (Betts et al., 1985). Condition score of the cows was correlated with corpora lutea weight, healthy cells and degenerative cells. They concluded that viability of the corpora lutea may be related to body condition of the cows. Wiltbank et al. (1962) found that cows and heifers in thin condition at calving, required more concentrate feed after calving if estrus was to occur during the breeding season. However, feeding diets high in concentrates to thin cows after calving is expensive and can result in adverse effects on postpartum reproduction by stimulation of milk production, thus

increasing the suckling effect, and, in turn, lengthen the postpartum anestrous period (Bellows and Short, 1978).

Beal et al., (1978) studied the effect of changes in body weight and condition of cows on pituitary and luteal function. After a prolonged period (90 d) of feed restriction, cows fed the restricted diet lost .37 kg/d, compared with cows that gained .36 kg/d. Carcass weight, backfat thickness and kidney fat weight were significantly reduced by restricting the intake. Cows in thin condition had greater concentration of LH and greater total LH release following GnRH administration compared to cows fed the adequate ration. Restricted intake decreased the pituitary content of LH and peripheral serum concentrations of progesterone tended to be reduced. This suggests that thin body condition may influence LH release directly at the pituitary level, as well as, indirectly through effects on ovarian steriod production.

Corah et al., (1975) studied the effect of changes in maternal body weight in the later stages of gestation on reproductive performance of beef heifers. Heifers were assigned to a high or a low level of energy 100 days prior to predicted calving. Heifers fed the high ration gained 36 kg while the heifers on the low ration lost 6 kg. Restriction of energy prepartum decreased birth weight, survival rate and weaning weight of calves. In addition, there was a tendency for a reduced percentage of cows to exhibit estrus by day 40 post partum. Donaldson et al. (1967) found that pregnancy rates were less in cows with poor body condition at calving. Pregnancy rate was 10% in cows in thin condition compared to 89% for cows in fat condition.

Holnes and Hopley (1978) investigated the effects of both long- and short term feed restriction and changes in liveweight on the occurrence of postpartum estrus in beef cows. Cows were fed either to gain 13% (high) or to lose 13% (low) of their maximum body weight (early pregnancy) by mid breeding season. Half the cows in each group were subjected to an increase or a decrease in nutrient intake for a 25-d period starting at 25 d post partum. Estrus occurred significantly earlier for the cows on the high nutrient intake than for low cows (66 vs 75 d post partum), but short-term fluctuations in nutrient supply had no apparent effect on the incidence of estrus. Postpartum anestrous was shorter in cows that lost weight post partum. A loss in live weight occurs in cows that are in better condition at calving. Also, they mobilize tissue reserves more rapidly and are better equipped to provide for normal metabolic function during the time of heavy demand for available nutrients.

Cows fed 60% of the energy requirements starting 30 d before their expected calving date lost more weight through the first 39 d after parturition compared to cows fed 115% of the energy requirements (Lishman et al., 1979). However, level of feeding had no effect on size of the largest ovarian follicle during the first estrus. The occurrence of corpora lutea after GnRH was not related to body weight post partum, weight changes during lactation or nutrient intake.

Wettemann et al. (1980) studied cows that maintained or lost body condition during the winter. Fewer cows losing condition exhibited estrus by 80 d post partum and pregnancy rate was 71% compared with a pregnancy rate of 85% for cows maintaining condition. Birth weight of the calves was reduced in cows that lost condition. Similarly, Bellows

and Short (1978) observed that decreasing precalving nutrient intake affects the dam and the calf. Precalving feed intake (90 days) significantly affected precalving body weight and condition score of the cow, length of the post partum anestrous interval, percent of cows exhibiting estrus before the breeding season, birth weight of the calves and the percentage of cows pregnant at weaning.

Weight changes from fall to spring and during the breeding season were found to be related with calving percent. There was a reduction of .12% in calving rate for each kg of body weight lost from fall to spring and an increase of .2% in calving rate with each kg gained during the summer. Also, Gardner (1969) noted that cows fed either low or high energy pre and post partum had similar fertility. Average birth weights, days from calving to first estrus, calving intervals and services required per conception were not different. Good body condition at calving may lead to dystocia. Makarechian et al. (1982) reported that dam weight at calving and calf birth weight had the most significant influence on problems associated with dystocias.

Infertility due to undernutrition is not a major problem in dairy herds because sufficient amounts of concentrate are usually fed to attain satisfactory milk production. However, high-producing cows fed adequate amounts of concentrates had prolonged calving intervals and more services per conception than control cows (Morrow et al., 1969).

Badinga et al. (1985) suggested a substantial antagonism between milk yield, body weight change and efficient reproduction. Cows with a greater than average milk yield had a decrease in conception rates at first service compared with cows that had below average milk production (Spalding et al., 1975). Also, cows that produced more milk were

heavier at the initiation of lactation, had more days open and tended to require more services per conception. Correlations between milk yield and services per conception were positive, indicating that high-producing cows required more services per conception than low-producing cows. Similarly, the interval from parturition to first ovulation was longer in cows with a genetic potential for greater milk yield (Whitmore et al., 1974). Animals with the genetic potential for greater milk production had longer intervals to estrus (41 d) than cows with genetic ability for less milk production (31 d; Hansen and Hauser, 1983). During the postpartum period, cows in good condition had shorter intervals to first ovulation and first estrus than cows with poor condition (Coppock et al., 1974). Cows producing greater amounts of milk cannot maintain a positive energy balance during early lactation and must mobilize energy reserves. In these cows, postpartum ovarian activity is more closely associated with milk production than with total digestible nutrient intake. Butler et al. (1981) observed that energy balance during the first 20 d of lactation was inversely related to days to ovulation ($r=-.60$) and to milk production ($r=-.80$). On the average, ovulation and the initiation of the first luteal phase occurred approximately 10 d after the energy balance was no longer negative. During this 10-d interval, serum progesterone increased in 60% of the cows. Fulkerson (1984) found that the percentage of dairy cows submitted for first service during the first 24 d of the mating season increased from 60 to 97% as cow condition score improved from 3 to 5.5 (1=emaciated, 8=overfat).

Energy balance during the first 20 d of lactation influences the onset of ovarian activity following parturition. Rutter and Randel

(1984) noted that if beef cows maintained body condition from calving to first estrus, they had a short postpartum inteval to first estrus (32 d) compared with cows that lost weight (60 d). Body weight changes may be a poor measure of energy balance in lactating cows (Coppock et al., 1974) and may be confounded with body condition at calving. Stevenson and Britt (1980) noted in dairy cows that the percentage change in body weight was inversely related to days first ovulation. Cows that had the smallest weight losses during the postpartum period had the shortest intervals to formation of the first postpartum corpora lutea (Menge et al., 1962). King (1968) observed that increases in body weight around parturition caused an increase in conception rate at first service (78%) compared with cows that lost weight (16%). McClure (1965) noted that the infertile cows were those which lost the most weight between calving and mating and/or were still losing weight at the time of mating, whereas, the mean body weight of fertile cows was increasing at the time of mating.

Under tropical and sub-tropical conditions where animals obtain most of their nutrients from the pastures, the situation is more critical. Lamond (1970) observed that the effects of undernutrition on fertility are more commonly observed in tropical and sub-tropical regions than in herds in temperate regions. Young (1968) found a greater pregnancy rate in lactating beef cows than in non-lactating cows in Australian herds in temperate regions. Evidently, in herds in which satisfactory nutritional conditions prevail, adult lactating cows have greater fertility. Fertility of lactating, adult beef cows may be a good indicator of the nutritional status of a herd.

Baker (1969) studied the relationship of pregnancy rate to body condition in cattle. Cows in thinner body condition were less fertile. Bos indicus crossbred cows maintained in thin condition over a suckling period of 180 d, had a postpartum interval to first estrus of 220 d. The incidence of pregnancy was influence by body condition in both weaned and unweaned cows, however, weaning influenced the incidence of pregnancy only if the cows were in poor condition. The proportion of cows cycling at 120 d post partum was correlated with the average live weight of the cows at 60 d post partum (Gauthier et al., 1984). The percentage of cows with ovarian activity, calculated for consecutive 30 kg increments in liveweight from 250 to 400 kg, was less for cows under 250 kg (approximately 25%), increased between 250 and 310 kg and was about 100% for cows that weighed more than 340 kg.

Henneke et al. (1984) studied the relationship between body condition in mares at the onset of the breeding season, post partum nutrition and reproductive performance. Mares were fed to have either good or thin body condition from 90 d before foaling and good or thin condition during the first 90 d post partum. After 3 y of treatments, pregnancy rate at 30 d post partum was significantly less (50%) in mares losing body condition pre partum and maintaining thin body condition post partum compared to 100% in the mares that gained body condition before or after foaling or gained condition during both periods. Maintenance of pregnancy to 90 d was also reduced in mares that lost condition both before and after foaling. Interval to the onset of estrus and ovulation and pregnancy rates were reduced and number of cycles/conception were increased for mares in thin condition at the start of the breeding season and for pregnant mares foaling in thin

condition. In another study, Henneke et al. (1983) observed that mares in thin condition at foaling had longer postpartum intervals to onset of estrus. Conception rates for mares in good body condition at foaling that lost weight during lactation were as good as those for mares in good or thin condition at foaling that gained or maintained weight during lactation.

Severe loss of body weight in humans leads to endocrine malfunction; amenorrhea in women is commonly associated with decreases in body energy reserves. Menstrual disfunction in athletes is associated with reduced body weight, which is associated with smaller amounts of body fat (Carlberg et al., 1983). Runners with the least body weight and body fat had the greatest incidence of amenorrhea (Baker et al., 1981). In non-athletic women, amenorrhea is often associated with weight loss or chronic malnutrition. Total body weight, percent ideal body weight, percent body fat and weight of body fat were significantly less in the oligo/amenorrheic athletes compared with women exhibiting normal menstrual cycles.

Boyden et al. (1984) did not find any significant correlations between changes in body composition and changes in gonadotropin responses in women. However, Russell et al. (1984) observed that average concentrations of LH and estradiol were decreased and concentrations of endorphins were increased under strenous exercise in women athletes. Rapid weight loss, decreased percentage of body fat and stress are key factors in decreased concentration of LH, FSH, estradiol and progesterone in plasma and amount and intensity of exercise may be more critical than changes in percentage of body fat in the cessation of menstrual function. Endorphins bind to hypothalamic cells which secrete

GnRH and blocks GnRH release by norepinephrine (Kalra and Simpkins, 1983). Increased concentrations of endorphins and dopamine during strenous exercise may interact to cause suppression of GnRH release.

Warren et al. (1975) demonstrated severely impaited gonadotropin responses to GnRH in women who were 25% underweight. Pulsatile administration of GnRH for ovulation induction in hypogonadotropic amenorrhea women is effective (Liu et al., 1983). The negative feedback effects of ovarian estradiol could modulate the GnRH-mediated gonadotropin release, and thus circumvent hyperstimulation and follicular development.

Relationships Among Reproductive, Endocrine and Metabolic Parameters

Nutrition has a major role in modification of the length of the postpartum anestrous interval of cows. But, there is some controversy about the optimal nutritional conditions for the prompt return to normal estrous cycles.

There is a positive effect of increased dietary nutrient intake on reproductive performance, including enhanced pituitary (Beal et al., 1978; Jordan and Swanson, 1979; Lishman et al., 1979) and ovarian (Wiltbank et al., 1962, 1964) function. Energy intake has either altered (Wiltbank et al., 1962, 1964; Dunn et al., 1969), or has had no effect on ovarian (Lishman et al., 1979; Carstairs et al., 1980) or pituitary activity (Hill et al., 1970; Dunn et al., 1974; Spitzer et al., 1978; Haresign, 1981).

The relationship between hypoglycemia and reproductive dysfunction has been studied (Oxenreider and Wagner, 1971; McClure, 1972; McClure

and Payne, 1978). Concentrations of glucose in blood have been observed to be either inversely (Kellogs and Miller, 1977) or positively (Patil and Deshpande, 1979) correlated with the postpartum interval to conception.

Kappel et al. (1984) and Selk (1986) observed that animals with greater fertility had greater concentrations of glucose in blood compared with less fertile cows. Nutrient intake prior to and following parturition influences follicular development and pituitary function. Hypoglycemia is associated with decreased follicular development (Oxenreider and Wagner, 1971) and infertile inseminations (Downie and Gelman, 1976). In young, lactating beef cows, concentrations of glucose in plasma are decreased and related to the lengthened anestrous period compared to mature cows (Chang et al., 1984). Rowlands et al., (1977) suggested that in postpartum lactating cows there is a threshold for plasma glucose concentrations below which fertility is impaired. Kellogs and Miller (1977) observed that concentrations of glucose in blood were less great for cows with the shortest postpartum interval. Selk et al. (1985) found that beef cows conceiving during the breeding season had increased plasma glucose during the first 10 wk post partum compared with cows that did not conceive. This suggests that the concentrations of glucose in plasma after nutritional restriction may be related to subsequent conception rate (Selk et al., 1985).

There is a correlation betweeen hypoglycemia and infertility in dairy cows when energy intake is restricted (McClure, 1970). The degree of infertility was correlated more strongly with blood glucose concentrations than with weight losses. It was also suggested that hypoglycemia was the cause of hypothalamic failure. Lotthamer (1982)

indicated that milking cows fed grass-silage and concentrates during 3 years had problems balancing energy requirements, indicated by decreased concentrations of glucose in plasma. These cows had reduced conception rates (45%). When energy was increased in the diet, there was an increase in conception rates (59%) along with an increase in plasma glucose. Carstairs et al. (1980) observed that the interval from parturition to the first observation of serum progesterone greater or equal to 3 ng/ml was correlated with glucose (r=-.33) and growth hormone (r=.51).

Infusion of glucose (iv) into postpartum cows did not affect progesterone in plasma, mean LH release after GnRH and basal secretion of LH (McCaughey et al., 1985). However, cows with greater ovarian activity had peak LH and greater area under the LH curve than cows that did not have elevated progesterone before day 53 post partum. Glucose infusion, that was sufficient to elevate plasma glucose and insulin and decrease plasma NEFA, did not affect return to estrous cyclicity in the postpartum beef cows.

A decrease in dietary energy intake may disrupt hypothalamic control of the pituitary gland (McClure, 1970). The use of an inhibitor of glycolysis, 2-deoxy-glucose, disrupted glucose metabolism and inhibited LH release, presumably due to a failure of the hypothalamus to release LHRH rather than failure of the pituitary to produce LH (Crump et al., 1985). Sen et al. (1979) examined the involvement of the energy in GnRH-stimulated LH release from the anterior pituitary. Inhibitors of both glycolysis and oxidative phosphorylation inhibited stimulation of LH release with GnRH. McClure and Payne (1978) observed energy deficiency and decreased concentrations of glucose in plasma, which were

associated with anestrous and reduced conception rates. Reducing glucose in blood by administering insulin altered ovarian function and reduced fertility in cattle. In rats, Lengyel et al. (1984) observed that basal LHRH was not influenced by either glucose or 2-deoxy-glucose.

The inhibition of glycolysis is associated with failure of both estrus and formation of functional corpora lutea. Administration of 2-deoxy-glucose to heifers just before and during estrus, or following the removal of the corpus luteum, prevented both the occurrence of estrus and the formation of corpora lutea. In addition, concentrations of progesterone in plasma were minimal for 21 d after treatment with 2-deoxy-glucose (McClure et al., 1978). They suggest that hypoglycemia is the primary biochemical change responsible for infertility induced by acute energy deficiency in cattle.

The brain is dependent on a constant supply of glucose in blood for energy because there is reduced carbohydrate storage in the brain (Lund-Andersen, 1979). Insulin causes an increase in glycogen synthesis in the brain and increased glucose consumption will cause an increase in the net transport of glucose from blood to brain.

Cellular metabolism of glucose in vitro is necessary for LH and progesterone production (McCann, 1984). Pituitary and steroidogenic cells have insulin receptors, suggesting that insulin regulates glucose metabolism and may be important in LH and progesterone production. Insulin and insulin receptors are abundant in the central nervous system (Havrankova et al., 1978). The preoptic area and the anterior hypothalamic area have numerous insulin receptors (Harvankova et al., 1978; Pacold and Blackard, 1979). Adashi et al. (1981) found that in rats, insulin for 2 d resulted in significant increases in both the

basal and the maximal release of LH and FSH. This suggests that the pituitary has target cells for insulin. Acute insulin-induced increases in glucose utilization did not affect progesterone production but suppressed LH production (McCann, 1984).

Poretsky et al. (1984) suggested that insulin might directly influence ovarian function. Insulin is capable of stimulating ovarian steroidogenesis in vitro of porcine theca cells (Barbieri et al., 1983) and granulose cells (May anad Schomberg, 1981), as well bovine granulose cells (Savion et al., 1981). Insulin is a regulator of cell growth and steroidogenesis in cultured granulose cells (Channing et al., 1976). Quantity of insulin in follicular fluid and the concentration of progesterone is correlated. Pancreatectomy and diabetes reduced the gonadotropin receptors in ovaries of rats and administration of insulin restored the binding capacity to normal values (Charreau et al., 1978). Isolated Leydig cells from diabetic rats were less sensitive to exogenous LH than the interstitial cells isolated from normal rats.

Decreased insulin concentrations, decreased glucose utilization and reduced progesterone production may explain in part the decreased ovarian function in fasted or chronically underfed animals (McCann, 1985). McClure (1968) compared cows mated after insulin injection for 3-4 d and cows treated with insulin daily during the first 4 d after mating. The later cows were significantly less fertile than either cows treated at other times, or control cows. Administration of protamine zinc insulin to lactating cows at proestrus delayed the onset of estrus and reduced pregnancy rates of cows in which estrus occurred at the normal time (McClure, 1968). Bines and Hart (1982) observed that insulin is responsive to brief changes in energy status of the cow.

Concentrations of insulin in serum are reduced in starved animals (Trenkle, 1978), and increases markedly after a meal. The amounts of insulin released at feeding is related to the amount of dietary energy consumed (Basset, 1978).

Hove (1978) observed an increase in insulin at 10 to 20 min after the start of a glucose infusion in normal animals, followed by a sustained increase. Concentrations of insulin were greater in fed than in starved animals. McAtee and Trenkle (1971) observed that concentration of insulin in plasma was not related to concentration of glucose in plasma after feeding or after 46 to 58 h of fasting. Intravenous infusion of glucose, propionate, or butyrate each increased concentration of insulin in plasma of steers fasted for 24 h.

In sheep, Basset et al. (1971) observed that mean insulin concentrations were closely correlated with glucose entry rate or infusion. However, plasma insulin concentrations were not related to the plasma glucose concentrations. Prior and Christensen (1978) observed that an injection of insulin into non-pregnant ewes produced an immediate increase in the rates of glucose clearance and glucose disappearance. Uterine glucose uptake in pregnant ewes was reduced after insulin infusion and tended to increase with an increased number of fetuses.

Glucose appears to be the primary energy source for the fetus. Boyd et al. (1973) calculated that the metabolism of glucose could account for about 50% of the oxygen uptake by the fetus. Glucose oxidized was unaffected by diet, but was reduced in pregnant when compared with dry or lactating ewes. Glucose tended to be greater in

plasma and significantly reduced in placenta and fetuses, due to reduced transport into the fetuses (Oddy et al., 1985).

The effect of energy status on LH release after GnRH treatment has not been established. Reduced energy intake decreased (Lishman et al., 1979), increased (Haresign, 1981) or had little effect (Lishman et al., 1974) on LH release. Changes in the hormone concentrations of underfed animals suggest that differences in energy intake may affect fertility by altering endocrine function. Increased amounts of energy and increased quality of the diet have been effective in decreasing the postpartum anestrous interval.

Easdon et al., (1985) observed that mean concentrations of LH were not different between cows fed either high or low plane of nutrition post partum. However, mean LH concentrations have been reduced (Gauthier et al., 1983) or have remained constant (Rone et al., 1982) during feed restriction in the postpartum period. Gombe and Hansel (1973) and Apgar et al. (1975) have suggested that restricting energy intake reduces the corpus luteum responsiveness to LH stimulation, resulting in the corpus luteum synthesizing and releasing less progesterone. The negative feed back effects of progesterone on LH is decreased. Therefore, systemic levels of LH are increased, indirectly, through the effects on the ovary. Concentrations of progesterone were slightly affected and concentrations of LH were significantly decreased in cows with restricted energy diet at estrus (Apgar et al., 1975). Gombe and Hansel (1973) observed that ovarian hypofunction under conditions of restricted energy intake is not due to reduced concentrations of LH in plasma, suggesting that the first effect is a reduced ability of the ovarian tissue to respond to LH. Dairy cows fed

reduced protein had decreased basal concentration of LH in serum, compared to cows fed either intermediate or elevated protein. Cows fed either a restricted or intermediate protein diet had a decreased response to GnRH compared to cows fed an elevated protein diet (Jordan and Swanson, 1979). Neither protein restriction nor time post partum had any effect on episodic LH release, duration of GnRH induced LH release, duration of estradiol induced LH release or maximal estradiol induced LH release of beef cows (Nolan, 1984). Protein restriction tended to alter time of maximal GnRH-induced LH release, suggesting that protein restriction may affect the ability of the pituitary to store and/or release LH.

Ewes receiving a grain diet had greater concentration of glucose and reduced NEFA compared with ewes fed only hay (Howland et al., 1966). Concentration of LH in pituitary, pituitary weight, ovulation rate, follicular fluid weight and number of large follicles were greater in ewes receiving grain, suggesting that elevated concentrations of glucose in plasma, via hypothalamic stimulation, lead to a greater gonadotropin production and subsequent greater ovarian activity.

Lamond (1970), McClure (1965) and McClure and Dowell (1969) reported reduced fertility in pastured cows. The decreased pregnancy rate was associated with a 10% reduction in live weight between parturition and mating and reduced concentrations of glucose in blood. Wiltbank et al., (1964) observed that follicular development and fertilization were more obvious when the TDN intake was elevated than when it was reduced.

In tropical conditions, Moore and Campos (1983) observed that in gyr cows, supply of energy during the postpartum period had no effect on

cow weight at weaning or conception, the interval from calving to first estrus or the number matings per conception; however, the interval to conception was reduced (116 d vs. 160 d) for cows on greater amounts of energy.

Studies designed to increase the availability of nutrients by altering rumen fermentation patterns (Randel and Rhodes, 1980; Randel et al., 1982) or by providing energy substrates post-ruminally (Rutter et al., 1983), appear to have a consistent enhancing effect on reproductive performance. Harrison et al. (1982) observed alterations in endocrine responses in cows after monensin consumption. Cows fed monensin had greater numbers of smaller corpora lutea, greater serum progesterone concentrations and more cows showed a LH pre-ovulatory surge. Monensin fed to cattle influences age at puberty (Moseley et al., 1977; McCartor et al., 1979), gross ovarian characteristics (Bushmich et al., 1980), pre partum steroid levels (Chew et al., 1978) and post-partum interval to first estrus post partum (Turner et al., 1977). Ortuno and Carson (1985) observed that monensin was able to increase the number of corpora lutea and the total mean luteal weight. Post partum cows fed with monensin had larger ovaries and greater number of follicles compared to control cows (Saturnino et al., 1985). Hardin et al. (1982) observed that monensin treatment did affect interval to LH response and interval to LH peak, while duration of LH peak, LH peak height and area under LH peak were not affected. However, when postpartum cows were fed lasalocid, another ionophore, reproductive performance and concentration of glucose and insulin in plasma were not altered (Fleck et al., 1985).

Condition of the cow at the moment of calving affects reproductive performance. Walters et al. (1984) observed that cows in good condition

and fed increased amounts of supplement post partum ovulated sooner compared with either cows in thin or good condition but with reduced nutrition post partum. Moss et al. (1985) indicated that neither a lack of GnRH nor pituitary LH and FSH is associated with the thin condition in cycling beef cows. An enhanced release of LH and FSH could account for reduced pituitary content of LH and FSH observed in cows fed high energy diets.

Estradiol in plasma did not vary with nutrition and, in contrast to the report of Fernandez et al., (1978) in dairy cattle, maximum LH was not correlated with concentration of estradiol prior to GnRH. Faltys et al., (1985) reported that diet did not affect the number of estrogen receptors either in the hypothalamus or pituitary.

Factors Associated with Onset of Estrous Cycles

Pubertal Cycles

Puberty is the limiting factor to the onset of reproductive function in heifers. In the female bovine, puberty is considered as the time when estrus and ovulation first occur simultaneously.

Age at puberty is influenced by nutrient intake (Joubert, 1955; Wiltbank et al., 1969), and prepuberal gains (Reynolds et al., 1964; Wiltbank et al., 1966; Short and Bellows, 1971; Arije and Wiltbank, 1971; Laster et al., 1971). When managed under similar conditions, faster growing heifers reach puberty at younger ages (Laster et al., 1971). Dairy heifers fed a high energy diet reached puberty at an earlier age and heavier weight (Sorensen et al., 1959). Rhodes et al. (1978) observed that increased growth rate and increased fatness in beef heifers does not lead to a reduction of age at puberty. Bovine growth

hormone may augment the ability of the pituitary to respond to GnRH and this effect may be more pronounced as the heifer approaches pubertal age and weight (Moseley et al., 1984).

Grass and Hauser (1981) found that unilateral ovariectomy and mastectomy of Angus heifers did not influence the age at puberty, age at first conception or services required for first conception. Mastectomy reduced the number of days from parturition to ovulation, the interval from parturition to first estrus, and the intervals between calvings were shorter.

Progesterone has a key role in the changes leading to the establishment of the phasic LH release characteristic of the cyclic bovine female. Gonzalez-Padilla et al. (1975) observed an increased response to endogenous LH by prepuberal ovaries primed with progesterone. Heifers do not have altered ovarian function during the estrous cycles leading to an anestrus condition. Hill et al. (1970) found no change in basal plasma LH in beef heifers under restricted energy and protein intake (85% NRC).

Increases in LHRH release due to hypothalamic maturation is the key factor controlling the onset of puberty in Rhesus monkeys (Loose and Terasawa, 1984). A pulsatile infusion of LHRH induced precocious vaginal opening followed by ovulation in female guinea pigs. An increase in endogenous LHRH release is responsible for the onset of puberty in guinea pigs. However, constant infusion of LHRH appears to delay onset of puberty in heifers (Skaggs et al., 1985).

Overfeeding dairy heifers increased frequency of LH pulses, but amplitude, baseline, and overall LH concentration were not affected (Spicer et al., 1984). Release of LH induced LHRH was reduced in

heifers with ad libitum intake but FSH secretion was not affected. In prepuberal heifers, excess feeding did not affect anterior pituitary gland weight or its content of LH and FSH at first estrus (Pritchard et al., 1972), but, can increase the frequency of pulsatile LHRH release from the hypothalamus.

Monensin treatment accelerates the onset of puberty in heifers (Moseley et al., 1977). McCartor et al., (1979) found that treatment with monensin decreased age at puberty in beef heifers and monensin treatment of prepuberal heifers caused an enhanced ovarian response to gonadotropin stimulation (Bushmich et al., 1980).

Randel and Rhodes (1980) observed that dietary monensin for prepuberal heifers appears to increase hypophyseal capabilitity of releasing LH after a first and second GnRH challenge. Monensin also appeared to enhance the LH response in prepuberal heifers given exogenous estrogen (Randel and Rhodes, 1980; Randel et al., 1982). Monensin causes increased propionate production by the rumen. Rutter et al. (1983) reported that abomasal infusion of propionate enhances the ability of prepuberal heifers to release LH after GnRH treatment.

Photoperiod (Hansen and Hauser, 1983) and season (Hansen, 1985) may influence age at puberty. Specifically, fall and winter environments during the first 6 m of life hasten puberty, while the same conditions after 6 m delayed puberty. Zinn et al. (1983) observed that photoperiod may affect eating patterns but did not affect body growth.

Suckling

General endocrine changes during the post partum period in cows have been reviewed (Wagner and Oxenreider, 1971; Arije et al., 1974;

Goodale et al., 1978; Wettemann, 1980; Edgerton and Hafs, 1972; Lamming et al., 1981). In beef cows, suckling delays the first postpartum ovulation by suppressing episodic LH secretion (Carruthers and Hafs, 1980), average LH concentrations and frequency of LH pulses (Garcia-Winder et al., 1984), and number and amplitude of LH pulses (Graves et al., 1968; Saiduddin et al., 1962; Carruthers et al., 1980; Walters et al., 1982). Suckling reduced the frequency of corpora lutea formation in response to GnRH (Lewis et al., 1983) and increased the postpartum interval to first estrus (Hansen and Hauser, 1983).

Suckling reduced follicular concentrations of estradiol and the percent of normal follicles (Bellin et al., 1984). Carruthers et al., (1980) observed that reduced frequency and amplitude of episodic LH and decreased capacity of pituitary to respond to LHRH may be the cause of suckling induced inhibition of postpartum ovulation in cattle. Suckling may increase the time to the first estrus by increasing the sensitivity of the hypothalamus to the negative feed back of estrogens and causing decreased LH release (Acosta et al., 1983). It also prolongs the postpartum interval by reducing the frequency of pulsatile GnRH release from the hypothalamus. Suckling cows failed to show estrus or to exhibit LH release in response to estradiol injection, which is considered to be indicative of malfunction of the hypothalamic mechanism responsible for the establishment and maintenance of ovarian function. In ovariectomized rats, suckling inhibits LHRH release from the hypothalamus (Culler et al., 1982).

Removal of the suckling stimulus in cattle increases pituitary responsiveness to GnRH and increases basal LH and FSH concentrations (Walters et al., 1982). Early weaning of swine increases GnRH

concentrations (Cox and Britt, 1982), increases concentration of in serum FSH and LH (Stevenson et al., 1980) and these changes are accompanied by increased development of ovarian follicles (Lauderdale et al., 1965; Palmer et al., 1965; Cox and Britt, 1982) and secretion of estrogens (Ash and Heap, 1975). Average interval from parturition to conception was reduced by early weaning of calves from heifers (Lusby and Wettemann, 1980). Ovarian activity and conception rates were also increased. Postpartum weight losses and intervals to conception were reduced by weaning under tropical conditions (Moore and Campos, 1983). Calf removal at 60 d post partum caused concentrations of LH to increase only in cows fed high energy after calving (Whisnant et al., 1985). Inadequate dietary energy delays the LH response to calf removal.

Calf removal hastens reestablishment of postpartum reproductive activity be eliminating a suppressive effect on pituitary gonadotropin release. Thus, calf removal hastens follicular development (Carter et al., 1980). Troxel et al. (1983) reported that calf removal enhanced the GnRH-induced LH release. Limited nursing initiates earlier ovarian activity post partum (Randel and Welker, 1976; Flood et al., 1979). Alves-Torres et al. (1984) observed that limiting the suckling by calves increased conception rates at first insemination, but days open were not affected. Similarly, once-a-day nursing decreased the time to the first estrus post partum, but did not affect the interval from calving to conception (Reeves and Gaskins, 1981). After 72 h calf removal, there is an increase in the pituitary responsiveness to GnRH (Dunn et al., 1985). Edwards (1985) observed increases in both LH concentrations and LH pulse frequency at 48 to 76 h after calf removal. Calf return decreased LH concentrations and LH pulse frequency within 8 h in

anestrous cows. Holness and Hopley (1978) significantly reduced the mean time from calving to first estrus only in cows fed increased nutrient intake. Once-daily suckling decreased the post partum interval with heifers heavier at weaning (Randel, 1981) but without affecting the weight of the calves at weaning. Bastidas et al. (1984) reported that twice-daily suckling improved pregnancy rate without depressing preweaning calf performance.

Treatment with GnRH (Britt et al., 1974; Erb et al., 1977; Lishman et al., 1979; Fonseca et al., 1980; Kesler et al., 1980; Troxel et al., 1980) and sex steroids (Walters et al., 1977; Smith et al., 1979; Troxel et al., 1980) may induce ovulation in anestrous beef cows. However, Britt et al. (1974) reported that treatment with GnRH did not reduce the percent of suckling cows in anestrous.

Suckling intensity increases the length of the postpartum interval to ovulation and first postpartum estrus (Casida, 1971). This increase is proportional to the number of calves suckled (Wettemann et al., 1978), frequency of suckling (Reeves and Gaskins, 1981) and appears to be independent of nutritional factors (Wettemann et al., 1978).

Flushing

An increased plane of nutrition before estrus is commonly associated with increased ovulation rates in ewes (Thomas et al., 1984). Feeding additional supplement to cows may shorten the interval from first follicle to first ovulation (Eduvie, 1985).

Wettemann et al. (1984) demonstrated that conception rate and days post partum to conception for cows in thin to moderate body condition were not influenced by flushing or calf separation. Flushing may

increase calf weaning weight. In another study, flushing did not affect either estradiol of progesterone during the postpartum period in beef cows; pregnancy rate was 82% and 87% for flushing and control, respectively (Westfall et al., 1984).

Control of postpartum reproductive activity requires a clear understanding of the roles played by the hypothalamus, pituitary and ovaries and their interrelationships and how these roles are affected or modified by external factors as suckling and nutritional level.

It remains to be demonstrated whether the delayed and reduced response of LH to GnRH in the underfed, lactating cows was simply the result of deficient pituitary reserves or inadequate sensitization by ovarian steroids.

In summary, postpartum reproductive function may be influenced by nutrition around the time of calving. Changes in the concentrations of energy metabolites in plasma may alter reproductive and endocrine function following parturition.

CHAPTER III

INFLUENCE OF NUTRITION, WEANING, INFUSION WITH GLUCOSE AND INSULIN INJECTIONS ON PLASMA CONSTITUENTS AND LUTEINIZING HORMONE IN POSTPARTUM ANESTROUS BEEF COWS

Abstract

Thirty mature postpartum Hereford cows were used to determine the effects of altered energy on serum luteinizing hormone (LH), ovarian function and concentrations of glucose, insulin and non-esterified fatty acids (NEFA) in plasma. On day 25 post partum, 5 cows were assigned to each of six treatments for 17 d: continuous jugular infusion with glucose (1.2 g/kg bw/d); twice daily injection of 50 IU insulin (subcutaneous, protamine zinc); fed an additional 5 kg/d of a 20% crude protein feed (flushed); calves were weaned at 32 d post partum; continuous jugular infusion with saline and non injected control. Average body condition score at treatment was 4.7 .1 (1=emaciated, 9=obese). Plasma glucose and NEFA and serum insulin and LH were quantified in daily samples between 25 and 42 d post partum. LH was quantified in serum samples taken at 10 min intervals for 4 h at 35, 37, 39 and 41 d, post partum. Concentrations of insulin were increased ($P<.05$) in cows treated with glucose and flushed cows and concentrations of NEFA were decreased ($P<.05$) compared to control cows. However, treatments did not affect ($P>.10$) either plasma glucose or LH secretion.

We conclude that reducing fat mobilization by infusion of glucose or feeding additional energy in anestrous beef cows during 4 to 6 w post partum did not influence LH secretion.

Introduction

Length of the postpartum anestrous interval of beef cows influences reproductive efficiency. Bellows et al. (1979) determined that 17% of the cows exposed to bulls failed to wean a calf the subsequent year because they were not pregnant at the end of the breeding season.

The establishment of pulsatile LH secretion is necessary for the initiation of ovarian activity in postpartum cows (Peters et al., 1981). Body energy reserves and/or restricted intake influences the length of the postpartum anestrous interval (Wettemann et al., 1980; Bellows et al., 1982; Selk, 1986).

Increased nutrient intake may enhance (Beal et al., 1978; Lishman et al., 1979) or not influence (Dunn et al., 1974; Spitzer et al., 1978; Carstairs et al., 1980) ovarian and pituitary function. The variability in response may be related to the amount of body energy reserves.

The mechanism by which energy intake and body energy reserves regulate pituitary and ovarian function is not clear. Inhibition of glycolysis inhibits pituitary (Sen et al., 1979) and ovarian function (McClure et al., 1978). Receptors for insulin are present in the brain of rats (Havrankova et al., 1978) and insulin may affect ovarian function (Savion et al., 1981; May and Schomberg, 1981; Poretsky et al., 1984). However, insulin administration reduced fertilization and decreased the onset of estrus in lactating cows (McClure, 1968).

The suckling stimuli increases the post partum anestrous interval (Hansen and Hauser, 1983). But, calf removal increases LH concentration in the serum of cows fed additional energy after calving (Whisnant et al., 1985). This experiment was conducted to determine the effect of glucose infusion, insulin administration, feeding additional energy and protein and weaning on LH secretion, ovarian function, serum insulin and concentrations of glucose and NEFA in plasma during the first 45 d post partum in beef cows.

Materials and Methods

Thirty mature anestrous Hereford cows at 25 (SD=2.3) d post partum were used to determine the effect of glucose infusion, insulin injection, feeding additional energy and protein or weaning on LH secretion, ovarian function and glucose, insulin and NEFA in blood. Cows received rations during the last 90 d of gestation so that their weights and body condition scores (1=emaciated, 9=obese, Wagner et al., 1986) at parturition were 401 $\pm$ 12 kg and 4.6 $\pm$ .1, respectively. Such cows usually exhibit their first estrus between 70 and 90 d post partum.

Cows were cohabited with sterile bulls with chinball markers and estrous detection as well as concentrations of progesterone in plasma collected each week were used to select anestrous cows. During the first 85 d after calving, cows were fed to maintain body weight. Body weights and body condition scores were recorded weekly. On day 24 post partum, cow and calf pairs were transported 10 km from range pastures and pairs were maintained in individual pens in a total confinement building at 21 $\pm$ 4 C, 50 $\pm$ 10% relative humidity with 14 h of fluorescent light daily.

On day 25 post partum, five cows were randomly assigned to each of six treatments based on calving date: (1) continuous infusion with a 40% glucose solution via a jugular cannula for 17 d (days 25-42 post partum, a total of 1.2 g/kg bw/d); (2) injection at 12 h intervals with 50 IU insulin (Protamine zinc insulin, Eli Lilly Co.) during days 25-42 post partum; (3) fed an additional 5 kg of a 20% crude protein diet daily from 25-42 d post partum (flushing); (4) calves were weaned from the cows at 32 d post partum; (5) continuous infusion with saline via a jugular cannula from 25-42 d post partum and (6) non-injected control. Cows and calves were constantly together except for animals assigned to the weaning treatment.

A cannula was inserted into the jugular vein of each cow on day 25 post partum. A second cannula was inserted in the contralateral vein of cows assigned to continuous infusion treatments. Blood samples were obtained daily at 0800 and at 10 min intervals for 4 h on the morning of days 35, 37, 39 and 41 post partum to assess LH secretion. Plasma and serum were obtained from daily blood samples and serum was obtained from the samples collected every 20 min. Blood (40 ml) was added to 32 mg oxalic acid, cooled at 4 C and centrifuged (2500 X g) to obtain plasma. Plasma was stored at -20 C until glucose (Sigma Chemical Co.), progesterone (Lusby et al., 1981) and NEFA (Patterson, 1963) were quantified. Samples of blood (10 ml) were allowed to clot at room temperature for 20 min, then stored at 4 C for 24 h until centrifuged (2500 X g). Serum was decanted and stored at -20 C until LH and insulin (Selk, 1986) were quantified.

On day 43 post partum, cows were returned to range pasture and cohabited with fertile bulls until at least 100 d post partum. Cows

were exposed to bulls until Aug. 1. Progesterone was quantified in weekly blood samples between 43 and 85 d post partum to assess ovarian luteal activity. Pregnancy rate and days to conception were used to determine treatment effects on reproductive performance.

Concentrations of LH in bovine serum were quantified a heterologous double antibody radioimmunoassay similar to that described by Niswender et al. (1969). Ovine LH (LER-1374A) and NIH-LH-B9 were used as radiolabeled ligand and standard, respectively. The primary antisera used at a dilution of 1:50,000, (TEA #35, produced against ovine LH and supplied by Dr. J.J. Reeves, Washington State University, Pullman, Washington) bound 15% of ^{125}I-LH in the absence of nonlabeled LH. Quantities of standard LH ranging from .0625 to 8 ng/tube were included in each assay. The lower limit of sensitivity of the assay was .45 ng LH/ml serum. Duplicates (200 and 300 ul) of each serum sample were assayed. Increasing quantities (1, 2, 4, and 8 ng) of NIH-LH-B9 were added to 1 ml samples of bovine serum and 1.6 ± .3 (n=4), 2.5 ± 0.4 (n=3), 5.2± 0.6 (n=3) and 9.3 ± 0.8 ng (n=3), respectively, were measured with the assay. The intra-assay and inter-assay coefficients of variation were 5.5% and 8.5%, respectively (n=12).

Dose response curves for dilutions of bovine serum and a bovine pituitary homogenate were parallel to the standard curve (Figure 1). The cross-reactivities of NIH FSH-B-1, NIH GH-B-18, NIH Prl-B-4, and NIH TSH-B-7 in this LH assay were .6%, 2%, .2% and 37%, respectively. The crossreactivity of TSH could be caused by contamination of the TSH with immunologically active LH since these two hormones are immunologically similar (Selenkov et al., 1976; Guillemin, 1967).

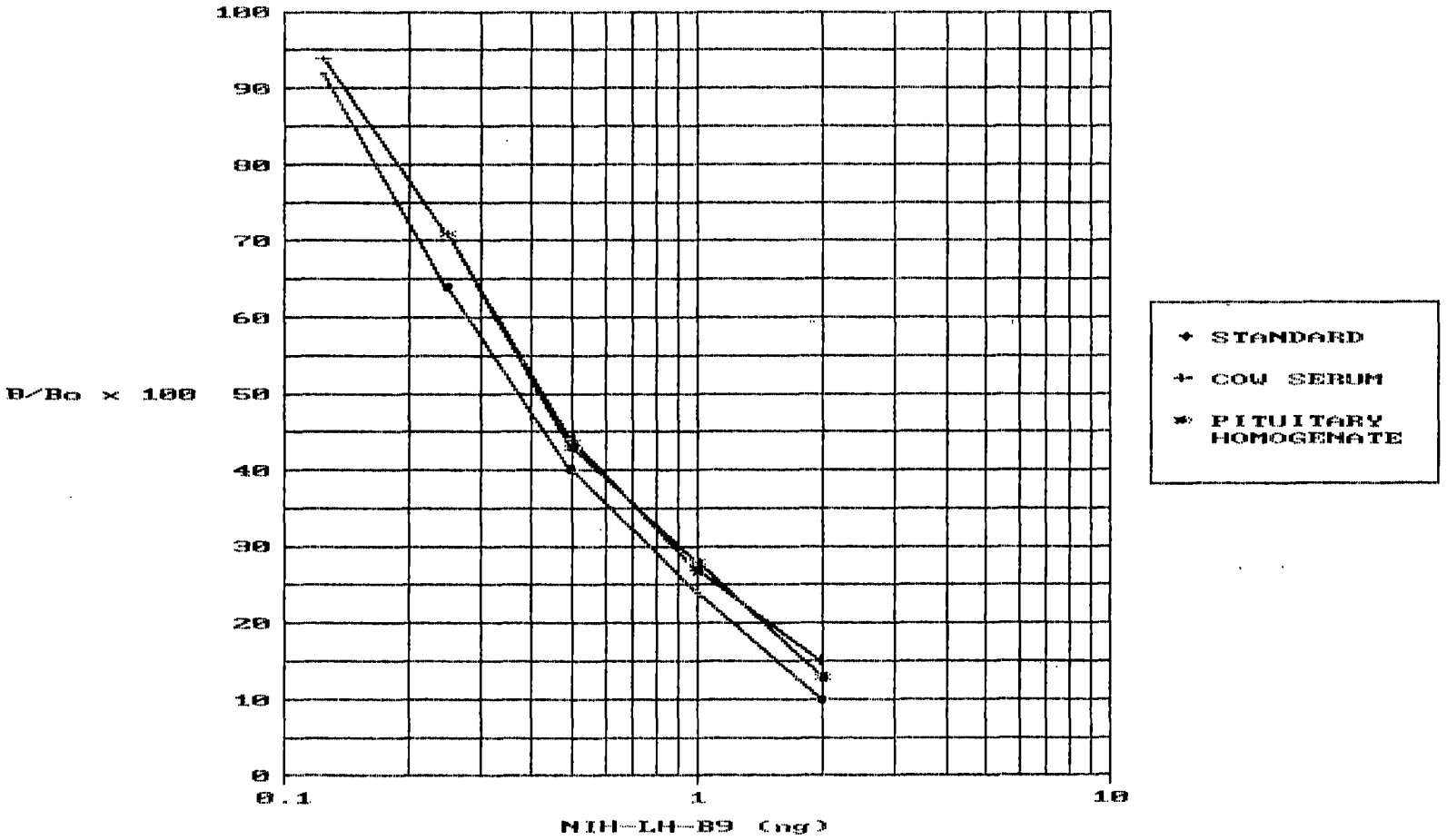

Figure 1. Displacement of ^{125}I-NIH-LH-B9 by NIH-LH-B9, cow serum and cow pituitary homogenate (1:5000) in the luteinizing hormone assay.

Concentration of LH for a cow on a day was obtained by averaging the LH concentrations in every sample taken during the bleeding period. An LH pulse was defined as any value larger than 1 standard deviation above the mean for a cow on a day, that was followed by at least 2 values of lesser concentrations. Pulse interval was the time between two consecutive pulses and pulse amplitude was defined as the difference in LH between the greatest value during a pulse and the smallest concentration within 30 min before the pulse.

Treatment effects on daily post partum samples for plasma glucose and NEFA and serum LH and insulin were analyzed with split-plot analyses of variance. Full model analyses of blood constituents indicated nonsignificant treatment*day interaction. For instance, the reduced model included treatment, cow(treatment) and day effects. Luteinizing hormone analyses of variance during the bleeding periods indicated nonsignificant day*treatment, sample*treatment and sample*day interactions. Therefore, the reduced model included treatment, cow(treatment), day and sample. Polynomial response curves were used to describe concentrations of hormones and constituents in samples taken daily and orthogonal comparisons and tests of heterogeneity of regression were used to determine if time trends between treatment were different.

Results and Discussion

Average concentrations for glucose, NEFA, insulin and LH for the total treatment period (days 25-42) are summarized in Table I. Since concentrations of these blood constituents varied over time due to

TABLE I

INFLUENCE OF TREATMENTS ON ENERGY METABOLITES AND HORMONES IN POSTPARTUM BEEF COWS

	TREATMENT						
	Control	Saline	Glucose	Insulin	Wean	Flush	EMS
Glucose (mg/100 ml)	67.4[a]	55.8	73.9	59.6	68.0	70.2	9.02
NEFA (uE/1)	671	645	482	694	568	533	6950
Insulin (ng/ml)	2.0	1.5	6.4	3.6	3.2	6.1	4.7
LH (ng/ml)	1.2	1.2	1.5	1.7	2.3	1.5	.1

[a]LS means for the 17 day treatment period (n = 5 cows).

treatment, the effect of treatment on these characteristics are not presented but the values are presented to indicate average values.

A linear regression equation best described the response curve for concentrations of glucose in plasma (Table II). The response curve for cows infused with glucose was different ($P<.001$) from that for cows infused with saline (Table III). The curves were not parallel and concentrations of glucose were greater in the infused cows. The response curve for cows treated with insulin was different ($P<.001$) from that for cows that had their calves weaned or those that were fed additional energy and protein (Figure 2). Concentrations of glucose were greater for cows that had weaned calves or were flushed compared to control cows.

During lactation, there is a large net uptake, of both glucose and lactate by the mammary gland, for lactose synthesis (Garner and Hogue, 1964). In this way, a large proportion of glucose is excluded from participation in whole body metabolic conversions. McNiven (1984) observed that concentrations of glucose in plasma were reduced during the first 28 d post partum, probably due to lactational stress. Similarly, Wanger and Oxenreider (1971), found decreased concentrations of glucose in plasma when cows were fed a restricted energy intake during the post partum period. In lactating cows, glucose infusion for 48 h significantly increased concentrations of glucose in plasma up to 24 h after the beginning of the infusion, but, in non-lactating cows, the increase in glucose concentrations continued during the experimental period (Lomax et al., 1978). In sheep, Judson and Leng (1973) observed that only 10% of the glucose infused was apparently retained in extracellular fluid.

TABLE II

R^2 AND PROBABILITY LEVELS OF POLYNOMIAL REGRESSION EQUATIONS FOR CONCENTRATIONS OF METABOLITES AND HORMONES IN POSTPARTUM BEEF COWS

	Treatment			
Order	Glucose	NEFA	Insulin	LH
Linear	.22[ac]	.146	.138	.448[c]
	<.14[b]	<.0005	<.0065	<.0001
Quadratic	.222	.156	.162[c]	.448
	<.29	<.0126	<.0001	<.607
Cubic	.222	.167[c]	.164	.449
	<.67	<.0176	<.248	<.784
Quartic	.222	.167	.164	.449
	<.63	<.35	<.827	<.68
Quintic	.227	.168	.169	.449
	<.07	<.38	<.09	<.978

[a] R^2 value.

[b] Probability level for the term in the model.

[c] Curve used in analyses.

TABLE III

ORTHOGONAL COMPARISONS USED TO TEST FOR HETEROGENEITY OF REGRESSION COEFFICIENTS FOR POLYNOMIAL RESPONSE CURVES TO DETERMINE WHETHER TIME TRENDS FOR POST PARTUM CONCENTRATIONS OF GLUCOSE IN PLASMA AMONG TREATMENTS WERE NOT PARALLEL

	IC, GL vs. C, IN, W, FL			
Error	df	SS	MS	F
IC, GL	175	7802		
C, IN, W, FL	318	15302		
Total	493	23104	48.9	
C, IC, GL, IN, W, FL	494	24732		
Difference	1	1628	1628	35.0**
	C vs. IN, W, FL			
C	78	2475		
IN, W, FL	239	12784		
Total	317	15259	48.1	
C, IN, W, FL	318	15302		
Difference	1	43	43	.90
	IC vs. GL			
IC	79	2322		
GL	95	6399		
Total	174	8721	50.1	
IC, GL	175	9181		
Difference	1	460	460	9.2**
	IN vs. W, FL			
IN	79	4421		
W, FL	159	7929		
Total	238	12350	51.9	
IN, W, FL	239	12783		
Difference	1	433	433	8.5**
	W vs. FL			
W	79	3727		
FL	79	4168		
Total	158	7895	50	
W, FL	159	7829		
Difference	1	34	34	.68

**($P<.01$)

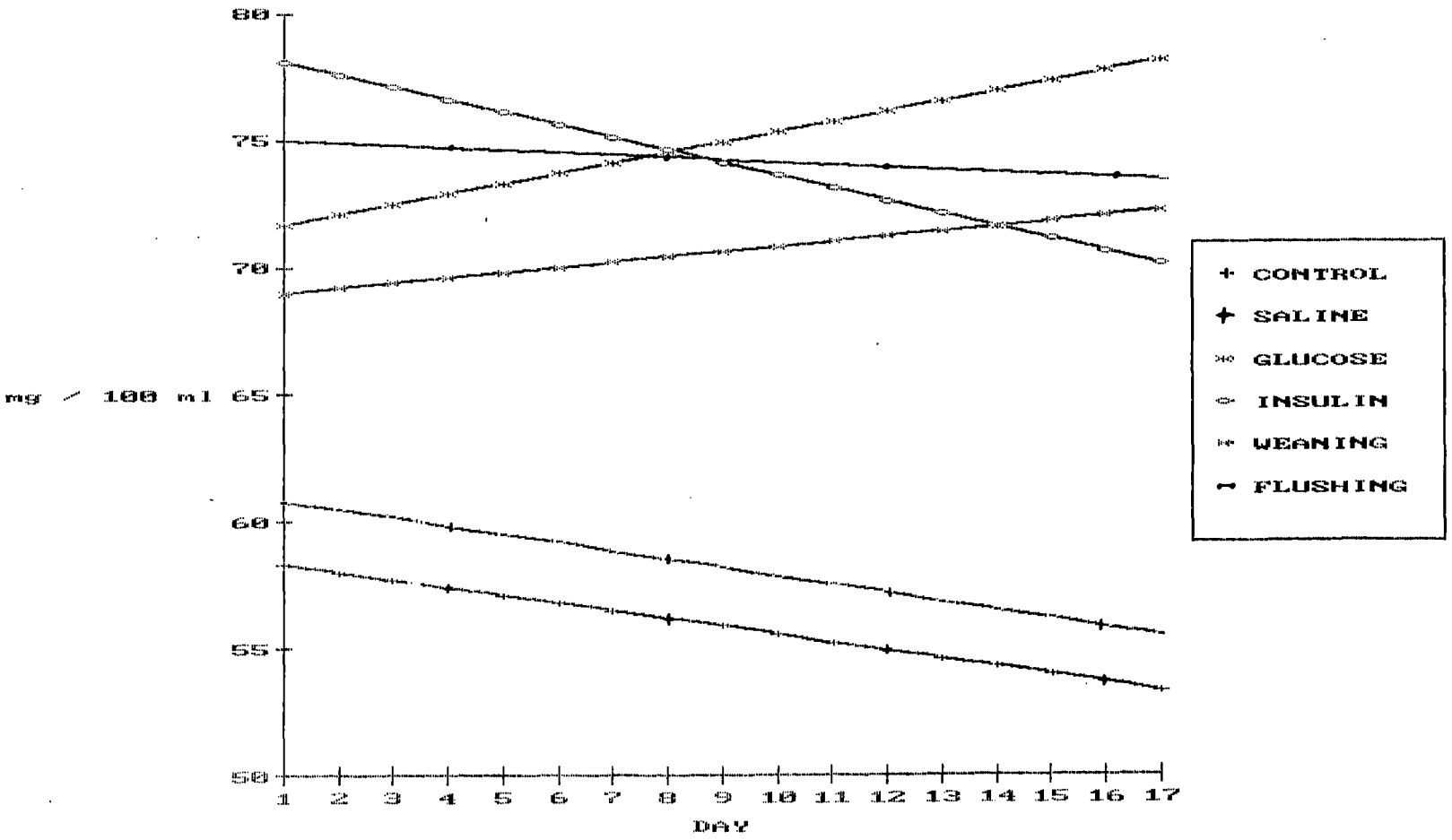

Figure 2. Concentrations of glucose in plasma (mg/100 ml) of cows during infusion with glucose, insulin treatment, flushing, weaning, infusion control and control.

A third order polynomial regression equation best described the response curve for NEFA during the experimental period (Table II). The response curve for concentrations of NEFA in cows infused with glucose was different ($P<.05$) from that for cows infused with saline (Table V). During treatment with glucose, concentrations of NEFA were reduced compared to cows infused with saline. In addition, response curves for cows on weaning and flushing treatments were not parallel ($P<.05$) and the response for cows treated with insulin was similar to that for cows with weaned calves or fed additional energy and protein (Figure 3). In general, infusion with glucose and weaning the calves resulted in reduced fat mobilization and decreased concentrations of NEFA in plasma.

Non esterified fatty acids are a major transport form of lipids under conditions of fat mobilization (Engel and White, 1960). Changes in concentration of NEFA in plasma during feed restriction are consistent with increased mobilization of energy from tissues for utilization (Gow et al., 1981). Concentration of NEFA in plasma may be a sensitive index of fat mobilization. Fritz (1961) observed that concentration of NEFA in plasma of cows reflect the rate of release of NEFA from adipose tissue as it does in other species.

During early lactation, milk synthesis has a high priority for energy in the cow and milk synthesis may continue despite insufficient dietary energy intake. Under such conditions, the cow must mobilize body tissue reserves to provide the energy which is lacking in the diet (Moe et al., 1971; Metz and Van der Bergh, 1977; Roberts et al., 1978). A marked lipid mobilization in early lactation is accompanied by depletion of triglycerides in adipose cells (Elias et al., 1973) and elevated plasma NEFA concentration (Radloff et al., 1976).

TABLE V

ORTHOGONAL COMPARISONS USED TO TEST FOR HETEROGENEITY OF REGRESSION COEFFICIENTS FOR POLYNOMIAL RESPONSE CURVES TO DETERMINE WHETHER TIME TRENDS FOR POST PARTUM CONCENTRATIONS OF NEFA AMONG TREATMENTS WERE NOT PARALLEL

Error	df	SS	MS	F
IC, GL vs. C, IN, W, FL				
IC, GL	173	5555812		
C, IN, W, FL	318	12516732		
Total	491	18072544	36807	
C, IC, GL, IN, W, FL	494	18609131		
Difference	3	536587	178862	4.9**
C vs. IN, W, FL				
C	77	2818010		
IN, W, FL	237	9582976		
Total	314	12400986	39494	
C, IN, W, FL	317	12516732		
Difference	3	115476	38492	.97
IC vs. GL				
IC	77	2808257		
GL	93	2463481		
Total	170	5271738	31010	
IC, GL	173	5555812		
Difference	3	284074	94691	3.1*
IN vs. W, FL				
IN	77	3155389		
W, FL	157	6258787		
Total	234	9414176	40232	
IN, W, FL	237	9582976		
Difference	3	168800	433	8.5**
W vs. FL				
W	77	3341985		
FL	77	2618251		
Total	154	5960236	38703	
W, FL	157	6258787		
Difference	3	298551	99507	2.6*

** ($P<.01$)
* ($P<.05$)

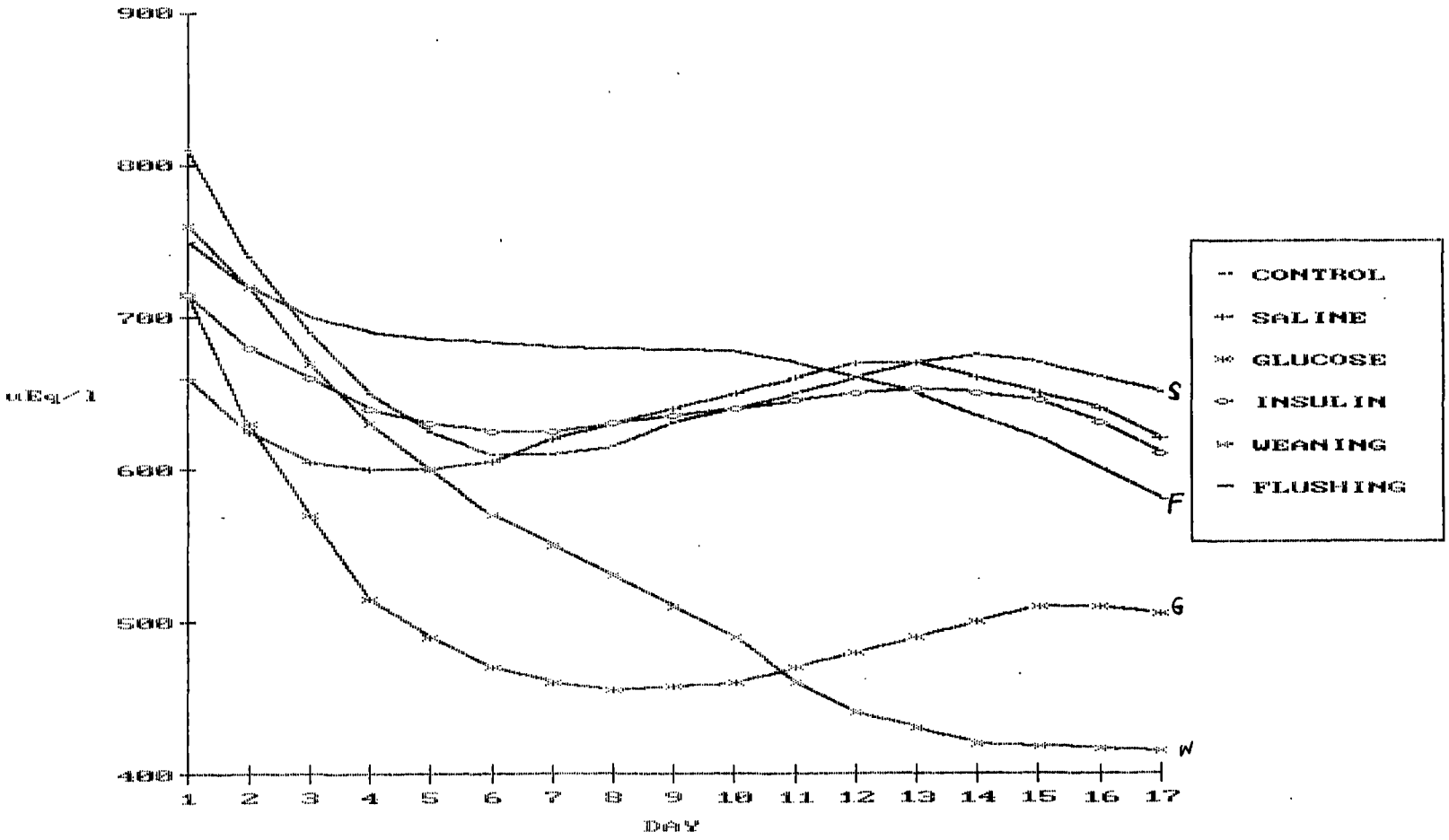

Figure 3. Concentrations of non-esterified fatty acids in plasma (uEq/l) of cows during infusion with glucose, insulin treatment, flushing, weaning, infusion control and control.

Consequently, a negative energy balance leads to increased concentrations of NEFA in plasma and increased peripheral utilization of NEFA for synthesis of milk fat. The rate of NEFA production from adipose tissue, as well as the rate of NEFA utilization, is closely correlated with the concentration of NEFA in plasma (Reid and Hinks, 1962).

Concentrations of NEFA in plasma were not correlated ($P>.10$) with concentrations of glucose in animals with similar body condition (Table IV). Reid et al. (1979) found that concentrations of glucose in plasma were negatively correlated with concentration of NEFA in plasma of dairy cows, indicating that fat mobilization occurs upon reduced energy intake and minimal plasma glucose concentrations. Cows mobilizing more adipose tissue after calving, as evidenced by increased concentration of NEFA in plasma, had reduced concentration of glucose in plasma compared to cows with less fat mobilization. Similarly, de Boer et al. (1985) found that intense fat mobilization during the first 3 w post partum, to support milk production, significantly decreased concentration of glucose in plasma. Annison (1960) observed that during hypoglycemia, concentrations of NEFA were elevated. On the contrary, glucose infusion reduced NEFA concentrations (Fritz, 1961).

Concentrations of insulin in serum of cows during the experimental period were best described by a second order polynomial response curve (Table II). The response curve for cows infused with glucose was different ($P<.001$) from that for cows infused with saline (Table VI). Moreover, the response curves for cows that had their calves weaned, were flushed or were injected with insulin were not parallel ($P<.01$) (Table VI) and were also different from the response curve for control

TABLE IV

POOLED WITHIN CLASS CORRELATION COEFFICIENTS FOR BLOOD PARAMETERS OF POSTPARTUM BEEF COWS[a] ADJUSTED BY BODY CONDITION

	NEFA	INSULIN	LH
Glucose	.02	.10*	-.02
NEFA		-.04	-.18**
Insulin			.05

[a] N = 30

*(P<.01)

**(P<.05)

TABLE VI

ORTHOGONAL COMPARISONS USED TO TEST FOR HETEROGENEITY OF REGRESSION COEFFICIENTS FOR POLYNOMIAL RESPONSE CURVES TO DETERMINE WHETHER TIME TRENDS FOR POST PARTUM SERUM INSLUIN CONCENTRATIONS AMONG TREATMENTS WERE NOT PARALLEL

	IC, GL vs. C, IN, W, FL			
Error	df	SS	MS	F
IC, GL	174	6769		
C, IN, W, FL	318	5204		
Total	492	11973	24.3	
C, IC, GL, IN, W, FL	494	12638		
Difference	2	665	332.5	13.6**
	C vs. IN, W, FL			
C	78	101		
IN, W, FL	238	5031		
Total	316	5132	16.2	
C, IN, W, FL	318	5284		
Difference	2	152	76	4.7**
	IC vs. GL			
IC	78	150.4		
GL	94	6259		
Total	172	6409.4	37.3	
IC, GL	174	6769		
Difference	2	359.6	179.8	4.8**
	IN vs. W, FL			
IN	78	1963		
W, FL	158	2409		
Total	236	4372	18.5	
IN, W, FL	238	4542		
Difference	2	170	85	4.6**
	W vs. FL			
W	78	484		
FL	78	2348		
Total	156	2832	18.2	
W, FL	158	2943		
Difference	2	111	55.5	3.0*

** (P<.01)
* (P<.05)

cows (Figure 4). Concentration of insulin in the serum of control and saline infused cows averaged about 1 ng/ml during treatment, whereas, concentration of insulin in cows treated with insulin, supplied with addditional energy (flushed or glucose infusion) or with weaned calves averaged greater than 4 ng/ml.

Hove (1978) observed a biphasic increase in insulin within a maximum of 10 to 20 min after the start of glucose infusion in lactating dairy cows. Mean insulin concentrations in sheep are correlated with rate of infusion of glucose (Basset et al., 1971). Glucose infusion for 20 min resulted in increased insulin concentrations at 1 h after infusion. Prior and Christenson (1978) observed that an injection of insulin into non-pregnant ewes produced an immediate increase in the rates of glucose clearance and disappearance. Glucose infusion (75 g/h) during 2 h significantly increased insulin in serum of lactating cows (Laarveld et al., 1981).

A linear regression equation best described daily LH concentrations during treatment. Infusion with glucose did not influence the LH response curve compared with cows infused with saline (Table VII; Figure 5). The response curve for cows on the insulin treatment was different ($P<.01$) from that for cows with weaned calves or flushed. In addition, the response curves differed ($P<.05$) for cows with weaned calves and cows that were flushed. Increased concentrations of LH in cows with weaned calves compared with flushed cows is related to removal of the suckling inhibition on LH secretion (Graves et al., 1968; Walters et al., 1982; Garcia-Winder et al., 1984).

Days after calving did not affect any of the LH characteristics studied when cows were bled every 10 min for 4 h on 35, 37, 39 and 41 d

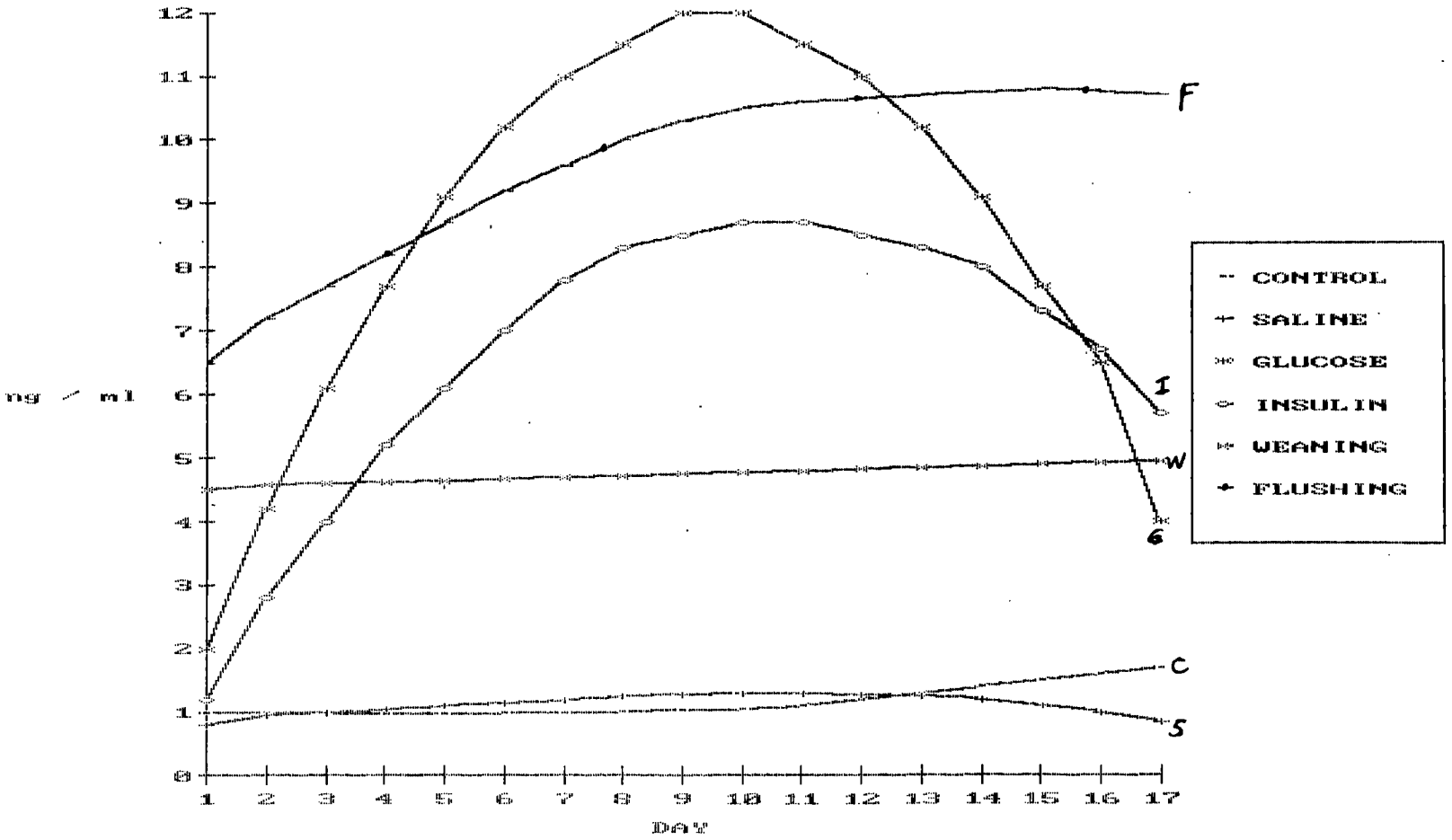

Figure 4. Concentrations of insulin in serum (ng/ml) for cows during infusion with glucose, insulin treatment, flushing, weaning, infusion control and control.

TABLE VII

ORTHOGONAL COMPARISONS USED TO TEST FOR HETEROGENEITY OF REGRESSION COEFFICIENTS FOR POLYNOMIAL RESPONSE CURVES TO DETERMINE WHETHER TIME TRENDS FOR LUTEINIZING HORMONE CONCENTRATION AMONG TREATMENTS WERE NOT PARALLEL

	IC, GL vs. C, IN, W, FL			
Error	df	SS	MS	F
IC, GL	175	105.10		
C, IN, W, FL	318	139.70		
Total	493	244.80	.50	
C, IC, GL, IN, W, FL	494	244.82		
Difference	1	.02	.02	.04
	C vs. IN, W, FL			
C	78	18.8		
IN, W, FL	239	119.8		
Total	317	138.6	.44	
C, IN, W, FL	318	139.7		
Difference	1	1.1	1.1	2.5
	IC vs. GL			
IC	79	39.5		
GL	95	65.6		
Total	174	105.1	.60	
IC, GL	175	105.2		
Difference	1	.1	.1	.17
	IN vs. W, FL			
IN	79	17.1		
W, FL	159	95.1		
Total	238	112.2	.47	
IN, W, FL	239	119.8		
Difference	1	7.6	7.6	16.01**
	W vs. FL			
W	79	46.8		
FL	79	45.9		
Total	158	92.7	.6	
W, FL	159	95.1		
Difference	1	2.4	2.4	4.0*

** (P<.01)
* (P<.05)

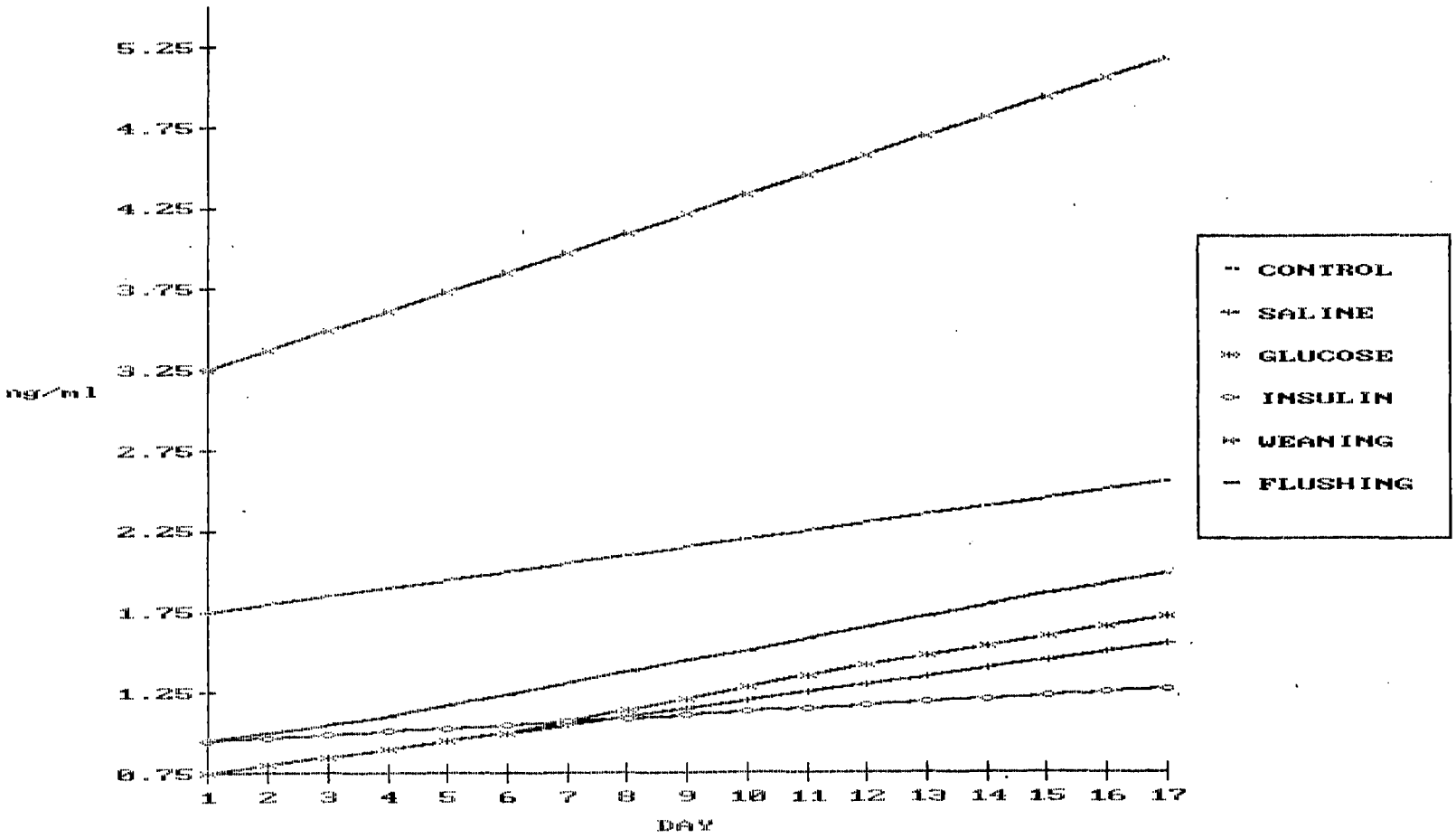

Figure 5. Concentrations of LH in serum (ng/ml) of cows during infusion with glucose, insulin treatment, flushing, weaning, infusion control and control.

post partum (Table VIII). Mean concentrations of LH were 1.1, 1.4, 1.3 and 1.2 ng/ml on days 35, 37, 39 and 41, respectively. Similarly, days post partum did not influence either the number of pulses during each 4 h bleeding period, the pulse frequency or the magnitude of the pulse.

Treatments did not influence ($P>.10$) characteristics of LH secretion when samples were taken every 10 min during 4 h on 35, 37, 39 and 41 d post partum (Table IX). Although not significant, concentrations of LH and the pulse magnitude tended to be greater in cows which had their calves weaned at 32 d post partum compared to cows on the other treatments. Frequency of LH pulses were similar for all the treatment groups and averaged 120 min for the 4 sampling days.

Serum concentrations of LH were negatively correlated ($r=-.18$; $P<.01$) with NEFA, indicating that concentrations of LH were decreased when greater rates of fat mobilization occurred.

The lack of treatment effect on secretion of LH by 41 d post partum could be related to the length of the interval from calving until the onset of ovarian activity of these cows. The earliest that any cow exhibited ovarian activity was 57 d and by 85 d post partum only 25% of the control cows had ovarian activity. Evaluation of LH secretion at some time between 46 and 60 d post partum would have been useful to evaluate treatment effects.

Suckling of beef cows delays the first post partum ovulation by suppressing episodic LH secretion (Carruthers and Hafs, 1980), average concentrations of LH, and frequency (Garcia-Winder et al., 1984) and amplitude (Graves et al., 1968; Saiduddin et al., 1968; Carruthers et al., 1980; Walters et al., 1982) of LH pulses. However, other studies did not find an effect of suckling on concentration of LH in serum

TABLE VIII

INFLUENCE OF DAY POSTPARTUM ON
LUTEINIZING HORMONE SECRETION

	Days Postpartum				
	35	37	39	41	EMS
Mean LH (ng/ml)	1.1[a]	1.4	1.3	1.2	1.07
Pulse number / 4 h	2.1	2.3	1.8	2.2	.12
Pulse Frequency (min)	114	104	133	109	627
Pulse Magnitude (ng/ml)	.71	1.59	.98	.77	3.15

[a]LS means (n = 30)

TABLE IX

INFLUENCE OF TREATMENTS ON LUTEINIZING HORMONE SECRETION OF POST PARTUM COWS ON DAYS 35, 37, 39 AND 41 POST PARTUM

	TREATMENT						
Item	Control	Saline	Glucose	Insulin	Wean	Flush	EMS
Mean LH (ng/ml)	1.1[a]	1.3	1.1	1.1	1.7	1.3	1.09
Pulse Frequency (min)	130	119	97	106	119	126	715
Pulse Magnitude (ng/ml)	.62	.87	.83	.73	2.0	1.1	5.15

[a]LS means (n = 20)

(Convey et al., 1977; Echternkamp, 1978; Chang et al., 1981; Convey et al., 1983). Similarly, suckling did not reduce the concentration of LH in the pituitary (Carruthers and Hafs, 1980; Peters et al., 1981; Chang et al., 1984; Walters et al., 1982) interval to peak LH or magnitude of LH release (Dunn and Kaltenbach, 1980). Differences may depend on times of sampling or days post partum.

Calf removal may increase pituitary responsiveness to GnRH and increase basal concentrations of LH (Walters et al., 1982). Edwards (1985) observed increased LH concentrations and pulse frequency 48 to 72 h after calf removal. Calf return decreased LH concentration and pulse frequency within 8 h in anestrous cows.

The effects of restricting energy intake on LH secretion may depend on body energy reserves of the cow as well as the severity of the dietary energy restriction. If cows have body energy reserves to mobilize, dietary restrictions of energy may have little or no effect on reproductive or endocrine function.

Some studies suggest that alteration of the energetic condition of the cow does not affect characteristics of LH secretion. Infusion of glucose in postpartum cows did not affect individual LH characteristics (McCaughey et al., 1985). Similarly, Harrison et al. (1982) observed that energy restriction or insulin administration did not alter LH in beef heifers. Easdon et al. (1985) found that average LH concentrations did not differ between cows fed either a high or low plane of nutrition post partum. However, mean concentration of LH may be reduced due to feed restriction during the postpartum period (Gauthier at al., 1984). Alteration of blood glucose in cows will affect reproductive performance. Reducing blood glucose by administering insulin or

blocking glucose metabolism by 2-deoxy-glucose, altered ovarian function and reduced fertility in cattle (McClure and Payne, 1978).

McCann (1984) observed that pituitary cells have insulin receptors, suggesting that insulin and the regulation of glucose metabolism may be important for normal pituitary function. Treatment with insulin resulted in significant increases in both the basal and the maximal release of LH (Adashi et al., 1981). After GnRH treatment of rat anterior pituitary cells in vitro, supraphysiological concentrations of insulin suppressed LH production (McCann, 1984). Moore and Campos (1983) observed that inadequate dietary energy delays the LH response to calf removal and increases the LH response to exogenous GnRH.

Postpartum reproductive performance is summarized in Table X. Limited numbers of cows per treatment restrict the conclusions that can be made. Treatments did not significantly influence reproductive criteria; however, some trends emerged. Fewer cows in the control, saline control and insulin treated groups exhibited estrus by 85 d post partum. Improving the energetic condition of the cows by flush, weaning or infusion of glucose tended to increase the number of cows that exhibited estrus within 85 d after calving. Similarly, more cows on the weaning and glucose infusion treatments tended to exhibit ovarian activity by 85 d after calving.

All cows on the glucose infusion and weaning treatments were pregnant at the end of the breeding season. Seventy-five percent of the cows on the control, saline and insulin treatments and 67% of the cows on the flushing treatment, were also pregnant at the end of the breeding season. The interval from parturition to conception tended to be shorter for cows infused with glucose or flushed during the experimental

TABLE X

INFLUENCE OF TREATMENTS ON POSTPARTUM REPRODUCTIVE PERFORMANCE OF RANGE COWS

	Control	Saline	Glucose	Insulin	Weaning	Flushing
Cows (no.)	4[a]	4	5	4	4	3
Estrus by 85 d (no.)	1	1	4	1	3	2
First estrus for cows that exhibited estrus during breeding season	85± 11[b]	68± 12	60± 10	54± 13	58± 12	60± 10
Ovarian activity by 85 d postpartum (no.)	1[c]	2	4	0	3	2
Onset of ovarian activity during the first 85 d postpartum (d)	76	64	66	--	56	64
Pregnant (no.)	3[d]	3	5	3	3	2
Parturition to Conception (d)	97± 18[e]	96± 13	77 ±10	101± 3	94± 7	79 ±3

[a]Reproductive data were not obtained for all treated cows.

[b]Means S.E.

[c]The onset of ovarian activity was characterized by concentration of progesterone in plasma equal to or greater than 1 ng/ml for two consecutive weeks.

[d]Date of conception was calculated by subtracting 282 days from the subsequent calving date.

period (77 and 79 days, respectively) compared to cows on control, saline infusion, insulin or weaning treatments (97, 96, 101 and 94 days, respectively).

Concentrations in blood of compounds related to energy metabolism have been used in an attempt to monitor the reproductive and nutritional status of the postpartum cow. Concentrations of glucose in blood have been observed to be either negatively (Kellogs and Miller, 1977; Chang et al., 1984) or positively (Patil and Deshpande, 1979) correlated with the length of the post partum interval to conception. However, Blowey et al. (1973) found no relationship between concentrations of glucose and fertility.

Howland et al. (1966) suggested that continuously elevated concentrations of glucose in plasma of ewes caused greater gonadotropin production and subsequent greater ovarian activity. Rutter and Randel (1984) observed that postpartum nutrient intake did not affect LH secretion at day 21 after calving. However, there was a significant decrease in the postpartum interval to first estrus with increased levels of nutrient intake. Similarly, energy balance during the first 20 d of lactation influences the interval to the onset of ovarian activity following parturition. Rutter and Randel (1984) noted that cows that maintained body condition from calving to first estrus had a shorter postpartum interval to first estrus (32 days) compared with cows that lost weight (60 days).

Variation in reproductive performance is related to the level of nutrition around parturition and to changes in weight and condition of the cow (Lamond, 1970; Selk, 1986). Condition of the cow at calving is correlated with length of the interval from calving to first estrus

(Whitman, 1975; Bellows and Short, 1978; Bellows et al., 1982). Wiltbank et al. (1962) and Dunn et al. (1969) found that dams that were thin at calving required greater amounts of supplementation after calving if estrus was to occur early or at all during the breeding season. However, feeding extra energy to thin cows after calving can result in adverse effects on postpartum reproduction by stimulation of milk production, thus, increasing the suckling effect (Bellows and Short, 1978). Restriction of energy prepartum decreases the percentage of cows exhibiting estrus by day 40, post partum (Corah et al., 1974; Selk, 1986) and underfeeding, either pre or post partum, can delay onset of estrus cycles following calving (Dunn et al., 1969; Whitman et al., 1975). McCann (1984) found that decreased insulin concentrations and glucose utilization resulted in decreased progesterone production. This may explain in part, the decreased ovarian function in chronically underfed animals. Insulin administration reduced fertility in cows (McClure, 1968), while injection of protamine zinc insulin to lactating cows at proestrus delayed the onset of estrus and pregnancy rate. Eduvie (1985) observed that feeding a 3 kg supplement per day after calving shortened the interval from first follicle to first ovulation compared with cows only grazing pasture. Also, supplemented cows had their first follicle 2 days before and ovulated 18 days earlier than cows that only grazed.

Suckling intensity increases the length of the postpartum interval to ovulation and first postpartum estrus (Casida, 1971). This increase is proportional to the number of calves suckled (Wettemann et al., 1978), frequency of suckling (Reeves and Gaskins, 1981) and appears to be independent of nutritional factors (Wettemann et al., 1978).

Removal of the suckling stimulus reduced the average interval from parturition to conception of cows (Lusby et al., 1981). However, inadequate energy delays the LH response to calf removal and increases the LH response to exogenous GnRH (Whisnant et al., 1985).

An increased plane of nutrition before estrus is commonly associated with an increased ovulation rate in ewes (Thomas et al., 1984). However, in cows with thin to moderate body condition, conception rates and days post partum to conception were not influenced by flushing (Wettemann et al., 1984).

In conclusion, glucose infusion and feeding additional energy and protein during the postpartum period, increased serum concentrations of insulin and reduced plasma concentrations of NEFA; however, neither treatment altered LH secretion by 41 d post partum.

CHAPTER IV

SECRETION OF LUTEINIZING HORMONE IN POSTPARTUM COWS INFUSED WITH GLUCOSE

Abstract

Eighteen mature anestrous Hereford cows were used to determine the effect of glucose infusion on LH secretion. At 30 (SD=2.1) days post partum jugular cannulae were inserted into both veins and cows were randomly assigned to continuous infusion for 12 d with either a 40% glucose solution (1.4 g/kg bw/d) or 0.85% saline. On day 12 of treatment, cows were bled frequently for 38 h. During the next 8 h period, samples were obtained every 20 min and 1 ug of LHRH was infused (iv) after each sample. Then, blood samples were taken every 30 min for an additional 14 h. Body condition of the cows during treatment averaged 4.4 ±.4 (1=emaciated; 9=obese). Glucose infusion significantly increased concentrations of glucose in plasma ($P<.10$) and insulin in serum ($P<.05$) and concentration of NEFA in plasma were decreased ($P<.01$). Concentrations of NEFA in plasma were negatively correlated ($P<.05$) with serum insulin, whereas concentrations of glucose in plasma were positively correlated with insulin in serum ($P<.10$). Glucose infusion increased the number of LH pulses before treatment with hormones ($P<.05$) and mean concentrations of LH and total response area during the LHRH infusion ($P<.10$) were greater for cows infused with

glucose compared to controls. Approximately half of the cows on each treatment exhibited estrus within 3 days after estradiol treatment. These results suggest that increased concentrations of glucose and insulin and decreased concentrations of NEFA in plasma may be associated with increased LH secretion in post partum cows.

Introduction

Nutrient intake and body energy reserves influence reproductive performance of postpartum beef cows (Wiltbank et al., 1964; Corah et al., 1974; Dunn and Kaltenbach, 1980). Concentration of glucose in plasma after calving may be associated with the initiation of estrous cycles (Selk, 1986). Hypoglycemia in postpartum cows has been associated with decreased follicular development (Oxenreider and Wagner, 1971) and infertile inseminations (Downie and Gelman, 1976). Reduced fertility associated with decreased nutrient intake may be caused by altered hypothalamic or pituitary functions that result in reduced LH secretion. Since function of brain tissue depends on glucose for energy source, even milk hypoglycemia may depress hypothalamic function and thus indirectly influence ovarian activity (Howland et al., 1966).

Pulsatile LH secretion increases before the initiation of ovarian activity in postpartum cows (Humphrey et al., 1976; Goodale et al., 1978; Stevenson and Britt, 1979). Restricted intake of energy reduced concentrations of LH in plasma and reduced the sensitivity of the ovaries to LH (Apgar et al., 1975). Greater prepartum energy intake increased the maximum LH after GnRH and reduced the time to the maximum concentration in postpartum beef cows (Sprott et al., 1981).

Treatment of cows with estradiol in the absence of progesterone usually causes increased concentrations of LH in blood (Beck and Covey, 1977). But, the positive effect of estrogens on LH secretion is absent during the early postpartum period in beef cows (Radford et al., 1978). A biphasic effect of estrogens upon pituitary responsiveness to LHRH has been demonstrated in rats (Moll and Rosenfield, 1984) ovariectomized ewes (Nett et al., 1984) and anestrous cows (Kesner et al., 1981). Schoenemann et al. (1985) demonstrated that estradiol increases the concentration of bovine pituitary LHRH receptors before the surge of LH.

This study was conducted to test the hypothesis that concentrations of glucose in the blood of lactating anestrous beef cows influence pulsatile and GnRH induced release of LH. Cows were continuously infused with glucose or saline for 12 days and LH secretion and the responsiveness of the pituitary to estradiol and GnRH were determined.

Materials and Methods

Eighteen mature anestrous Hereford cows without luteal activity at 30 5 d post partum were used to determine the effect of glucose infusion on LH secretion. Cows were fed during late pregnancy so that they had a body condition score of 4.4 ± .1 (1=emaciated and 9=obese); Wagner et al., 1985) at parturition. Such cows generally exhibit their first estrus after 60 d post partum.

At 30 d post partum, cow and calf pairs were transported 10 km from range pastures and pairs were maintained in a barn at 21± 4 C, and 50± 10% relative humidity with 14 h of fluorescent light daily. A complete ration (14% crude protein) was fed to maintain the condition and weight of the cows during the experimental period. A cannula was inserted into

each jugular vein of cows. Then cows were assigned at random (based on days post partum) to either continuous infusion witha 40% glucose solution (1.4 g/kg bw/d) via the jugular cannulae for 12 d (commencing at day 30 ±5 post partum) or continuous infusion with a saline solution (.85%). Cows and calves were constantly together.

After 12 days of treatment (at 42± 5 d post partum), all cows were bled frequently for 38 h. During the first 8 h period, blood samples were obtained at 10 min intervals. Then, each cow received an injection of estradiol-17B (1 mg; im) in 5 ml corn oil and samples were taken for a second 8 h at 20 min intervals. During the next 8 h, samples were obtained every 20 min and 1 ug of LHRH (Sigma Chemical Co.) was infused (iv) after each sample. Then, blood samples were taken every 30 min for an additional 14 h.

Plasma and serum were obtained from daily blood samples as described in experiment 1. Serum was obtained from all samples obtained on day 42± 5 and plasma was obtained at infrequent times to assess concentrations of estradiol. Concentration of glucose (Sigma Chemical Co.), NEFA (Patterson, 1963), estradiol (Hallford et al., 1979), and progesterone (Lusby et al., 1978) were quantified in plasma and concentrations of insulin (Selk, 1986), LH (Niswender et al., 1969, with revisions described in experiment 1) were determined in serum.

On day 44 ± 5 post partum, cows were returned to range pastures and cohabited with fertile bulls. Progesterone was quantified in weekly blood samples obtained until 85 d post partum to assess the onset of ovarian luteal activity. Days to conception and estrus data were used to determine any effects of treatments on reproductive performance.

To determine the amount of LH secreted during a period (i.e., the first 8 h of sampling) the order of the polynomial response curve that best fit the LH concentrations for the period was determined using treatments as the main effect. After the level of fit was determined for each period, equations were developed for each cow. The integrals were evaluated over the range of the time periods, to determine the area under the curve for each cow.

Concentration of LH was obtained by averaging the LH concentrations in every sample taken during the bleeding period for a cow. An LH pulse was defined as any value greater than 1 standard deviation above the mean and followed by at least 2 lesser values. Pulse interval was the time between two consecutive pulses and pulse amplitude was the amount of the LH increase from a lesser concentration within 30 min before the pulse and the greatest value during the pulse. An LH surge, similar to a naturally occurring preovulatory LH surge, was considered to have occurred if concentrations of LH in serum were greater than 10 times the baseline LH concentration for more than 3 h. Baseline LH concentrations were defined as the lowest LH concentration between pulses. Duration of the surge was defined as the period during which concentrations of LH were greater than 10 times the baseline value and the onset of the LH surge was the time period when concentration of LH in serum was first greater than 10 times the baseline value. Characteristics of LH secretion were analyzed by analyses of variance.

Characteristics in daily blood samples were analyzed by analyses of variance (split plot) with body condition score as a covariable. Polynomial response curves were used to describe concentrations of LH and insulin in serum and concentrations of glucose and NEFA in plasma

over days and tests of heterogeneity of regression were used to determine if time trends between treatments were different.

Results and Discussion

Concentrations of glucose in plasma during the infusion were affected by treatment ($P<.10$; Table XI). Cows infused with glucose had greater concentrations of glucose in plasma (76.8 mg/100 ml) when compared with control cows (60.8 mg/100 ml). The response for concentrations of glucose during treatment was best described by a linear regression equation (Table XII; Figure 6). The response curve for cows infused with glucose was parallel to that for cows in the control group (Table XIII).

Glucose infusion decreased concentrations of NEFA in plasma ($P<.01$). During the 12 d treatment, concentrations of NEFA averaged 559 uEq/l for control cows and 383 uEq/l for cows infused with glucose. A third order polynomial regression equation best described concentrations of NEFA in plasma over time (Figure 7). The response curve for cows infused with glucose was not parallel ($P<.05$) with the curve for the control cows (Table XIV).

A quadratic polymonial regression equation best described the concentrations of insulin in serum during the infusion of glucose (Figure 8). Concentrations of insulin in cows infused with glucose were almost twice the concentrations ass those in control cows (3.4 and 1.8 ng/ml, respectively, $P<.05$). The response curve for insulin in the serum of cows infused with glucose was parallel to that for cows infused with saline (Table XV).

TABLE XI

LEAST SQUARE MEANS FOR BLOOD CONSTITUENTS IN POSTPARTUM COWS INFUSED WITH GLUCOSE OR SALINE SOLUTIONS

Item	Treatments		EMS
	Saline	Glucose	
Cows (no.)	9	9	
Glucose (mg/100 ml)	60.7	76.8*	20.6
NEFA uEq/l Palmitate	559	383***	3141
Insulin (ng/ml)	1.8	3.4**	.56

*(P<.10)

**(P<.05)

***(P<.01)

TABLE XII

R^2 AND PROBABILITY LEVELS OF POLYNOMIAL REGRESSION EQUATIONS FOR CONCENTRATIONS OF GLUCOSE IN PLASMA AND NEFA AND INSULIN IN SERUM OF POSTPARTUM BEEF COWS

	Treatment		
Order	Glucose	NEFA	Insulin
Linear	.44[ac]	.18	.22
	<.05[b]	<.0001	<.13
Quadratic	.45	.20	.26[c]
	<.06	<.06	<.05
Cubic	.45	.22[c]	.27
	<.49	<.02	<.13
Quartic	.46	.22	.27
	<.13	<.69	<.82
Quintic	.46	.22	.27
	<.39	<.46	<.63

[a] R^2 value.

[b] Probability level for the term in the model.

[c] Curve used in analyses.

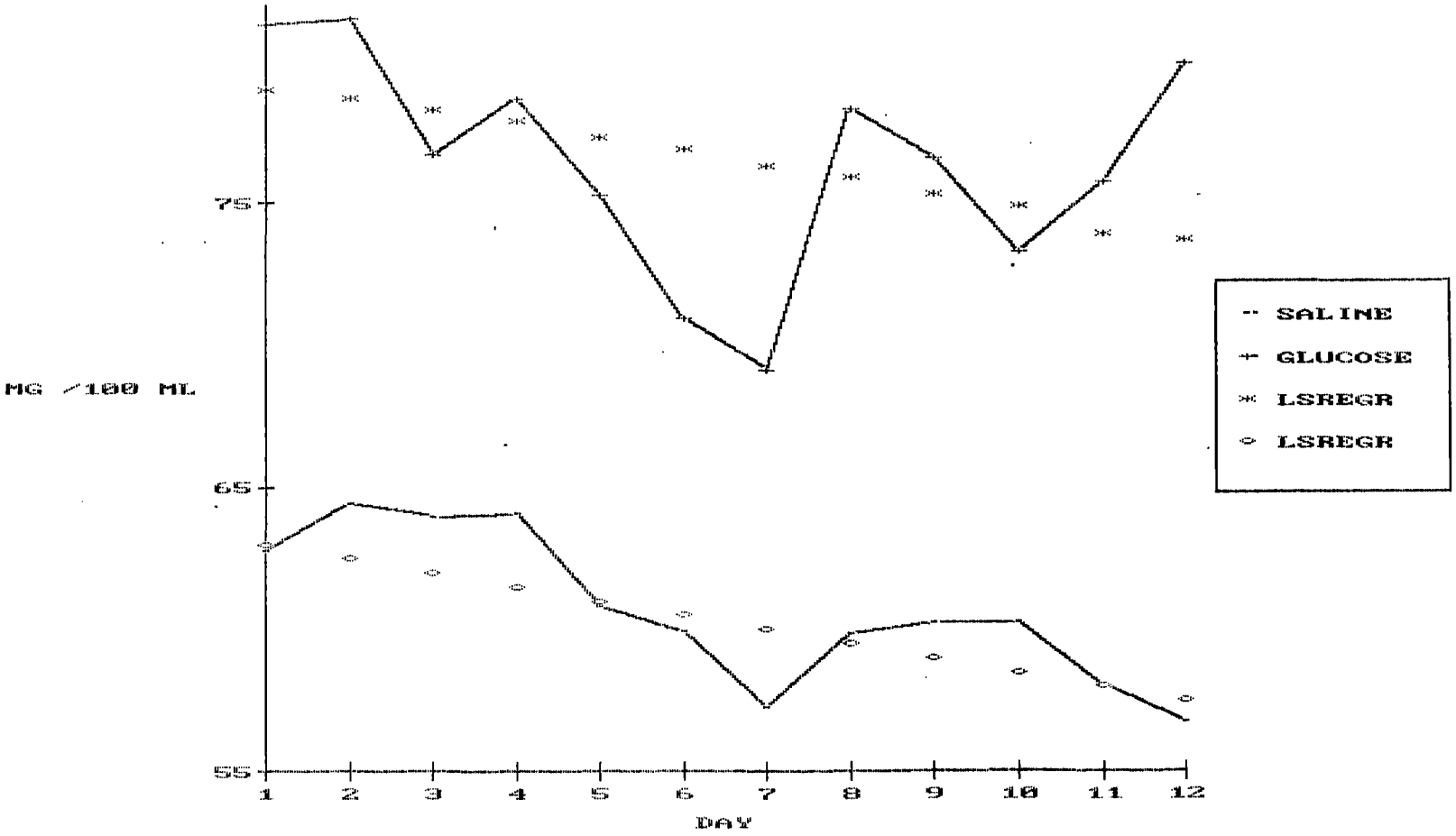

Figure 6. Concentrations of Glucose in Plasma (mg/100 ml) of Beef Cows Infused with Glucose or Saline Solutions During Days 32 to 44 Post Partum

TABLE XIII

ORTHOGONAL COMPARISONS USED TO TEST FOR HETEROGENEITY OF REGRESSION COEFFICIENTS FOR POLYNOMIAL RESPONSE CURVES TO DETERMINE WHETHER DAILY TRENDS FOR CONCENTRATIONS OF GLUCOSE BETWEEN GROUPS WERE NOT PARALLEL

	Control vs Glucose			
Error	D.F.	S.S	M.S.	F
Control	105	5267		
Glucose	105	13464		
Total	210	18731	89.2	
Control, Glucose	211	18736		
Difference	1	5	5	.06

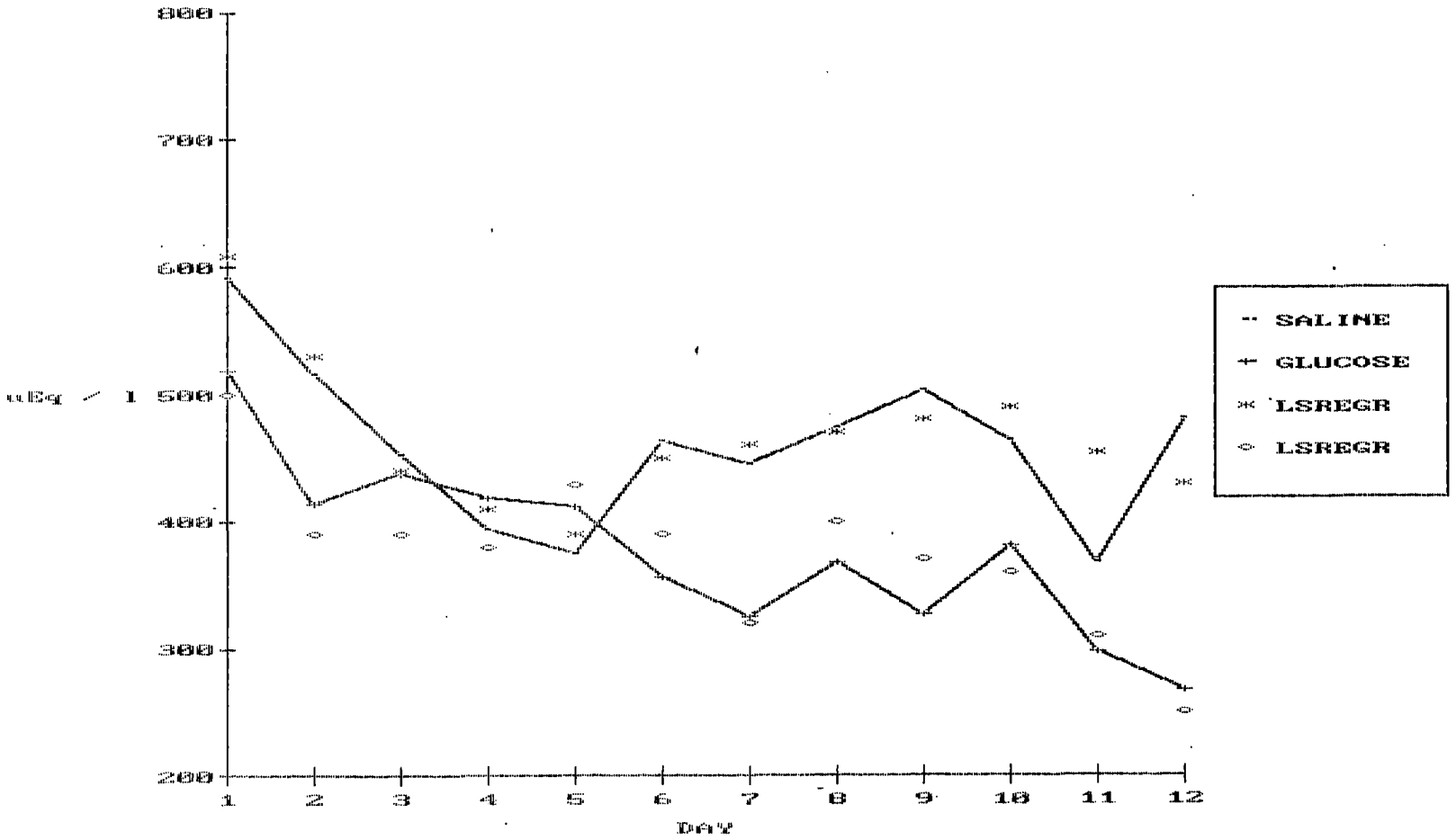

Figure 7. Concentrations of Non-Esterified Fatty Acids (uEq/l) in Plasma of Beef Cows Infused with Glucose or Saline Solutions Days 32 to 44 Post Partum.

TABLE XIV

ORTHOGONAL COMPARISONS USED TO TEST FOR HETEROGENEITY OF REGRESSION COEFFICIENTS FOR POLYNOMIAL RESPONSE CURVES TO DETERMINE WHETHER DAILY TRENDS FOR NEFA BETWEEN GROUPS WERE NOT PARALLEL

	Control vs Glucose			
Error	D.F.	S.S	M.S.	F
Control	103	2135947		
Glucose	103	1288852		
Total	206	3424799	16625	
Control, Glucose	209	3562024		
Difference	3	137225	45741	2.75*

*(P<.05)

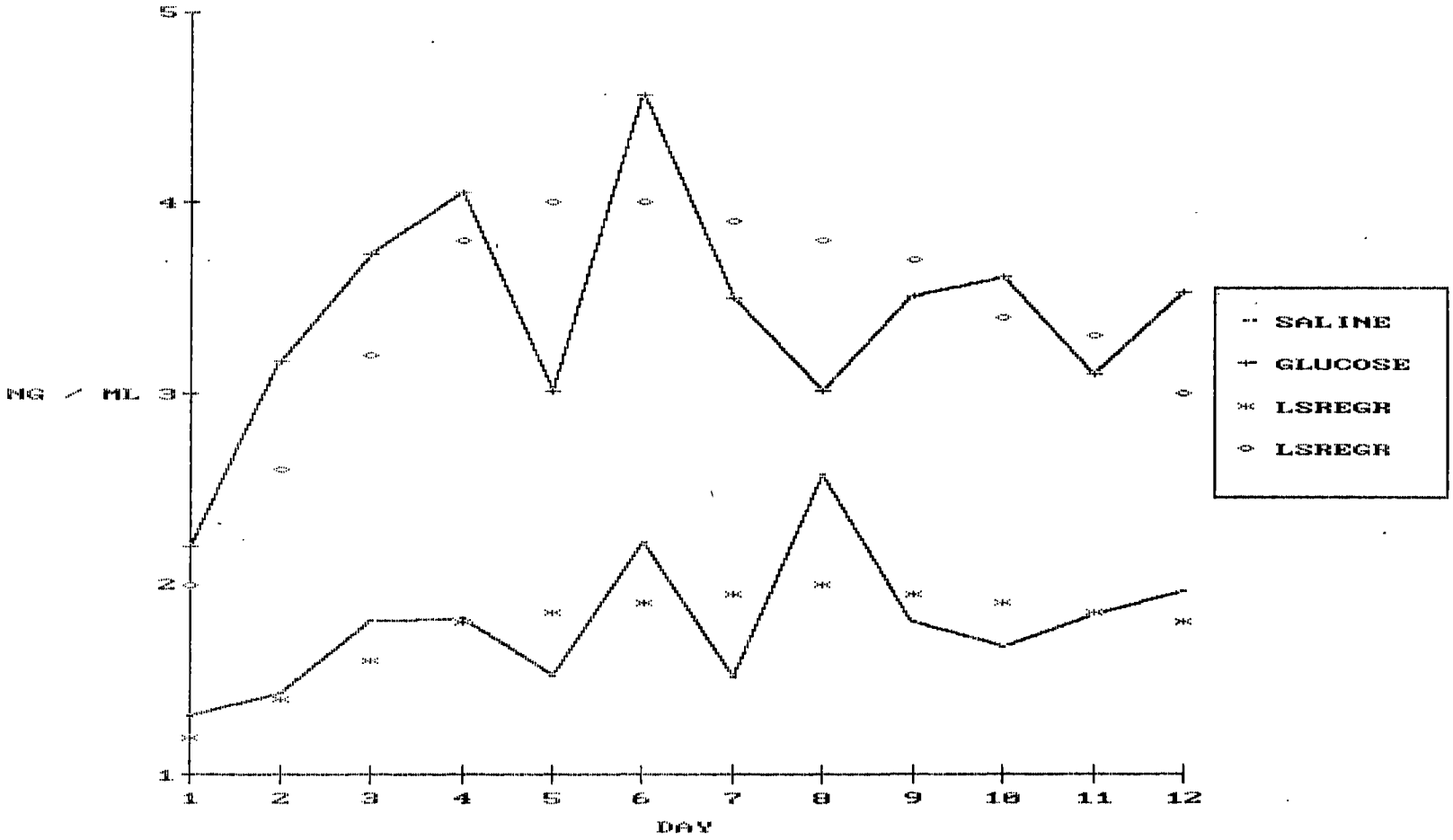

Figure 8. Concentrations of Insulin in Serum (ng/ml) of Cows Infused with Glucose or Saline Solutions During Days 32 to 44 Post Partum.

TABLE XV

ORTHOGONAL COMPARISONS USED TO TEST FOR HETEROGENEITY OF REGRESSION COEFFICIENTS FOR POLYNOMIAL RESPONSE CURVES TO DETERMINE WHETHER DAILY TRENDS FOR INSULIN BETWEEN GROUPS WERE NOT PARALLEL

	Control vs Glucose			
Error	D.F.	S.S	M.S.	F
Control	104	143.4		
Glucose	104	335.0		
Total	208	478.4	2.3	
Control, Glucose	210	479.7		
Difference	2	1.3	0.65	.28

TABLE XVI

PARTIAL CORRELATION COEFFICIENTS FOR GLUCOSE, NEFA AND INSULIN IN POST PARTUM COWS, ADJUSTED FOR TREATMENT, DAY OF SAMPLING AND BODY CONDITION

	NEFA	Insulin
Glucose	.01[a]	.13*
NEFA		-.14**

[a] N = 18 cows

* (P<.10)

** (P<.05)

Concentrations of NEFA in plasma were negatively correlated ($P<.05$) with concentrations of insulin in serum. The correlation between concentrations of glucose and insulin was .13 ($P<.10$).

Concentrations of glucose in plasma can be increased by infusion of cows with glucose. De Boer et al. (1984) observed that plasma glucose concentrations were increased to 175 mg/100 ml at 1 h after infusion of a 50% dextrose solution. But by 3 h after infusion, concentrations of glucose had returned to preinjection values. In lactating cows, a period in which ruminants are very susceptible to hypoglycemia, Lomax et al. (1978) found that infusion of a 50% glucose solution during 2 d significantly increased concentrations of glucose in plasma for only 24 h after the beginning of the infusion. However, in non-lactating cows, the increase in glucose in plasma was constant during the infusion period, indicating that milked cows utilized glucose for milk production. Glucose infusion of sheep suppressed endogenous production of glucose to about 50-60% of that normally produced (Judson and Leng, 1973).

Kellogs and Miller (1977) observed that as the supply of energy from the ration was reduced, blood glucose declined as the demand for energy increased. Since Bergman (1974) reported that the major proportion of glucose available to the ruminant has to be supplied by gluconeogenesis because little glucose is absorbed from the gut, reduced endogenous concentrations of glucose in plasma after glucose infusion may indicate a reduction in gluconeogenesis.

Concentrations of NEFA in plasma of cows generally reflect the rate of release of fatty acids from adipose tissue (Fritz, 1961). In addition, there is a simple reciprocal relationship between glucose

utilization and fatty acid release from adipose tissue. An increase in carbohydrate utilization inhibits the net release of fatty acids from tissue stores while conversely, conditions associated with impaired glucose utilization accelerate the release of fatty acids (Fredrickson and Gordon, 1958; Dole, 1958). In cows and goats, Radloff et al. (1966) observed that upon fasting, concentrations of NEFA in plasma increased, whereas concentrations of glucose in blood were depressed and blood ketones were increased. In heifers, Annison (1960) observed that during hypoglycemia, there were elevated concentrations of NEFA and injections of glucose reduced concentrations of NEFA. Although adipose tissue is mobilized during feed restriction, largely to supply energy in the form of NEFA (Patterson, 1963), the concomitant release of glycerol, a glucose precursor, may make a significant contribution to the glucose supply.

Infusion of glucose usually results in increased concentrations of insulin in the blood of cows (Brockman, 1983). Glucose infusion during 2 h (75 g/h) increased insulin concentration in serum (Laarveld et al., 1981). In addition, one hour after infusion of a 50% dextrose solution, concentrations of insulin increased (de Boer et al., 1984). In sheep, insulin concentrations were closely correlated with rate of glucose infusion (Basset et al., 1971). However, plasma insulin concentrations were not related to the concentrations of endogenous glucose in plasma.

During feed restriction, when dietary precursors to gluconeogenesis are limited, the body attempts to spare glucose in several ways: insulin concentrations in blood decrease, which decreases peripheral uptake of glucose; reesterification of adipose tissue is depressed, thus decreasing requirements for glucose; mobilization of NEFA from adipose

tissue is increased, and since NEFA is the preferred substrate, it will spare glucose to some extent (McNiven, 1984). Animals in thin body condition and fasting, generally exhibit decreases in glucose and insulin concentrations in blood and an increase in concentrations of NEFA in plasma.

The effect of glucose infusion on secretion of LH is summarized in Table XVII. Cows infused with glucose had 4 pulses of LH during 8 h ($P<.05$) whereas, cows infused with saline only had 3 pulses/8 h. However, mean LH concentration and the magnitude of the LH pulses were not different ($P>.10$). Area under the response curve for the concentrations of LH was determined using a third order polynomial regression equation. Infusion of cows with glucose did not alter the area compared with control cows.

Secretion of LH during the first 4 h after estradiol injection is summarized in Table XVIII. Estradiol administration reduced ($P<.01$) number and magnitude of LH pulses when compared with samples obtained during the previous 8 h but did not significantly influence the area under the response curve. After treatment of cows with estradiol, mean LH and the number of pulses per 4 h were greater ($P<.05$) in cows infused with glucose compared with control cows. Magnitude of pulses and area under the response curve were similar in glucose infused and control cows during the first 4 h after estradiol treatment.

Characteristics for LH during 4 to 8 h after estradiol injection of postpartum cows infused with glucose or saline solutions are presented in Table XIX. When compared with LH characteristics before estradiol treatment, magnitude of pulses were greater ($P<.05$), but the number of pulses were reduced ($P<.05$). Area under the LH response curve at 4 to 8

TABLE XVII

LEAST SQUARE MEANS FOR LH CHARACTERISTICS ADJUSTED FOR BODY CONDITION IN POSTPARTUM COWS INFUSED WITH GLUCOSE OR SALINE SOLUTIONS

Item	Treatments		EMS
	Saline	Glucose	
Serum Mean (ng/ml)	1.2	1.2	.04
Number of pulses / 8 h	3.0	4.0*	.13
Magnitude of pulses (ng/ml)	1.1	1.0	.30
Area (ng/ml.h)	1.2	1.1	.03

*(P<.05)

TABLE XVIII

LEAST SQUARE MEANS FOR LH CHARACTERISTICS DURING THE FIRST 4 H AFTER ESTRADIOL INJECTION IN POSTPARTUM COWS INFUSED WITH GLUCOSE OR SALINE SOLUTIONS

Item	Treatments		EMS[a]
	Saline	Glucose	
Mean LH (ng/ml)	.42	.77*	.19
Number of pulses / 4 h	.21	.65*	.50
Magnitude of pulses (ng/ml)	.70	.82	.76
Area (ng/ml.h)	.75	.82	.57

*($P<.05$)

[a]Error mean squares

TABLE XIX

LEAST SQUARE MEANS FOR LH CHARACTERISTICS DURING 4 TO 8 H AFTER ESTRADIOL INJECTION IN POST PARTUM COWS INFUSED WITH GLUCOSE OR SALINE SOLUTIONS

Item	Treatments		EMS[a]
	Saline	Glucose	
Mean LH (ng/ml)	.98	1.3*	.16
Number of pulses / 4 h	.6	1.2*	.82
Magnitude of pulse (ng/ml)	3.0	4.2	1.26
Area (ng/ml.h)	.7	1.2*	.91

*(P<.05)

[a]Error mean squares

h after estradiol was similar to the area before estradiol treatment. Cows infused with glucose had greater ($P<.05$) concentrations of LH in serum, more pulses and the area under the response curve was greater compared to the control cows during 4 to 8 h after estradiol. However, magnitude of the pulses were similar. A third order polynomial regression best described the response curve for LH after estradiol injection. Response of LH for cows infused with glucose was similar to the response observed in the control cows (Table XX; Figure 9).

Concentrations of LH in serum during treatment with GnRH are summarized in Table XXI. The area under the curve was determined using a sixth order polynomial regression equation (Figure 10). Glucose infusion increased both the area under the LH secretion curve ($P<.10$) and mean concentrations of LH ($P<.05$). The greatest concentrations of LH during treatment with GnRH occurred at similar times after the beginning of glucose or saline infusion of cows. Cows infused with glucose had a slightly greater ($P<.10$) maximum LH during GnRH treatment than control cows (64 vs 42 ng/ml).

Concentrations of LH in the serum of glucose infused and control cows were similar during 16 to 30 h after estradiol treatment (8 to 22 h after the start of the GnRH infusion; Table XXII). A third order polynomial regression curve was used to determine area under the curve (Figure 11). Onset, magnitude and duration of the LH increase were similar ($P>.10$) for cows on both treatments. However, cows infused with glucose had more surges than control cows (66% vs 44%, respectively).

Decreased dietary energy intake may affect hypthalamic control of the pituitary gland (McClure, 1970). Glucose inhibitors that disrupt glucose metabolism can inhibit release of LH (Sen et al., 1979; Crump et

TABLE XX

ORTHOGONAL COMPARISONS USED TO TEST FOR HETEROGENEITY OF REGRESSION COEFFICIENTS FOR POLYNOMIAL RESPONSE CURVES TO DETERMINE WHETHER LUTEINIZING HORMONE RESPONSE TO ESTRADIOL BETWEEN GROUPS WERE PARALLEL

	Control vs Glucose			
Error	D.F.	S.S	M.S.	F
Control	222	124.7		
Glucose	222	240.6		
Total	444	365.3	.82	
Control, Glucose	447	369.7		
Difference	3	4.4	1.47	1.79

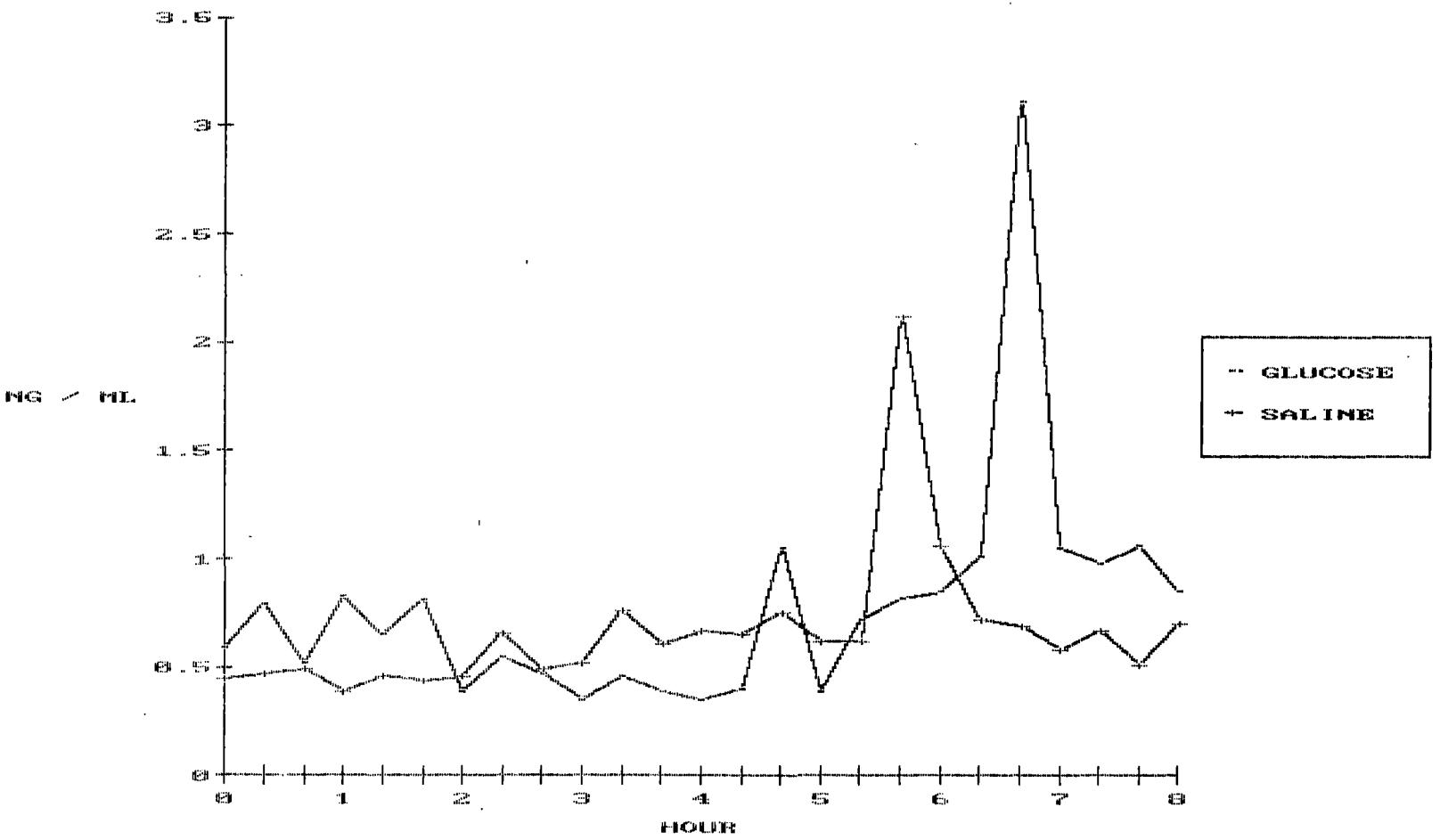

Figure 9. Pulsatile Patterns of LH Release (ng/ml) During 8 h After Estradiol Injection of a Representative Cow from Each of the Treatment Groups.

TABLE XXI

LEAST SQUARE MEANS FOR LH CHARACTERISTICS DURING GONADOTROPIN ADMINISTRATION IN POSTPARTUM COWS INFUSED WITH GLUCOSE OR SALINE SOLUTIONS

Item	Treatment		EMS
	Saline	Glucose	
Serum Mean (ng/ml)	18.0	24.9**	6.4
Area (ng/ml.h)	9.0	11.6*	10.9
Magnitude (ng/ml)	42	64	70
Interval to maximum LH (min)	68	69	633

*(P<.10)

**(P<.05)

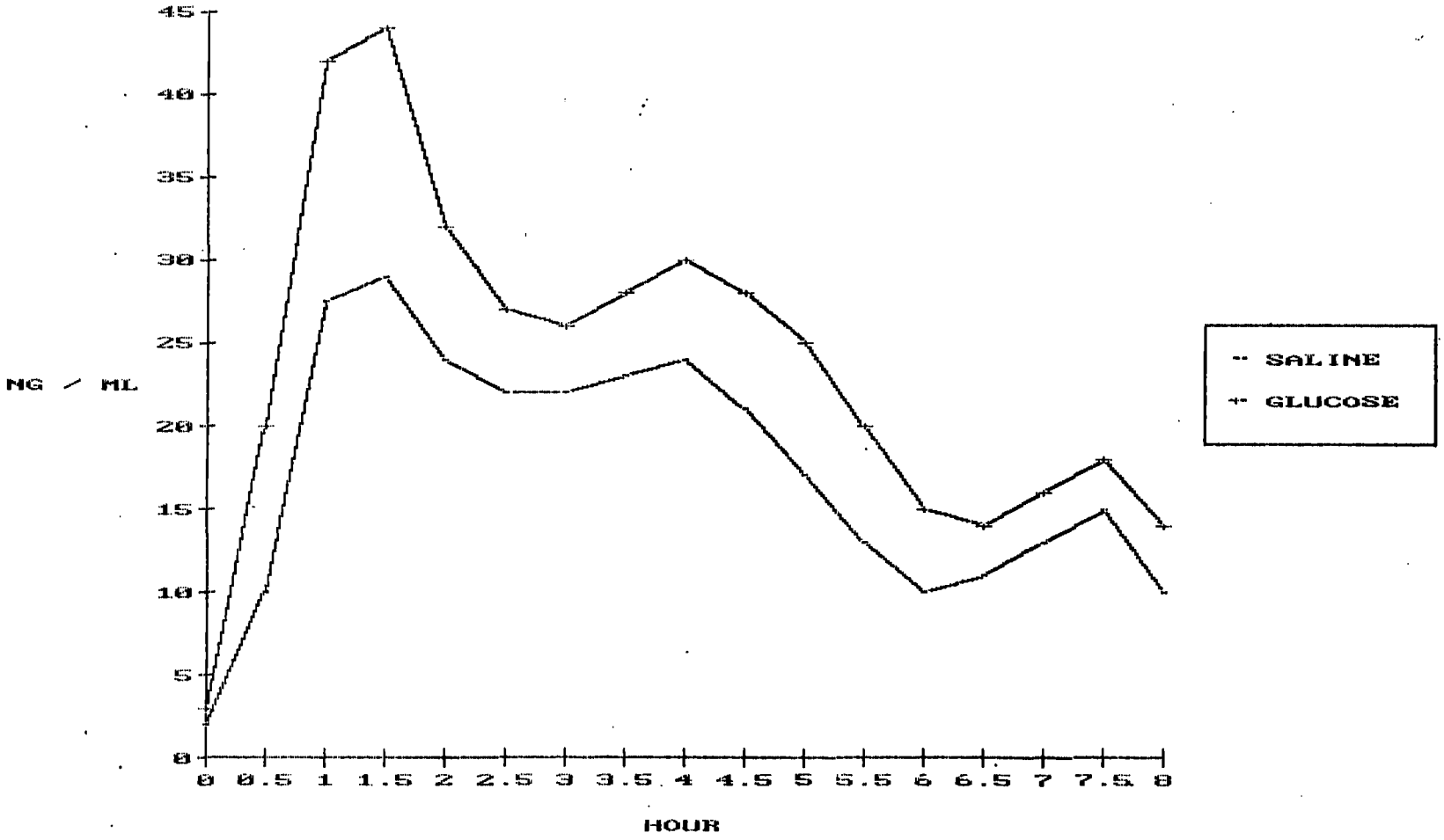

Figure 10. Concentration of LH in Serum of Cows (ng/ml) During LHRH Injections and Infusion with Glucose or Saline Solution.

TABLE XXII

LEAST SQUARE MEANS FOR LH CHARACTERISTICS AFTER GONADOTROPIN ADMINISTRATION IN POSTPARTUM COWS INFUSED WITH GLUCOSE OR SALINE SOLUTIONS

Item	Treatment		EMS
	Saline	Glucose	
Serum Mean (ng/ml)	3.2	3.2	.67
Area (ng/ml.h)	3.1	3.1	.68
Onset of surge after estradiol (h)	25.6	26.5	.50
Surge magnitude (ng/ml)	11.5	13.1	3.4
Surge duration (h)	3	3.9	.6

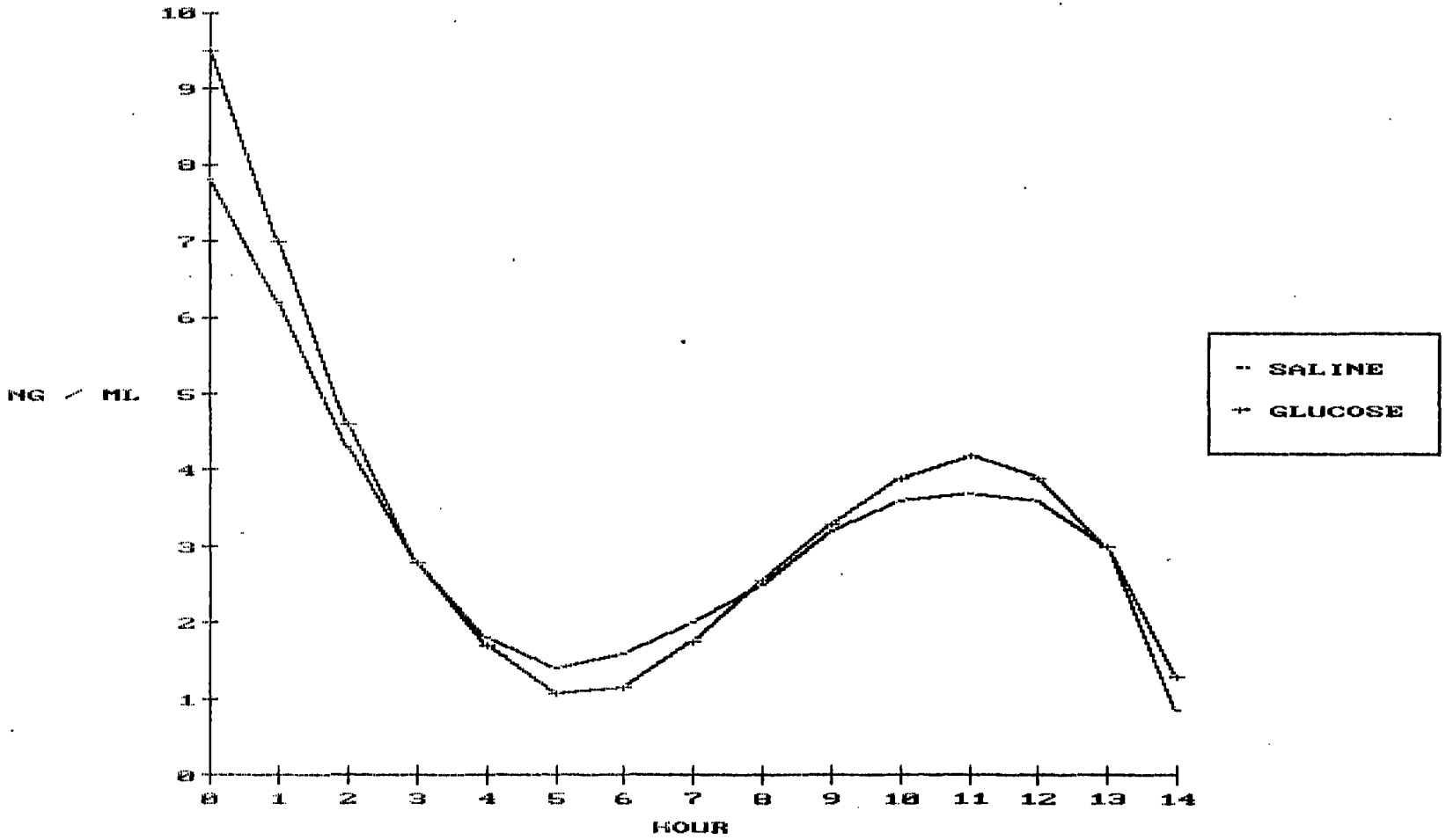

Figure 11. Concentration of LH in Serum of Cows (ng/ml) During 16 to 30 h After Estradiol Treatment (at 8 to 22 h After LHRH Injections) and Continuous Infusion with Either Glucose or Saline Solutions.

al., 1982) and can block the occurrence of estrous and formation of corpora lutea in heifers. This suggests that hypoglycemia may be related to infertility induced by acute energy deficiency in cattle (McClure et al., 1978).

Glucose metabolism is necessary for LH production (McCann, 1984). The presence of insulin receptors in the central nervous system has been well documented in other species (Havrankova et al., 1978; Havrankova and Roth, 1978; Pacold and Blackard, 1979), suggesting that insulin is necessary for glucose metabolism in nervous tissue. However, there is controversy about the effect of nutritional regimes on secretion of LH. Glucose infusion of postpartum cows did not affect either concentration of progesterone in plasma or LH secretion (McCaughey et al., 1985). Similarly, energy restriction of heifers did not alter concentrations of LH or progesterone in plasma and increased energy intake did not affect mean LH, number of LH pulses or the area under the LH curve (Harrison et al., 1984). Decreased pituitary LH content in intact cows has been observed after nutrition restriction (Beal et al., 1978). Easdon et al. (1985) also observed that average concentrations of LH were similar for cows fed either high or low planes of nutrition post partum. Rone et al. (1982) observed that nutrient intake of postpartum beef cows did not affect mean concentrations of LH but did affect the number of secretory spikes of LH. Luteinizing hormone secretion by cows is probably influenced by body energy reserves in addition to nutrient intake.

Estrogens influence LH secretion (Reeves et al., 1971). Single injections of estradiol in ovariectomized sheep caused biphasic changes in plasma LH (Coppins and Malven, 1976); there was an initial 8 h period of LH inhibition with increased LH release 12 to 20 h after estradiol

treatment. A similar effect has been demonstrated in rats (Vilchez et al., 1974). Treatments of heifers with estradiol will stimulate secretion of LH similar to preovulatory surges of LH (Kessner et al., 1982). In postpartum cows, estradiol treatment decreased the frequency of LH pulses and the interval to first estrus was increased by 10 d compared to control cows (Walters et al., 1984). Restriction of feeding did not affect plasma estradiol at 30 d post partum and, in contrast of the report of Fernandez et al. (1978), maximum LH was not correlated with concentration of estradiol prior to GnRH (Lishman et al., 1979). Faltys et al. (1985) observed in beef cows that diet did not increase estrogen receptors either in the hypothalamus or pituitary on days 23 and 25 post partum. However, body condition and interval before first estrus may influence concentrations of estrogens in post partum cows.

In ruminants, the effect of energy intake on LH release after GnRH treatment has been contradictory. Reduced energy intake has decreased (Lishman et al., 1979), increased (Haresign, 1981; Rasby, 1986) or had little effect (Lishman et al., 1974) on LH release. Glucose infusion during the postpartum period did not influence mean LH release after GnRH (McCaughey et al., 1985). Basal concentrations of LHRH in rat hypothalamic fragments were not influenced either by glucose or 2-deoxy-glucose during incubation in vitro (Lengyel et al., 1984). In heifers, low energy did not influence LH release after a GnRH injection, while in cows it decreased the pituitary LH content (Beal et al., 1978). Cows maintaining weight post partum had greater basal concentration of LH, greater GnRH induced maximum LH concentrations, greater LH concentrations throughout the GnRH induced LH surge, and greater areas

under release curves for the endogenous, GnRH induced and total LH release (Rutter and Randel, 1984).

Protein restriction in beef cows did not influence either episodic LH release, duration of GnRH induced LH release, duration of estradiol induced LH release or maximal estradiol induced LH release (Nolan et al., 1984). Whether energy intake has a greater role in control of LH secretion than does protein intake is yet to be determined.

Only 33% of the saline infused cows and 55% of the glucose infused cows exhibited estrus during days 1 to 3 after the estradiol injections. In addition, only one of the 9 cows infused with saline and none of cows infused with glucose conceived within 85 d after calving. Twenty two percent of the saline infused cows and eleven percent of the glucose infused cows had ovarian luteal activity by 85 d post partum.

Body condition of the cows during the infusion period averaged 4.4± .1. This thin body condition may be related to the anestrous condition during the first 85 d post partum. Selk (1986) determined that body condition score at calving was the most important factor influencing pregnancy rate.

Continuous intravenous infusion of lactating anestrous beef cows with glucose significantly increased concentrations of glucose in plasma and insulin in serum and reduced concentrations of NEFA in plasma. These alterations in glucose, insulin and NEFA were associated with an increased number of pulses of LH after 12 d of glucose infusion, increased positive feed back of estradiol on LH secretion and increased secretion of LH during GnRH infusion after estradiol treatment. Alteration of available energy in postpartum cows may influence the

response of hypothalamic and pituitary tissues to the positive feed back effects of estradiol.

CHAPTER V

SUMMARY AND CONCLUSIONS

In the first experiment, thirty cows were used to evaluate the effects of altered energy on serum LH, ovarian function and concentrations of glucose, insulin and NEFA in plasma. On day 25 post partum, 5 cows were assigned to each of six treatments for 17 d: continuous jugular infusion with glucose; twice daily insulin injections; fed an additional 5 kg/d of a 20% CP feed; calves were weaned at 32 d post partum; continuous jugular infusion with saline or non injected control.

Glucose infusion and feeding additional supplementation increased concentrations of insulin in serum and decreased NEFA in plasma compared to control cows. However, treatments did not influence either concentrations of glucose in plasma or secretion of LH on days 35 to 41 post partum.

To evaluate the hypothesis that concentrations of glucose in blood of anestrous beef cows affected LH secretion, eighteen cows were continuously infused with glucose or saline solutions for 12 d beginning at 30 d post partum (experiment 2). Secretion of LH and the responsiveness of the pituitary to estradiol and LHRH were determined.

Concentrations of glucose in plasma and insulin in serum were increased and concentrations of NEFA in plasma were reduced. Concentrations of glucose in plasma were correlated with insulin in

serum. Infusion of cows with glucose increased the number of LH pulses before treatments with hormones and also increased the mean concentrations of LH and total response area during the LHRH infusion. In cows that were infused with glucose, estradiol had a greater positive feed back effect on secretion of LH compared with control cows.

Changes in nutrition around the time of parturition influence reproductive performance during the subsequent breeding season. Cows that are in thin body condition at calving, and are inadequately fed during early lactation, will continue to lose weight and will have reduced reproductive function. Such cows usually have an extended interval from calving until the first estrus.

Associated with postpartum anestrous, there is often a reduction in concentrations of glucose in plasma and concentrations of NEFA are increased, indicating active fat mobilization to supply energy for body function. Since glucose is the main supply of energy for brain function, reproductive endocrine function may be altered.

Short term changes in energy supply for two weeks around day 30 post partum may improve the energetic balance of the cows. To induce such a change, we either infused glucose intravenously, gave extra supplementation or weaned the calves. With these treatments, there was a tendency to increase the number of cows that exhibited estrus and ovarian activity within 85 d post partum. In addition, all cows on the glucose infusion and weaning treatments were pregnant at the end of the breeding season and the interval from parturition to conception tended to be shorter in cows infused with glucose and given extra supplementation.

An increase in the number of LH pulses and a greater response of the pituitary to exogenous estradiol and LHRH may indicate an effect of increased glucose supply on pituitary function. Cows infused with glucose had greater mean LH concentration, more pulses of LH and the area under the response curve from 4 to 8 h after estradiol was greater compared to the control cows. However, reproductive function was not improved in the postpartum cows infused with glucose for 12 d (second experiment) when compared with that of cows with slightly better body energy reserves and infused with glucose for 17 days (first experiment). This could be caused by a shorter treatment period or to the treatment with estradiol which was used to evaluate pituitary function. Other studies have indicated a longer postpartum anestrous interval after estradiol treatment.

It is concluded that pituitary function in cows in thin body condition is impaired after calving. However, supplying energy during this critical period may produce beneficial changes in pituitary endocrine function. Therefore, increased nutrient intake of thin cows after calving may increase gonadotropin secretion and decrease the interval to first estrus. However, the response of cows to increased energy intake will probably be influenced by the body condition of the cow and the number of days post partum.

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VITA 2

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