ASSOCIATION OF METABOLIC AND
ENDOCRINE FACTORS WITH
PRODUCTIVITY OF
BEEF COWS

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CHAPTER I

INTRODUCTION

Successful cow-calf production requires an understanding of the resource inputs (forage), manufacturing processes (cow herd), product outputs (pounds of calf weaned) and the interaction of these components. Beef cows have the ability to convert the cellulose in native and improved grass into beef. Forage from the approximately one billion acres of pasture and range land in the U.S. is most economically harvested by cattle. Producers must balance the needs of the cow herd with the needs of the grass plant to maximize forage utilization. Proper grazing management will promote a pasture or range condition capable of supplying adequate forage to the cow herd.

Nutrients derived from forage have major influences on reproductive function. Large amounts of energy are required for gestation, lactation, and repair of the reproductive tract for the initiation of fertile estrous cycles. For a cow to maintain a 365-day calving interval, she must conceive by 82 days postpartum. Body energy reserves are often required to make up the deficit in nutrient intake. Body condition of beef cows at the time of calving is an important factor that influences rebreeding performance.

Body condition influences endocrine and metabolic regulatory mechanisms that cause the onset of ovarian cycles. Metabolic cues, such as concentrations of insulin, glucose and non-esterified fatty acids in plasma, may influence hypothalamo-pituitary-ovarian function. An understanding of how energy constituents are regulated in cows with varying production capability, may help explain the control of postpartum reproduction.

The success of calf production is dependent upon the maternal ability of the dam. The reproductive efficiency of a cow-calf operation is affected by the ability of cows to rebreed quickly following calving. The ability to both produce and reproduce must be evaluated early in life to achieve maximum genetic progress.

The objectives of this research were to: (1) determine the repeatability of cow rebreeding performance and calf growth during the first and subsequent parities; (2) to evaluate endocrine and metabolic factors that may be related to above average or below average calf growth and reproductive performance of range cows; and (3) to evaluate the effect of epinephrine and fasting on concentrations of glucose, insulin and non-esterified fatty acids in the plasma of lactating beef cows.

CHAPTER II

LITERATURE REVIEW

Factors Influencing the Postpartum Anestrous Interval in Beef Cows

Nutritional Regulation of Reproduction

Nutritional requirements of breeding females must be met throughout the reproductive process for successful livestock production. The stages of reproduction include the production of gametes, fertilization, embryonic and fetal development, parturition, lactation and rebreeding. The area of investigation in this thesis is the effect of nutrition on the endocrine system which regulates reproductive performance from parturition, through the first postpartum estrus and initiation of pregnancy. The period from parturition to first estrus, commonly referred to as the postpartum anestrous interval, is extended when cows receive inadequate nutrients and body energy reserves are reduced (Wiltbank et al., 1964; Dunn and Kaltenbach, 1980; Selk et al., 1988).

Reproductive performance in cattle is influenced by dietary energy levels during both the pre- and postpartum periods (Corah et al., 1974; Dunn and Kaltenbach, 1980; Dziuk and Bellows, 1983). Dietary energy intake influences the secretion of gonadotropic and gonadal hormones in beef heifers during both the follicular and luteal phases of the estrous cycle (Hill et al., 1970; Imakawa et al., 1986). The anterior pituitaries of beef and dairy cows exhibit increased responsiveness to gonadotropin releasing hormone (GnRH) as days following parturition increase (Kesler et al., 1977; Fernandes et al., 1978; Nolan et al., 1988). The pulse frequency of luteinizing hormone (LH) secretion increases with time post partum, and is influenced by nutrient intake during the pre- and postpartum periods (Humphrey et al., 1983; Nolan et al., 1988). When postpartum beef cows were fed diets deficient in crude protein, the ability of the anterior pituitary to store and/or release LH was affected (Nolan et al., 1984) and a decreased pituitary responsiveness to GnRH may delay the return to estrus. Postpartum dairy cows fed a ration containing 12.7% crude protein (CP) had decreased basal concentrations of LH in serum and a decreased response to GnRH when compared to cows fed 19.3% CP (Jordan and Swanson, 1979). In addition, Sasser et al. (1988) found that CP-restricted beef cows had increased intervals from calving to first estrus, to first service and conception. The number of cows exhibiting estrus, that conceived, was also reduced. Beef cows receiving a postpartum diet deficient in both energy and protein [90% of the National Research Council

(NRC) recommendations] had an extended postpartum interval to estrus when compared to cows fed 100% or 110% of the NRC recommendations (Rutter and Randel, 1984).

Ovarian follicular activity and estrous cycles of beef cows are dependent upon nutrient intake. Inadequate nutrition may result in loss of body weight (BW) and reduced body condition. When postpartum beef cows were fed a ration deficient in dietary CP, .32 vs. .96 kg crude protein per head daily, Sasser et al. (1988) observed that postpartum BW and weight change were negatively correlated with the interval post partum to first estrus. Richards et al. (1989b) observed the cessation of ovarian luteal activity in non-lactating beef cows that lost 24% of their initial weight and attained a body condition score (BCS) of 3.5 following a reduction in nutrient intake. Undernourished anestrous cows that were fed to resume fertile estrous cycles were heavier, and at a higher BCS (4.6) upon the return to, than at the cessation of ovarian activity (Louw et al., 1988; Richards et al., 1989b). These results would suggest that greater body energy stores are required to re-initiate gonadotropin release, ovarian activity and estrous cycles than to maintain them.

<u>Prepartum Nutrition</u>. Prepartum nutrition influences early postpartum ovarian function in beef cows (Corah et al., 1974; Bellows and Short, 1978; Wettemann et al., 1980). Pregnant heifers and cows with reduced prepartum energy intake had increased postpartum anestrous intervals

(Wiltbank et al., 1964; Dunn et al., 1969; Bellows and Short, 1978; Dunn and Kaltenbach, 1980; Selk et al., 1988).

Luteinizing hormone secretion is a limiting factor to the onset of estrus following parturition (Lamming et al., 1981). Nett et al. (1988) suggested that pituitary LH content is a primary factor delaying the first postpartum estrus in beef cows. Beal et al. (1978) observed that cows with restricted dietary energy intake had similar pituitary weights but reduced pituitary LH content compared to cows not restricted in energy intake. A decrease in LH release following parturition was associated with a prepartum loss of body weight caused by nutritional restriction of beef heifers during gestation (Killen et al., 1989). Nolan et al. (1988) found that cows consuming a prepartum diet with adequate CP (.96 kg/d) had increased LH pulse amplitude and frequency as time postpartum increased, while cows that were deficient in dietary CP (.32 kg/d) did not exhibit a similar increase in LH pulse amplitude and frequency. Changes in concentrations of steroids in plasma during pregnancy may influence synthesis of gonadotropins and secretion of LH and FSH post partum. During late gestation, increased nutrition was associated with reduced concentrations of estrone sulfate in serum (Mobley et al., 1983; Boyd et al., 1987). Concentrations of progesterone and estrone in plasma were reduced in cows losing weight and body condition during late pregnancy (Mobley et al., 1983).

Body energy reserves influence the effects of prepartum nutrition on reproductive function. Cows which maintain or have limited BW loss prior to calving, have a shorter postpartum anestrous interval and greater conception rates than cows fed to lose weight during mid to late gestation (Dunn and Kaltenbach, 1980; Selk et al., 1988). Changes in prepartum nutrient intake which caused alterations in prepartum body condition, influenced subsequent pregnancy rates of beef cows (Selk et al., 1988). By increasing nutrient intake 1 to 3 months prior to parturition, beef cows that lost BW or condition during the second trimester of pregnancy had improved pregnancy rates over cows that continued to lose BW during gestation (Selk et al., 1988). Body condition of the cow at parturition may influence the response to postpartum nutrition (Dunn and Kaltenbach, 1980; Wettemann et al., 1987). When cows are in good body condition at the time of calving, prepartum nutrition has a minimal effect on the postpartum anestrous interval and subsequent conception (Richards et al., 1986; Boyd et al., 1987; Selk et al., 1988).

Postpartum Nutrition. The postpartum anestrous interval is prolonged in cows receiving inadequate energy and protein following parturition (Wiltbank et al., 1962, 1964; Dunn et al., 1969; Sommerville et al., 1979; Sasser et al., 1988). Reduced dietary energy intake following calving decreases pregnancy rate in beef heifers and cows (Wiltbank et al., 1962, 1964; Dunn et al., 1969; Spitzer et al., 1978;

Dunn and Kaltenbach, 1980; Dzuik and Bellows, 1983). However, feeding beef cows more energy than required for maintenance may not improve pregnancy rates (Loyacano et al., 1974; Wettemann et al., 1986; Warren et al., 1988). The duration of feeding, amount of energy and interval postpartum may influence the response.

Reproductive performance of postpartum cows with adequate body energy reserves was not improved by feeding additional energy and protein (Moore and da Rocha, 1983; Wettemann et al., 1986; Warren et al., 1988). Richards et al. (1986) found that feeding additional energy to postpartum cows that calved in thin body condition (BCS ≤4) decreased the interval to first estrus and increased conception during a finite breeding season. Therefore, the response to postpartum nutrition may depend on body condition, weight change and the prepartum energy intake of the cow (Wiltbank et al., 1962; Dunn and Kaltenbach, 1980).

Body weight gain after calving, shortened the postpartum anestrous period for thin cows, especially if they lost BW prepartum (Dunn and Kaltenback, 1980). Pregnancy rates were improved when cows gained weight during the breeding season (Dunn and Kaltenbach, 1980; Dziuk and Bellows, 1983; Wettemann et al., 1987; Warren et al., 1988). Postpartum diets which allowed prebreeding weight loss were detrimental to reproductive performance (Rakestraw et al., 1986; Sasser et al., 1988) and can lengthen the postpartum anestrous interval. In addition, BW loss of cows during the early postpartum period may reduce ovarian function in cows that calve with adequate body energy reserves (Rakestraw et al., 1986). Thus if cows calve with adequate BCS, this does not guarantee good rebreeding performance. BW loss after calving may have a greater effect on fertility than actual BW at the time of breeding (Sommerville et al., 1979).

Suckling

A critical factor affecting the calving interval is the length of the postpartum anestrous interval. Therefore, return to estrus early in the breeding season is of great importance to the reproductive efficiency of a beef cow herd. Suckling lengthens the postpartum interval to ovulation and prolongs the interval from parturition to first estrus (Oxenreider and Wagner, 1971; Short et al., 1972; Carter et al., 1980; La Voie et al., 1981; Walters et al., 1982b; Garcia-Winder et al., 1984). Normal suckling behavior in range beef calves includes an average of 5 suckling events per calf in 24 hours (Odde et al., 1985). Wyatt et al. (1977) observed the nursing behavior of Hereford X Holstein calves. Calves averaged 4 suckling events in 24 hours with a suckling duration of about 8.5 minutes per event. Manipulation of the frequency and intensity of suckling will influence postpartum ovarian activity. Once-daily-suckled cows (Randel, 1981; Reeves and Gaskin, 1981) or cows suckled twice-daily (La Voie et al., 1981; Bastidas et al., 1984) had shorter periods from parturition to first estrus and to the presence of the first follicle larger than 10 mm (Bastidas et al., 1984) than did cows that had calves with them continuously. Wettemann et al. (1978) found that increased suckling intensity lengthened the postpartum anestrous period in range cows, independent of nutritional factors. Temporary calf removal has been used as a management tool for reducing the length of the postpartum interval to estrus. Temporary calf removal resulted in increased concentrations of LH (Whisnant et al., 1986a) and an increased frequency of LH pulses at 48 h following calf removal (Edwards, 1985; Williams et al., 1987). In addition, temporary calf removal for 48 h (Beck et al., 1979) or 72 h (Dunn et al., 1985) reduced the postpartum anestrous period without detrimental effects on milk production of cows or subsequent calf performance. However, Wettemann et al. (1986) and Warren et al. (1988) found no beneficial effects of a 48 h temporary calf separation upon estrus or pregnancy rates for cows in thin to moderate body condition at parturition. These results suggest that the availability of body energy stores, interval after parturition and/or the duration of the weaning may influence the cow's reproductive performance. Williams et al. (1987) found a nearly linear increase in LH pulse frequency between day 0 and day 4 after weaning, which may explain why temporary weaning of shorter duration may not result in an ovulatory or estrus response in all cows.

Early weaning of calves will significantly shorten the postpartum anestrous interval of beef cattle (Bellows et al., 1974; Lusby et al., 1981). Laster et al. (1973a) found that early weaning was more effective at increasing the incidence of estrus during the first 21 days of the breeding season in younger cows compared to older cows. Early weaning has been used in conjunction with a hormone treatment to shorten the postpartum anestrous interval in beef cows (Smith and Vincent, 1972; Wettemann, 1980; Walters et al., 1984). Walters et al. (1984) found that the use of a progestin and estrogen treatment in conjunction with early weaning shortened the interval from parturition to conception and increased pregnancy rates of anestrous cows.

The period of ovarian inactivity following parturition is a result of inadequate LH secretion (Lamming et al., 1981). Suckled cows have reduced mean concentrations of LH in plasma, fewer LH pulses, and a decrease in LH pulse amplitude compared with nonsuckled cows (Radford et al., 1978; Dunlap et al., 1981; Walters et al., 1982a,b; Edwards, 1985). The amount of gonadotropin within the anterior pituitary is not reduced by suckling (Carruthers et al., 1980; Peters et al., 1981; Walters et al., 1982b) The endogenous release of gonadotropin-releasing hormone (GnRH) may be the limiting factor for the initiation of LH secretion during the postpartum anestrous period. Walters et al. (1982c) suggested that suckling extended the postpartum interval by reducing pulsatile GnRH secretion.

Exogenous GnRH treatment of postpartum cows can increase concentrations of LH in plasma and elicit ovulation or luteinization of follicles (Riley et al., 1981; Wettemann et al., 1982b; Troxel and Kesler, 1984). The responsiveness of the pituitary to GnRH is not decreased by suckling (Williams et al., 1982) and the response is enhanced with time after parturition (Jaeger et al., 1987). Estrogen exerts a negative feedback affect on the hypothalamus of suckled postpartum cows (Hinshelwood et al., 1985; Chang and Reeves, 1987). Acosta et al. (1983) suggests that suckling increases the sensitivity of the hypothalamus to the negative feedback effect of estrogen thereby reducing the secretion of GnRH. However Hinshelwood et al. (1985) found that upon removal of the ovaries on day 5 postpartum, suckled cows continued to have lower concentrations of LH compared to nonsuckled cows, suggesting that other inhibitory influences, in addition to ovarian secretions, may have an effect on suckled cows.

The endogenous opioid peptides have been implicated as inhibitors of gonadotropin secretion during the postpartum anestrous period of suckled beef cows (Whisnant et al., 1986b,c; Gregg et al., 1986; Cross et al., 1987) and will be discussed in a later section.

Body Condition

In addition to nutrient intake, body energy reserves influence reproductive function. When evaluating the response of reproductive performance to nutrient intake, body energy reserves must be monitored.

Body energy reserves of beef cows can be described using a body condition scoring system with a scale ranging from 1 = emaciated to 9 = extremely obese (Spitzer, 1986; Wagner et al., 1988). Body condition scores of beef cows were more highly correlated with estimates of the percentage of carcass fat (r = .91) and the energy content of the boneless carcass/kg live weight (r = .91), than either live weight or weight:height ratio (Wagner et al., 1988). Wright and Russel (1984) have also found that body condition score (0 = very thin, 5 = very fat) was a useful predictor of total carcass energy (r = .91) in beef cows. In addition, Dunn et al. (1983) demonstrated that body condition score was highly correlated with fat depth over the rib eye (r = .86) and fat content of the carcass (r = .77). Due to the close relationship between condition score and carcass energy or fat, condition score can be used to assess body energy reserves in cows.

Body condition may be an indicator of potential reproductive performance of beef cows. Rasby (1986) found greater concentrations of estradiol and estrone in plasma of thin cows than in moderate cows during late gestation. This indicates that pituitary, ovarian and placental function of cows with thin, moderate, and fat body condition may differ. Richards et al. (1989) observed that following a period of reduced nutrient intake, ovarian luteal activity ceased in non-lactating cows that lost 24% of their initial body weight and had a body condition score of 3.5. Cows maintaining body condition after calving, irrespective of nutrient intake, had a reduced postpartum interval to estrus compared to cows losing body condition (Rutter and Randel, 1984).

Body weight loss or change in body condition during pregnancy may be used to estimate potential reproductive performance of spring calving cows (Wettemann et al., 1982a). The percentage decrease in body condition score during the last half of gestation was correlated with days to first estrus (r = .61) and days to conception (r = .62). A 20 percent decrease in body condition score between November and parturition (March) was associated with an additional 16 days to conception when compared to cows that maintained body condition. Body condition score before parturition and at the beginning of the breeding season, are the dominant factors influencing subsequent pregnancy rates (Selk et al., 1988).

Relationships Among Metabolic and Endocrine Functions and Postpartum Reproduction

Following parturition, the beef cow undergoes a period of acyclicity termed the postpartum anestrous period. During this period, numerous endocrine and metabolic regulatory mechanisms influence the return to cyclic ovarian function. Characterization of the endocrine changes within the hypothalamic-pituitary-ovarian axis would contribute to an understanding of this transition period preceding the first postpartum estrus and ovulation. In addition, hypothalamic-pituitary-ovarian function may be directly affected by metabolic cues in blood such as concentrations of insulin, glucose or non-esterified fatty acids (NEFA). The availability of energy substrates may contribute to the regulation of the postpartum anestrous period in cows. In this section the possible roles of metabolic cues, including hormones, nutrients, blood constituents, and endogenous opioid peptides, will be associated with the postpartum anestrous period in beef cows.

Blood Constituents During the Postpartum Anestrous Period

Glucose. In ruminants, the major portion of circulating glucose is formed from propionate and amino acids via the gluconeogenesis pathway (Ballard et al., 1969;

Basset et al., 1971). Little glucose is normally absorbed directly from the bovine gut as a result of microbial fermentation in the rumen (Baird et al., 1983). Glucose is an important source of energy at the cellular level, including the central nervous system (Brockman and Laarveld, 1986) and glucose is required for the normal function of endocrine glands. Although specific glucose requirements of the reproductive organs have not been determined, glucose may regulate reproductive function by influencing the secretion of hormones.

Concentrations of glucose in the plasma of postpartum cows are influenced by energy intake and lactational status (Oxenreider and Wagner, 1971; Downie and Gelam, 1976). Richards (1987) found that restriction of nutrient intake which resulted in anestrous, was associated with reduced concentrations of glucose in the plasma of beef cows. Kellog and Miller (1977) observed a reduction in blood glucose concentrations of lactating cows when fed a diet restricted in energy. Lactation imposes increased demands for glucose on the cow. In postpartum dairy cows, concentrations of glucose in plasma are negatively related to milk production (Smith et al., 1976; Jenny et al., 1974). Chang et al. (1984) found that lactating beef cows had reduced concentrations of glucose in plasma (61 mg%) when compared to nonlactating cows (67 mg%). In addition, the lactating cows had an extended postpartum anestrous period.

Decreased concentrations of glucose in plasma have been associated with reduced fertility in beef and dairy cows (Oxenreider and Wagner, 1971; McClure et al., 1978; Patil and Deshpande, 1979; Kappel et al., 1984; Selk, 1986). Selk (1986) supplemented range cows with different amounts of protein and observed differences ($P<.1$) in plasma concentrations of glucose which were related to reproductive performance. Cows with extended postpartum anestrous intervals had reduced concentrations of glucose and body weights when compared with cows with shorter intervals (Patil and Deshpande, 1979). Oxenreider and Wagner (1971) found that concentrations of glucose in plasma were negatively correlated with the interval from calving to the occurrence of 10 mm follicles ($r=-.50$) and ovulation ($r=-.62$). McClure et al. (1978) prevented estrus in cyclic heifers through treatment with 2-deoxy-D-glucose, an inhibitor of glycolysis. When propionate, a gluconeogenic substrate, was infused directly into the abomasum of prepuberal heifers, concentrations of glucose in plasma were increased and pituitary responsiveness to GnRH was enhanced with the release of greater amounts of LH (Rutter et al., 1983). Secretion of LH was enhanced in response to estradiol and GnRH when postpartum anestrous cows were continuously infused with glucose, (500 g/d) for 12 days (Garmendia, 1986). In contrast, McCaughey et al. (1988) found that intravenous glucose infusion (500 g/d for 7 days) did not alter concentrations of LH in plasma after exogenous

GnRH. Infusion of phlorizin, a compound that causes glucosuria, inhibits weaning-induced increases in LH pulse amplitude in anestrous postpartum beef cows and suppresses the normal increase in LH pulse amplitude during the preovulatory period in cyclic postpartum beef cows (Rutter and Manns, 1987; 1988). These studies suggest that the metabolic regulation of LH secretion may be glucose-dependent.

Insulin. Concentrations of glucose, propionate and butyrate in serum of ruminants influence concentrations of insulin (Trenkle, 1970; McAtee and Trenkle, 1971). Glucose infusion resulted in a significant and sustained increase in concentrations of insulin in the serum of lactating cows (Hove, 1978; Laarveld et al., 1981; Garmendia, 1986). In ruminants, normal pituitary-ovarian functions are influenced by insulin and glucose metabolism (Downie and Gelam, 1976; McClure et al., 1978). A complete understanding of the relationship between insulin and reproductive performance has not been reached. However, exogenous insulin administration increases ovulation rates in gilts (Jones et al., 1983; Cox et al., 1987) and in energy deprived beef heifers (Harrison and Randel, 1986). Energy deprivation of postpartum beef cows decreased concentrations of both insulin and LH in serum (Hall et al., 1984). Insulin enhanced the GnRH-induced release of LH and FSH by rat anterior pituitary preparations in vitro (Adashi et al., 1981). Pituitary cells contain insulin receptors (McCann, 1984). Undernutrition and reduced concentrations of insulin may impair reproductive efficiency through reduced gonadotropin secretion.

Concentrations of insulin and glucose in plasma were reduced in cattle, in response to short-term fasting (McCann and Hansel, 1986) and long-term feed restriction (Blum et al., 1985). In addition, McCann and Hansel (1986) found decreased concentrations of LH in fasted dairy heifers when compared with control heifers, and upon refeeding of the fasted heifers, concentrations of LH and insulin increased significantly. Richards et al. (1989b) determined concentrations of glucose and insulin in serum after infusion of nonlactating beef cows with glucose when some were exhibiting normal estrous cycles and others were initiating nutritional anestrus. Glucose infusion resulted in increased concentrations of glucose and insulin in all cows. As anestrous occurred in nutritionally restricted cows (BCS of 3.5), concentrations of glucose were increased and concentrations of insulin were greater for a longer period following glucose infusion when compared to cows fed a maintenance diet. The increased concentrations of insulin without the subsequent decrease in plasma glucose concentrations, suggests that thin cows may become insulin resistant as anestrous is initiated. In addition, Wettemann and Castree (unpublished data) observed a decreased clearance rate of glucose from the plasma of thin (BCS of 4) vs. fat (BCS of 6) nonlactating beef cows following epinephrine infusion.

Insulin had a stimulatory effect on lipogenesis in adipose tissue of sheep (Hu et al., 1988) and in rat adipocytes (Haystead and Hardie, 1986). Lipogenic capacity of bovine adipose tissue was highly dependent on insulin (Etherton and Evock, 1986). Nutritionally obese heifers have greater secretion rates of insulin than do lean heifers (McCann and Reimers, 1985a). Obese heifers also are less sensitive to the glucoregulatory effects of exogenous insulin. In addition, obese heifers had greater insulin secretion during estrus than diestrus, while insulin was unaffected by stage of the estrous cycle in lean heifers (McCann and Reimers, 1985b).

Following continuous infusion of postpartum anestrous beef cows with glucose for 12 d, Garmendia (1986) observed an increase in the concentrations of glucose in plasma and insulin in serum. Concentrations of glucose in plasma were positively correlated with insulin in serum. Glucose infusion resulted in an increase in the number of LH pulses and greater mean LH concentrations. Similarly, Selk (1986) observed a positive correlation ($r=.20$; $P<.001$) between glucose and insulin in postpartum beef cows. Concentrations of insulin in serum postpartum were different in cows that became pregnant, compared to contemporaries that did not conceive. Therefore, glucose and its regulator, insulin, may have significant roles in the relationship between nutrition and reproductive function.

Non-esterified Fatty Acids. In ruminants, the primary site of fatty acid synthesis is adipose tissue (Ingle et al., 1971). Upon mobilization of adipose tissue, fatty acids leave the adipocytes and combine with albumin in plasma. These albumin bound long chain fatty acids are usually referred to as non-esterified fatty acids (NEFA) (Patterson, 1963). NEFA are a major transport form of lipids, which under conditions of fat mobilization, are transported to active tissues where they are oxidized to produce energy (Engle and White, 1960). Therefore fluctuations in the concentrations of NEFA in plasma may act as an index of fat mobilization (Fredrickson and Gordon, 1958; Fritz, 1961) in response to nutrient intake and production.

Ruminants in a negative energy balance have increased concentrations of NEFA in plasma as a result of fatty acid release from adipose tissue (Patterson, 1963; Bines and Hart, 1982). Concentrations of NEFA in the plasma of steers were elevated during a 5 month period of feed restriction (Blum et al., 1985). Similarly, a prolonged fast increased free fatty acid concentrations in steers (Blum et al., 1981; Rule et al., 1985). Richards et al. (1989b) restricted the nutrient intake of non-lactating cows, and BW and body energy reserves were depleted, resulting in a BCS of 3.5. As a result, nutritional anestrous occurred and was coincident with increased concentrations of NEFA and reduced concentrations of glucose, insulin and LH in serum. Endocrine changes may be responsible for increased rates of adipose tissue mobilization. Increased concentrations of NEFA and free fatty acids in fasted or feed restricted ruminants, were related to reduced plasma concentrations of insulin (Basset, 1968; Blum et al., 1985; Rule et al., 1985). The reduction in concentrations of insulin in blood could allow lipolysis due to the antilipolytic effect of insulin (Yang and Baldwin, 1973; Hu et al., 1988).

Garmendia (1986) infused postpartum anestrous beef cows with a 40% glucose solution for 12 d and found concentrations of NEFA in plasma were negatively correlated with concentrations of insulin in serum. In addition, glucose infusion decreased concentrations of NEFA in plasma, suggesting that fewer body fat reserves were mobilized when cows were supplied with additional energy. Concentrations of glucose in plasma are usually negatively correlated with concentrations of NEFA in the blood of ruminants (Annison, 1960; Reid et al., 1979). Radloff et al. (1966) found that concentrations of NEFA and glucose in blood were negatively correlated (-0.75).

During periods of increased nutrient requirements, elevated concentrations of NEFA in plasma indicate increased body fat mobilization to meet the increased energy requirements. Holmes and Lambourne (1970) observed that concentrations of NEFA in plasma varied inversely with the amount of energy intake. In dairy cows that produced larger quantities of milk, increased concentrations of NEFA indicate an energy deficiency (Baird, 1982). During early lactation the mobilization of adipose tissue reserves may be required to meet the increased nutrient requirements for lactation. Head et al. (1976) found the greatest concentrations of NEFA in plasma during the periods of maximum milk production in dairy cows.

Exogenous hormone treatments may alter the metabolism of cows, such that the utilization of fat as an energy yielding substrate is enhanced. The catecholamine, epinephrine, increases concentrations of NEFA in the plasma of ruminants (Radloff and Schultz, 1966; Blum et al., 1982; McCutcheon and Bauman, 1986) and increase lipolysis in bovine adipose tissue (Thorton et al., 1972; Yang and Baldwin, 1973; McNamara, 1988). Growth hormone (GH) elicits a lipolytic response in adipose tissue (Goodman and Grichling, 1983). Early work with ruminants indicated a dramatic increase in concentrations of plasma free fatty acids following administration of GH (Williams, 1963; Radloff and Shultz, 1966). This effect of GH and the importance of adipose tissue in maintaining energy homeostasis in ruminants may be dependent on the nutritional status of cows. Concentrations of NEFA in the plasma of lactating cows that are in a negative balance for energy and protein are elevated chronically by exogenous bovine GH treatment (Peel et al., 1981; Peel et al., 1983). However, treatment with bovine GH did not change concentrations of NEFA in the plasma of cows in a positive energy balance (Peel et al., 1982; McCutcheon and Bauman, 1986). These studies suggest that the two major metabolic activities of adipose tissue, lipogenesis and lipolysis, occur in response to endocrine and metabolic adaptations to alterations in energy intake and requirements.

Plasma hormones and reproductive function

Progesterone. Following parturition, concentrations of progesterone in plasma of cows are less than 1 ng/ml blood (Arije et al., 1974; Rawlings et al., 1980). Progesterone may be necessary for the re-establishment of normal estrus cycles following parturition (Ramirez-Godinez et al., 1982). Smith et al. (1987) suggests that progesterone may be required to organize endocrine events, which then require a gonadotropin to initiate ovarian cyclicity. A transient increase in the concentration of progesterone in the plasma of postpartum beef cows occurs about 4 days prior to the first postpartum estrus (Rawlings et al., 1980; Humphrey et al., 1983).

Following ovulation and the formation of a corpus luteum, concentrations of progesterone in plasma are greater than 1 ng/ml blood (Wettemann et al., 1972; Arije et al., 1974; Humphrey et al., 1983). Progesterone has a negative feedback effect on the frequency of pulsatile LH release in cattle (Ireland and Roche, 1982). Endogenous opioid peptides are thought to inhibit the release of LH (Malven, 1986). Progesterone may be a component in this endogenous opioid peptide inhibition (Brooks et al., 1986; Trout and Malven, 1987).

Estrogen. Concentrations of estrogen in serum of cows decrease following parturition and remain at minimal concentrations until just prior to the first postpartum estrus (Arije et al., 1974; Rawlings et al., 1980; Humphrey et al., 1983). During the postpartum period, concentrations of estradiol 17-β are between 5 and 7 pg/ml serum, followed by an increase approximately 2 d prior to estrus, reaching a maximum of 10 to 15 pg/ml serum at estrus (Corah et al., 1974; Humphrey et al., 1983). Estradiol influences LH release in cattle (Hobson and Hansel, 1972). Estradiol has a positive feedback effect on LH secretion (Beck and Convey, 1977) and this response to estradiol may change depending on the days postpartum (Garcia-Winder et al., 1988). Nolan et al. (1988) injected postpartum beef cows with 1 mg estradiol 17-β on d 19, 39 and 59 postpartum. An estradiol-induced LH release was evident only at 39 and 59 days. Similarly, Radford et al. (1978) found a suckling-mediated inhibition of an estradiol induced secretion of LH in beef cows during the early, but not late, postpartum period. Nancarrow et al. (1977) did not observe an estrogen-induced LH release during the early postpartum period in suckled beef cows. It would appear that the positive feedback response of LH to estradiol is reduced or nonexistent during the early postpartum period.

Luteinizing Hormone and Follicle Stimulating Hormone. Following parturition, concentrations of LH in the serum of suckled beef cows are minimal (Arije et al., 1974; Radford et al., 1978; Peters et al., 1981). As cows approach the first postpartum estrus, the frequency and amplitude of LH pulses increase (Rawlings et al., 1980; Humphrey et al., 1983). Secretion of GnRH from the hypothalamus of postpartum cows causes pulsatile release of LH. Pituitary LH content may be reduced following calving (Killen et al., 1989). Pituitary LH content was minimal from calving through day 15 postpartum (Moss et al., 1985; Nett et al., 1988). Pituitary content of LH in beef cows increased 6-fold from parturition to day 30 postpartum (Nett et al., 1988). During this same period concentrations of FSH in blood did not change. Concentrations of FSH in the blood of dairy cows from parturition to day 20 post partum were similar to concentrations on days 21 and 48 post partum (Dobson, 1978). Concentrations of FSH in the pituitary gland during the early postpartum period do not appear to limit the initiation of ovarian activity (Moss et al., 1985; Nett et al., 1988). Peck et al. (1988a) suggests that FSH secretion in the postpartum cow is not affected by the endogenous opioid peptides.

Endogenous Opioid Peptides. Endogenous opioid peptides act as neuro modulators in the central and peripheral nervous system to regulate hormone secretion. There are three families of opioid peptides: endorphins, enkephalins and dynorphins. These opiate-like peptides that are secreted by animal cells, are not able to induce activity on their own, but either stimulate or inhibit ongoing activity.

Pulsatile release of LH increases as time of first postpartum ovulation approaches in beef cows, reaching a maximum 2 to 3 weeks before the first ovulation (Rawlings et al., 1980; Humphrey et al., 1983). Endogenous opioid peptides (EOP) have been implicated as inhibitors of gonadotropin secretions in postpartum ewes and cows, and may play a role in the suckling-induced suppression of LH secretion (Whisnant et al., 1986a; Gregg et al., 1986; Cross et al., 1987). Gorden et al., (1987) observed a significant increase in concentrations of β-endorphin in hypothalamo-hypophyseal portal blood of ewes during 86% of suckling bouts. This supplies evidence of a link between suckling and an increase in EOP.

Treatment of suckled animals with the opioid receptor antagonist, naloxone, increases concentrations of LH in serum. This effect of naloxone on the postpartum opioid-mediated inhibition of LH release has been observed in rats (Bhanot and Wilkinson, 1983; Sirinathsinghji and Martini, 1984), lactating sows (Armstrong et al., 1986; Barb et al., 1986), fall-lambing lactating ewes (Gregg et al., 1986;

Leakakos et al., 1987) and suckled beef cows (Gregg et al., 1986; Whisnant et al., 1986b,c). Cross et al. (1987) found that both suckled and non-suckled cows (calf removed for 72 h) responded to naloxone (200 mg/hr for 8 h) at 24 days postpartum. Suckled and non-suckled cows had increased mean concentrations and pulse amplitude of LH. In addition, non-suckled cows had increased LH pulse frequency and decreased interpulse interval. Naloxone increased LH in 35-40 days postpartum suckled beef cows (Whisnant et al., 1986a), however following calf removal for 48 h, serum LH concentrations were already elevated and naloxone injection did not result in a further increase. Ewes lambing in the spring that nursed one or two lambs had increased LH release following naloxone administration (Malven and Hudgens, 1987). However, Knight et al. (1986) found that serum LH was not affected when suckled, spring-lambing ewes were injected with naloxone.

Morphine, an opioid agonist, has been used to investigate opioid modulation of gonadotropin secretion. In postpartum lactating sows, Armstrong et al. (1988) suppressed the secretion of LH associated with weaning and delayed estrus by activating EOP receptors with morphine. Peck et al. (1988a) suggested that morphine administration to postpartum weaned cows mimicked the suckling-activated EOP inhibition of LH secretion. Following morphine administration, both concentrations of LH in serum and the number of LH pulses were decreased. Because of the effects of the opioid receptor antagonist naloxone and the opioid receptor agonist morphine on secretion of LH, it appears that in postpartum cows and sows secretion of LH may be modulated in part by EOP.

Modulation of secretion of LH by endogenous opioid peptides may be dependent on gonadal steroids. In contrast to the effect of morphine on concentrations of LH in the serum of postpartum cows (Peck et al., 1988a), Peck et al. (1988b) found that in Angus steers, morphine had no significant effect on concentrations of LH in serum or frequency of LH pulses, while amplitude of LH pulses was decreased. This suggests that gonadal steroids may be necessary to mediate inhibition of LH secretion in cattle. Ovarian steroids, and progesterone in particular, appear to be essential in the naloxone-reversible inhibition of LH in ewes (Malven and Hudgens, 1987; Trout and Malven, 1987). In progesterone-treated ovariectomized ewes, Brooks et al. (1986) suggests that progesterone may have facilitated the opioid inhibition of LH which could be antagonized by naloxone. In postpartum beef cows treated with progesterone to produce concentrations of progesterone in plasma typical of those during the luteal phase of the estrous cycle, mean concentrations of LH, pulse amplitude and pulse frequency were suppressed and could not be overcome by naloxone (Cross et al., 1987). Exogenous estradiol-17β (E_2) treatment of ewes resulted in varied effects with respect to naloxone sensitivity. In ovariectomized ewes (Brooks et al., 1986) naloxone treatment failed to stimulate LH release and in postpartum lactating ewes (Leakakos et al., 1987) the naloxone-induced increase in serum LH was reduced. Trout and Malven (1987) observed that E_2 either enhanced or had no effect on the sensitivity of a naloxone-reversible inhibition of LH release in ewes.

Endogenous opioid peptides may act as an endogenous stimulator of prolactin release in many species. Concentrations of prolactin in serum decreased following naloxone administration in suckled female rats (Sirinathsinghji and Martin, 1984), postpartum ewes (Gregg et al., 1986; Malven and Hudgens, 1987) and lactating sows (Armstrong et al., 1988). In addition, Knight et al. (1986) found that naloxone blocked the suckling-induced increase in serum prolactin in ewes. In contrast to the effect of EOP on secretion of LH, modulation of prolactin may act independent of gonadal steroids. Following morphine administration in steers (Peck et al., 1988b) and postpartum cows (Peck et al., 1988a) prolactin secretion increased.

The involvement of EOP on the regulation of FSH has not been investigated to the extent that LH or prolactin have been studied. However, most studies would suggest that EOP do not influence secretion of FSH. In both suckled and non-suckled postpartum beef cows, naloxone infusions had no effect on FSH secretion (Cross et al., 1987; Wood et al., 1987). Treatment of suckled postpartum anestrous beef cows with morphine, an opioid agonist, had no effect on concentrations of FSH in serum (Peck et al., 1988a). Gindoff and Ferin (1987) found that EOP may modulate a CRF suppression of pulsatile FSH secretion in monkeys.

Opioid peptides may act at the hypothalamus and/or anterior pituitary to modulate gonadotropin secretion. Peck et al. (1988a) injected 5 µg GnRH into postpartum beef cows that were concurrently infused with either morphine or saline. Morphine-infused cows had a reduced LH response to GnRH injection, suggesting a direct effect of morphine on release of LH. Bovine anterior pituitary tissue contains opiate receptors (Simantov and Snyder, 1977; Gerstberger and Barden, 1986). In addition, Chao et al. (1986) reports a direct effect of EOP and naloxone on in vitro release of LH by bovine anterior pituitary cells. However, most evidence suggests that the hypothalamus rather than the pituitary is the site of action for opioid peptides and naloxone. Binding sites for [^{3}H] naloxone have been detected in the hypothalamic tissue of ewes (Trout et al., 1987) and suckled beef cows (Trout and Malven, 1988). Cross et al. (1987) suggested that the suckling stimulus inhibits LH release via an opioid mechanism which appears to function at the hypothalamic level in postpartum beef cows. Malven et al. (1986) found that early weaning in beef cows resulted in β-endorphin concentrations in the preoptic area and the hypothalamus, that were negatively associated with concentrations of LHRH in the stalk-median eminence. In conclusion, the hypothalamus appears to be the primary site of endogenous opioid peptide inhibition, which may influence the release of GnRH (Gregg et al., 1986).

Repeatability of Selection for Calf Growth and Reproductive Performance

Profitability of the cow-calf producer depends upon the efficiency of the cow herd to convert feed into pounds of calf. Cows which are most efficient in this conversion, maximize returns over production costs. To achieve maximum genetic progress within the beef herd, it is essential to accurately identify the production potential of cows early in life. Major emphasis should be placed on the evaluation of, and selection for, production traits which increase profitability. Such traits include age at puberty, calving ease, birth weight, preweaning growth, milk production, weaning weight and a short interval to estrus and conception following parturition. It would be advantageous to predict the lifetime efficiency of production of beef cows by evaluating their performance during the first parity.

Hickman and Henderson (1955) studied the relationship between first lactation performance and lifetime production of dairy cows. They concluded that selection based upon first lactation production could possibly favor increased lifetime production. White and Nichols (1965) found a positive correlation between first lactation production and later performance, concluding that higher milk producing heifers should continue to produce well throughout life. The genetic correlation between first lactation milk yield and lifetime production has been estimated at .85 (Hargrove et al., 1969), .34 (Norman and Van Vleck, 1972) and .56 (Hogue and Hodges, 1980). The correlation of heifer milk yield with last lactation milk yield was .83 (Hogue and Hodges, 1980). These large correlations between first lactation production and lifetime performance, indicate the importance of selecting dairy cattle for production yield early in life.

In beef cattle, preweaning calf growth is influenced by the calf's genotype for growth and the cow's genotype for maternal ability (Hohenboken and Brinks, 1971). In addition to genetic factors, the environment influences the care and nourishment provided by the dam during gestation and lactation (Koch, 1972). Cantet et al. (1988) studied the influence of maternal effects on the birth weight (BW) and weaning weight (WW) of Hereford calves. The basis for maternal effects on calf BW was mostly genetic, while the maternal effects for WW were found to be of genetic and environmental origin. Estimates of repeatability for BW and WW were .21 ± .03 and .30 ± .03 respectively. Repeatability estimates from seven lines of Hereford cattle were 0.27 ± .02 for BW and 0.44 ± .02 for 180-day weight (Kress and Burfening, 1972). Similarly, Hohenboken and Brinks (1971) found estimates of repeatability for WW in linecross

Hereford calves to be 0.33 ± .03 and 0.40 ± .03 for inbred Hereford calves.

Year to year variation in environmental conditions, food supply, sire selection and management ability may warrant the inclusion of second and possibly third parity data into the evaluation of a beef cow's lifetime production efficiency. Davis et al. (1987) predicted the life cycle efficiency of a cow's production. They determined that multiple regression equations based on first parity dam and calf traits were not of sufficient accuracy ($R^2<.30$) to be used in the prediction of life cycle efficiency. However by including second and third parity data, life cycle efficiency was predicted with improved accuracy ($R^2\geq.30$). When comparing the genetic correlations between lifetime milk yield and the milk yield of the first through third lactations, Taneja et al. (1982) found that the third lactation had the highest correlation (.83). In addition heritability estimates for milk production during the first, second and third lactations were 0.22, 0.33 and 0.49 respectively.

Birth Weight and Calving Ease

Birth weight and calving ease are important components that influence economic returns from a beef cow herd. BW of the calf influences calving difficulty (Rice and Wiltbank, 1972). Dystocia adversely affects reproductive efficiency of cows by increasing the number of days from calving to conception (Mangurkar et al., 1984) and results in greater death loss of calves (Laster et al., 1973a; Patterson, 1987). Cue and Hayes (1985) estimated the genetic correlation between calving ease and calf survival at -.82 for heifers and -.81 for mature cows, indicating that any improvement in calving ease will result in improved calf survival. Therefore, cattlemen must emphasize calving ease and carefully select replacement heifers, based on performance during the first parturition.

Younger cows experience calving difficulties more often than older cows (Mangurkar et al., 1984). Burfening (1988) observed a decrease in the percentage of assisted births as age of dam increased, (21 mo to 33 mo of age). Ahunu and Makarechian (1986) found a significant increase in BW of Hereford calves as age of dam increased. Heifers which experience calving difficulty during their first parity may continue to have difficult births in subsequent pregnancies. Genetic correlations for calving ease between first-calf heifer births and later parities have been estimated by Thompson et al. (1981) and Cue and Hayes (1985) at .84 and .995 respectively. These large genetic correlations between dystocia in the first parity with subsequent parities suggests a major influence of the same genes affecting dystocia in all parities (Thompson et al., 1981).

Preweaning Growth and Weaning Weight

Preweaning growth and weaning weight are performance traits which reflect both the growing ability of the calf and the environment created for the calf by the dam. A significant portion of the environment relates to the dam's milk producing ability. Milk yield of the dam influences calf production, accounting for 60% of the variance in 205-day WW (Rutledge et al., 1971). Koch (1972) summarized the correlations between total milk production of the dam and gain from birth to weaning of the calf, and found that they were from 0.50 to 0.80. This illustrates the importance of milk production in beef cows. Butson et al. (1980) found that a 1 kg increase in average daily milk yield was associated with a 7.7 kg increase in WW. In addition, 6-10% of the variance in WW was explained by milk yield variables, independent of cow age and breed, and age and sex of the calf.

Non-genetic sources of variation which influence preweaning growth and WW include the sex of calf, age of dam and year of birth (Singh et al., 1970; Baker et al., 1974; Pell and Thayne, 1978; Butson et al., 1980; Ahunu and Makarechian, 1986). Bull calves have greater BW, attain greater preweaning average daily gains and weigh more at weaning than heifer calves. Singh et al. (1970) found that Hereford bull calves were 2.35 kg heavier at birth, gained 0.047 kg more per day preweaning and were 10.66 kg heavier at weaning than heifer calves. Age of dam correction factors for WW are available (Cardellino and Frahm, 1971). Pell and Thayne (1978) found that WW of Hereford calves increased 23 kg as age of dam increased from 23 to 95 months. Butson et al. (1980) found that age of dam accounted for 48% of the variance in WW (P<.01). Ahunu and Makarechian (1986) found WW increased with increasing age of Hereford cows from 2 to 4 years, reaching a maximum in 5-year-old dams.

Reproductive Efficiency

A critical requirement for successful beef cattle production is good reproductive efficiency. Davis et al. (1985) indicated that lifetime cow efficiency is improved by breeding at puberty. Chapman et al. (1978) found that developing Hereford heifers to calve at 2 years of age improved their lifetime production. Cows calving first at 2 years of age could wean an additional calf in a lifetime compared to cows calving at 3 years of age. However, proper heifer development is required and management ability may be a limiting factor. Turman et al. (1963) evaluated the lifetime (14 year) reproductive performance of Hereford cows. Calving first at 2 years of age had no adverse effect on reproductive performance. The average calf crop born was 95.9% for 2-year-old cows and 95.5% for 3-year-old cows. In addition, the average calf crop weaned was 92.8% and 91.2% for 2- and 3-year-old cows respectfully. Goodrich (1985) compared the incidence of dystocia and reproductive performance of replacement heifers calving at 24 or 30 months of age. Conception rates at the initial breeding season were similar (95% and 100% for 24 month and 30 month respectively), however more of the heifers calving at 24 months experienced dystocia. Conception rate and the postpartum interval to conception were not different between groups at the second breeding.

Heifers calving at 24 months of age require expert attention at parturition and knowledgeable response to calving difficulty. Laster et al. (1973b) found that the incidence of dystocia was 36% greater in 2-year-old cows than in 3-year-old cows. Calving difficulty adversely affects reproductive efficiency by increasing days from calving to first service and conception (Mangurkar et al., 1984). Bellows et al. (1982) compared primiparous heifers and multiparous cows for incidence of dystocia and postpartum reproductive performance. Dystocia was more severe in heifers than cows, heifers had longer postpartum intervals to first estrus and a reduced percentage in estrus by the beginning of the breeding season. Meacham and Notter (1987) found that Simmental cows which experienced calving difficulty at first calvings were less likely to calve as 3-year-olds. In addition, cows which required an easy pull of the calf, a hard pull, or required cesarian section, had 4.9, 6.5 and 19.6 d longer intervals, respectively, to the birth of the next calf.

A definitive scale for measuring reproductive efficiency has not been established. Reproductive efficiency has been defined as percentage calves born of the number of beef cows in the breeding herd (Azzam and Nielsen, 1987). Calving interval is used to measure reproductive performance of dairy herds (Slama et al., 1976). Bourdon and Brinks (1983) suggested that when using a fixed breeding season, calving date is the reproductive measure of choice. For the producer, these reproductive measurements may be useful. The postpartum interval to conception, first estrus or ovarian luteal activity (OLA) have been measured. However, the interval to OLA would allow the most accurate measurement of reproductive function as it removes the opportunity for missed estrus by the bull or AI technician and failure to conceive. Concentrations of progesterone in plasma greater than 1 ng/ml blood are associated with the presence of a functional corpus luteum (Wettemann et al., 1972; Humphrey et al., 1983). Therefore, analysis of weekly blood samples for concentrations of progesterone during the postpartum period can define the postpartum interval to OLA.

Selection for a decrease in the postpartum interval to OLA could improve the efficiency of beef cattle production through subsequent calving earlier in the season which would allow a longer period between calving and the beginning of the breeding season and result in older, heavier calves at weaning. Azzam and Nielsen (1987) estimated the heritability of various reproductive traits using 12 years of records from cows of various beef breeds. The postpartum interval to first estrus was lowly heritable, for parity 1, parity 2 and the last parity (.05, .10 and -.03, respectively) of cows studied. In addition, measures of reproductive efficiency have very small genetic variance and heritability estimates near zero (Foote, 1970; Milagres et al., 1979).

CHAPTER III

RELATIONSHIPS AMONG METABOLIC FACTORS, COW REPRODUCTIVE PERFORMANCE, MILK PRODUCTION AND CALF GROWTH

Abstract

Twenty Hereford and Hereford X Angus cows were selected during their first lactation based on the average daily gain (ADG) of their calves and the interval from calving to the onset of luteal activity (LA). Cows were assigned to either an Above group (A) which had performance greater than the average of herdmates (n=10) for LA and ADG, or a Below group (B) which had performance less than the average of herdmates (n=10). During the first lactation, plasma samples were collected weekly for nine weeks from each cow during the breeding season and progesterone, glucose, insulin, and non-esterified fatty acids (NEFA) were quantified. Average daily gain of the calves and 205-day weaning weight (WW) were determined. The intervals from calving to conception (CC) and to the onset of luteal activity were measured. Estimates of cow 24-h milk production were determined at approximately 44 d, 88 d, and 124 d postpartum during the second or third lactation and glucose, insulin and NEFA were quantified in plasma samples collected weekly, prior to, during and following the 44 d milk production. Calves from the A cows had heavier weaning weights during lactations 1 and 2 (P<.01) and greater average daily gain (P<.06) during lactation 1 than B cows. Cows in the A group had shorter intervals from calving to conception (P<.02) and the onset of LA (P<.01) during the first lactation than B cows. During the third lactation, B cows had a shorter interval to conception (P<.01) than A cows. Cow group did not influence concentrations of glucose, insulin or NEFA in plasma during the first or subsequent lactation. We conclude that concentrations of glucose, insulin and NEFA in weekly plasma samples were not related to rebreeding or calf performance in first lactation cows. Rebreeding performance during the first lactation was not repeatable.

(Key Words: Beef Cow, Glucose, Insulin, Milk Production,
NEFA, Weaning Weight)

Introduction

The postpartum interval to the onset of luteal activity influences both the ability of cows to maintain a 365-d calving interval and the age and weight of the calves at weaning (Dunn and Kaltenbach, 1980). The weight of the calf at weaning is influenced by age of the calf and the maternal environment (Koch, 1972). A significant portion of this environment is the amount of milk produced by the cow (Neville, 1962; Rutledge et al., 1971; Wyatt et al., 1977; Clutter and Nielsen, 1987). The influence of milk production on weaning weight is a function of both the milk production potential of the cow and the ability of the calf to utilize the nutrition received through milk (Davis et al., 1985).

The ability of beef cows to partition nutrients to meet the requirements for reproduction and lactation is a critical function, and probably involves insulin and the plasma metabolites glucose and NEFA. Glucose is an important source of energy for the central nervous system (Brockman and Laarveld, 1986) and may regulate reproductive function by influencing the secretion of hormones. The uptake of nutrients for the synthesis of adipose tissue is decreased and body fat reserves are mobilized during lactation (Bauman and Currie, 1980). The negative energy balance is associated with increased concentrations of NEFA's in plasma (Patterson, 1963; Bines and Hart, 1982). Insulin depresses the concentration of glucose in plasma by inhibiting gluconeogenesis and glycogenolysis and stimulating the uptake of glucose by muscle (Hay et al., 1984) and adipose tissue (Vernon et al., 1985). Significant differences in the concentrations of insulin, glucose and NEFA in the plasma of high- and low- yielding dairy cows indicate that regulation of nutrient utilization may be related to production capabilities of cows (Hart et al., 1978).

Genetic differences in the ability of cows to partition nutrients to support reproductive function and milk synthesis may exist (Bauman and Currie, 1980). The objectives of this study were to 1) evaluate the relationship between concentrations of glucose, insulin and NEFA in plasma with rebreeding performance, milk production and growth of the calf and 2) to determine the repeatability of cow rebreeding performance and calf growth, during the first through third parities.

Material and Methods

Hereford and Hereford X Angus cows (n=42) were ranked according to average daily gain (ADG) of their calves and the interval from calving to the onset of luteal activity (LA) during their first lactation. Twenty pregnant cows were selected and assigned to either an Above group (A) which had performance greater than the average of herdmates (n=10) for ADG and LA, or a Below group (B) which had performance less than the average of herdmates (n=10). The study was initiated with one-half of the cows on each treatment in 1985 and the other half in 1986.

During the first lactation, blood samples (20 ml) were collected weekly by puncture of the tail vein for nine weeks during the breeding season (May 1-June 27). Cows were removed from feed and water for approximately 16-h prior to blood sampling. Blood samples (20 ml) were collected in tubes containing 32 mg of oxalic acid and cooled immediately to 5 C. Then samples were centrifuged (3200 x g for 20 min) and plasma was decanted and stored at -20C until quantified for glucose, insulin, non-esterified fatty acids (NEFA) and progesterone.

Biweekly weights and body condition scores (Wagner et al., 1988) were obtained for cows during the last trimester of pregnancy through the breeding season. During lactation one body weight and body condition score of cows in the Above group at 1 wk, 6 wk and 12 wk following parturition were (326 ± 4.9 kg, 4.9 ± 1.4), (343 ± 6.1 kg, 5.0 ± .13) and (363 ± 9.1 kg, 5.25 ± .11) respectively. Body weight and body condition score of cows in the Below group at 1 wk, 6 wk and 12 wk following parturition were (312 ± 6.8 kg, 4.4 ± .14), (325 ± 6.9 kg, 5.0 ± .07) and (369 ± 8.4 kg, 5.3 ± .11) respectively. Cows were maintained on native range and Bermuda grass pastures as a single herd. During pregnancy, cows were fed a 40% crude protein supplement so that they calved with an average body condition score (BCS; Wagner et al., 1988) of 5. Cows calved between the second week in February and the first week in May each year. Cows were supplied with hay during periods of extremely cold weather and when native pasture was covered with ice or snow. During the second and third lactations, weekly plasma samples were collected following parturition until approximately 80 d postpartum and progesterone was quantified.

Weight of the calves at weaning was adjusted to 205 d using the equation:

$$\frac{\text{Weaning weight - Birth weight}}{\text{Age}} \text{ X } 205 + \text{Birth weight}$$

Weaning weights of heifer calves were adjusted to a steer equivalent: Heifer weight X 1.07 = Steer equivalent weight.

Estimates of 24-h milk production were determined using the weigh-suckle-weigh technique at 8-h intervals during the second and third lactations (Totusek et al., 1973). Milk production was determined for each cow at 44.2 ± 2.6 d of lactation. In addition, milk production of all cows was determined on June 20, 1987 and July 30, 1987 when cows averaged 88 ± 25 and 124 ± 25 d respectively post partum. Plasma samples were obtained from each cow the week before, the week of, and the week following the 44 d milk production trial and concentrations of glucose, insulin, and NEFA were quantified. Cows and calves were gathered from their pastures and brought into a working area at approximately 0700 h and cows and calves were separated. Cows had access to feed and water and calves did not. At approximately 1500 h, calves were allowed to nurse. This initial nursing was used to standardize the time of suckling of all cows to begin measuring milk production. At approximately 2300 h, each calf was weighed, then paired with its dam. After suckling, each calf was weighed and separated from its dam until 0700 and 1500 h when the process was repeated. Calf weights were taken on an electronic digital scale which weighed to the nearest 0.5 kg. The difference in calf weight before and after suckling for each of the three 8-h weigh-suckle-weigh trials were summed to estimated the 24-h milk production of the cow.

Concentrations of progesterone in plasma were determined by radioimmunoassay (Lusby et al., 1981). The onset of luteal activity was estimated to occur when concentrations of progesterone in plasma were greater than or equal to 1 ng/ml for 2 consecutive weeks, followed by concentrations typical of normal estrous cycles or pregnancy. Conception dates were estimated from the subsequent calving date minus 280 d. Pregnancy was determined by rectal palpation at least 60 d after breeding.

Concentrations of glucose in plasma samples were quantified by an enzymatic, colormetric procedure (Sigma Chemical Co., Kit No. 510, St. Louis, MO). Concentrations of insulin in plasma samples were quantified by radioimmunoassay as described by Selk (1986). Antiserum (guinea pig anti-bovine insulin, lot GP 23; Miles-Yeda, Ltd. Research Products, Elkhart, Indiana) to bovine insulin was used at a dilution of 1:40,000. Sheep anti-guinea pig serum was used as the second antibody at a dilution of 1:20. Concentrations of NEFA in plasma samples were quantified using a colormetric procedure (Patterson, 1963).

Least squares analyses of variance were used to evaluate reproductive characteristics, calf performance, milk production and concentrations of plasma constituents. The experimental design was a split plot. For the weekly plasma samples, the main units Group, Year and the interaction were tested using cow (Group X Year) as the error term. Week was considered the subplot.

Analyses of calf performance, milk production and reproductive characteristics within a year had Group as the main plot, and cow (Group) was the error term. Day of lactation was considered the subplot. In statistical models for milk production, calving date was used as a covariate. Pooled within group and lactation, partial correlation coefficients were calculated to determine the association between plasma constituents, milk production, calf performance and reproductive characteristics.

Results and Discussion

Least-square means for rebreeding performance and calf growth of Above and Below cows are summarized in Table I. During the first lactation, cows in the Above group had shorter postpartum intervals to the onset of luteal activity (LA) ($P<.007$) and shorter intervals from calving to conception (CC; $P<.02$), averaging 17.6 ± 4.3 d and 22.5 ± 6.4 d fewer days, respectively, than cows in the Below group. Calves in the Above group had greater ADG ($P<.06$; 0.14 ± .05 kg) and greater WW (29.5 ± 5.3 kg, $P<.004$), respectively than calves in the Below group.

TABLE I

LEAST-SQUARES MEANS (±SE) FOR REBREEDING PERFORMANCE AND CALF GROWTH DURING THE FIRST LACTATION

	Group	
Trait	Above	Below
Weaning Weight, kg***	182.2 ± 5.3	152.7 ± 5.3
Average Daily Gain, kg*	0.70 ± .05	0.56 ± .05
Onset Luteal Activity, d***	89.5 ± 4.3	107.1 ± 4.3
Calving to Conception, d**	91.2 ± 6.4	113.7 ± 6.4

*P<.1, **P<.05, ***P<.01.

Concentrations of blood constituents in weekly plasma samples collected during the breeding season of the first lactation (May 1 - June 27) are summarized in Table II. Average concentrations of glucose in plasma during the sampling period were similar for cows in Above and Below groups and averaged 61.7 ± 1.4 mg% and 63.1 ± 4.1 mg%, respectively. During the breeding season, concentrations of glucose in plasma of cows in both groups decreased ($P<.001$) over the 9-week period and averaged between 58 and 66 mg% (Figure 1).

Concentrations of insulin in plasma during the sampling period were similar for cows in Above and Below groups and averaged 0.33 ± .02 ng/ml and 0.34 ± .02 ng/ml respectively. Week did not significantly influence concentrations of insulin in plasma samples during the breeding season of the first lactation (Figure 2). A group X year interaction ($P<.01$) for weeks 2, 7 and 8 was detected. The reason for this difference between years is not clear but may be related to the amount of nutrients available to the cows during those years. Insulin is a primary regulator of plasma glucose concentrations in ruminants (Brockman, 1978), Since concentrations of glucose and insulin in the plasma of Above and Below cows were similar during the breeding season, this suggests that the glucoregulatory effects of insulin were similar for both groups.

Average concentrations of NEFA in plasma during the breeding season were similar for cows in Above and Below

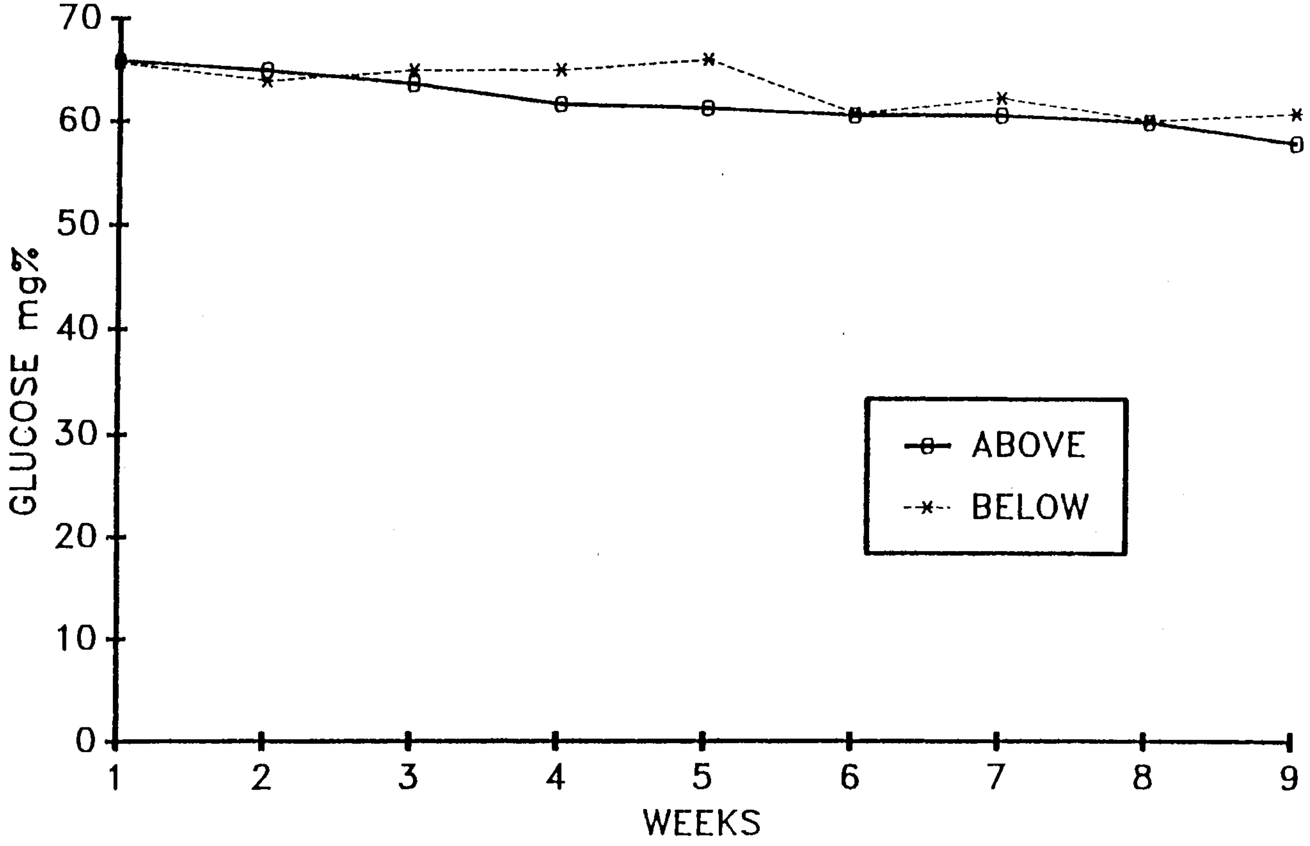

FIGURE 1. CONCENTRATIONS OF GLUCOSE (SE ± 1.34) IN PLASMA OF BEEF COWS DURING THE BREEDING SEASON OF LACTATION ONE

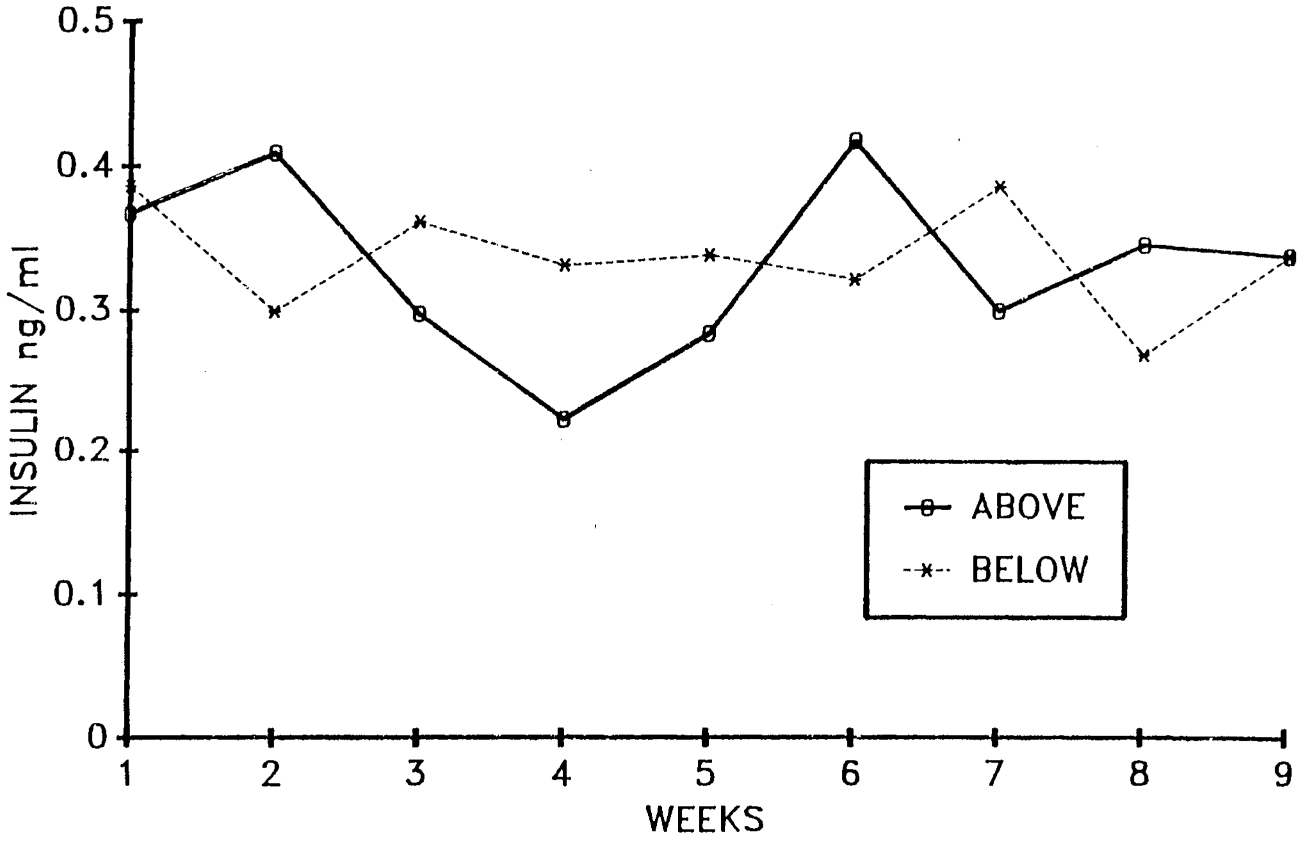

FIGURE 2. CONCENTRATIONS OF INSULIN (SE ± .04) IN PLASMA OF BEEF COWS DURING THE BREEDING SEASON OF LACTATION ONE

groups (Table II). There was not a group x week interaction (P>.10). However, cows in the Above group had greater (P<.01) concentrations of NEFA in plasma during week 2, and average concentrations of NEFA tended to be greater for weeks 3 and 4 (Figure 3). Bauman and Currie (1980) indicated that the adipocyte has two major functions, synthesis of lipids and the mobilization of lipids. The increase in concentrations of NEFA during weeks 1-5 of the breeding season, indicates a decrease in the uptake of nutrients for synthesis of lipids and a mobilization of lipid reserves to accommodate the nutrient demands of lactation and rebreeding. Metz and van den Bergh (1977) suggested that during early lactation, the increase in energy from NEFA is the result of enhanced lipolysis and reduced re-esterification in adipose tissue to accommodate the increased demand for energy. The pattern for concentrations of NEFA in plasma during lactation of Above and Below cows is similar to that reported by Blum et al. (1983). They found that plasma concentrations of NEFA were greatest in dairy cows during early lactation, then decreased until about 60 days postpartum. Concentrations of NEFA in plasma of cows in the Above group were consistently greater (P>.10) during the first 5 weeks of the breeding season (Figure 3). Hart et al. (1978) observed significantly greater concentrations of NEFA in the circulation of high-yielding vs. low-yielding dairy cows. Milk yield of the dam influences calf production, accounting

TABLE II

LEAST-SQUARES MEANS (±SE) FOR CONCENTRATIONS OF PLASMA CONSTITUENTS[a] DURING THE BREEDING SEASON OF THE FIRST LACTATION

	Group	
Constituent	Above	Below
NEFA μeq/l	1337 ± 60	1249 ± 60
Glucose mg%	61.7 ± 1.4	63.1 ± 1.4
Insulin ng/ml	0.33 ± 0.02	0.34 ± 0.02

[a] Average of 9-weekly samples.

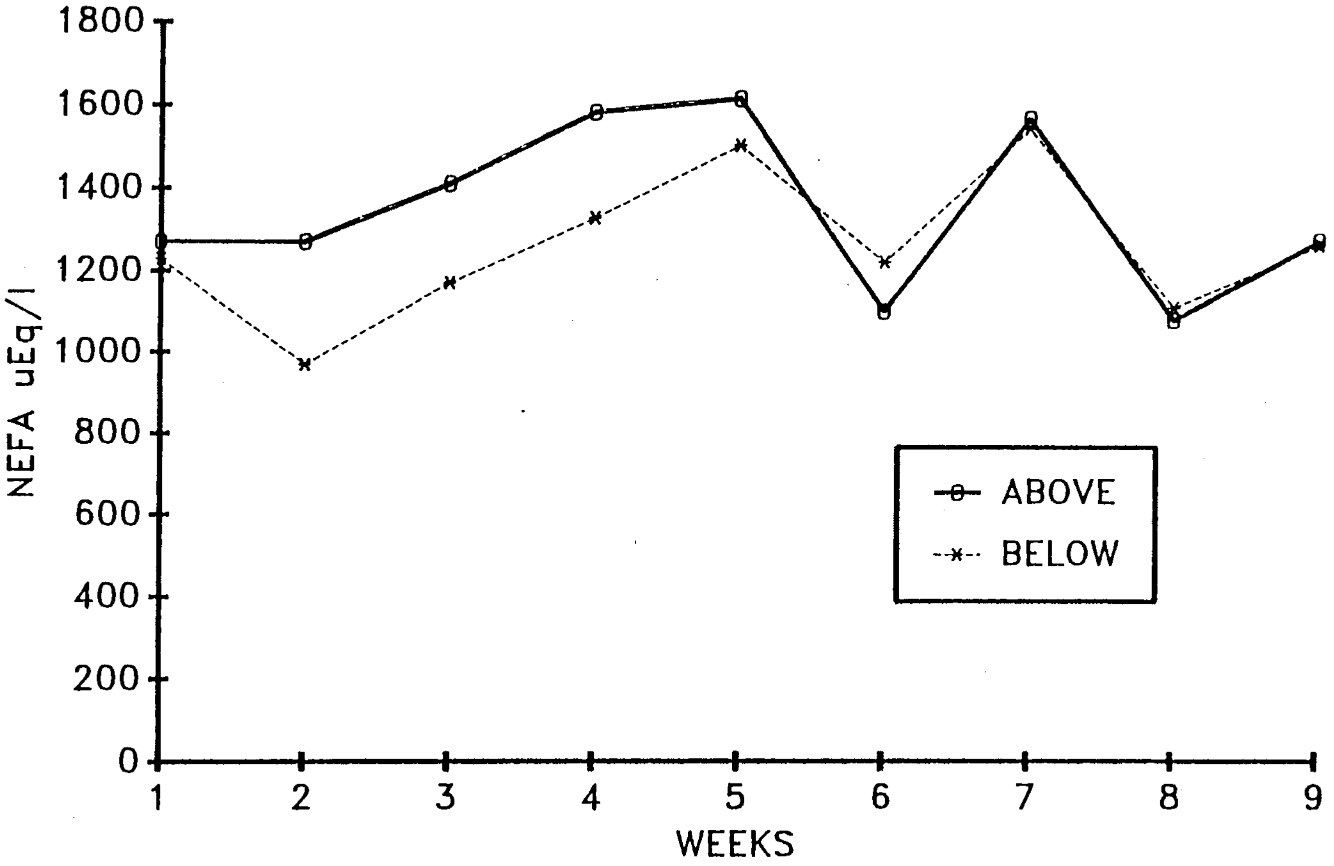

FIGURE 3. CONCENTRATIONS OF NEFA (SE ± 109.6) IN PLASMA OF BEEF COWS DURING THE BREEDING SEASON OF LACTATION ONE

for 60% of the variance in 205-day WW (Rutledge et al., 1971). Cows in the Above group weaned heavier calves. The greater weaning weights of calves in the Above group may indicate an improved ability of their dams to preferentially direct energy towards milk production.

Estimates of 24-h milk production for Above and Below cows at 44, 88 and 124 days postpartum are in Table III. The 44 d evaluation of milk production was conducted as each cow reached approximately 44 d postpartum (44.2 ± 2.6 d). Therefore, at the first evaluation of milk production the number of days postpartum was similar for all cows while environmental conditions varied. Estimates of 24-h milk production were not different (P>.10) for cows in the Above and Below groups at 44 d postpartum. The 44 d milk production trials were conducted during a 87 d period (3-30 to 6-25) and seasonal differences such as growing conditions of native range and ambient temperature varied. Milk production trials conducted on 6-25-88 and 7-30-88 represent averages of 88 ± 25.9 and 124 ± 25.9 d postpartum for all cows on the trials. Environmental conditions were similar for all cows on days 88 and 124, while days postpartum differed among cows from 1 to 71 days. Milk production estimates at these times represent measurements taken at various points in the cows lactation curves. Therefore calving date was entered as a covariate in the analysis. Estimates of 24-h milk production were not different (P>.10) for A and B cows at 88 and 124 d post partum (Table III).

TABLE III

LEAST-SQUARES MEANS (±SE) FOR 24-h MILK PRODUCTION (KG)

Group	Days Postpartum		
	44	88	124
Above	7.37 ± .55	6.42 ± .68	5.54 ± .77
Below	5.60 ± .75	4.59 ± .92	5.23 ± 1.05

Although not statistically different, cows in the Above group had consistently greater milk production during early lactation (Figure 4). This level of milk production by cows in the Above group may have contributed to heavier weaning weights of their calves, (224.0 ± 4.8 kg vs. 199.1 ± 6.5 kg for calves in the Below group). Studies suggest that by 9 weeks postpartum (Bartle et al., 1984) the average milk production of a beef cow would only meet the maintenance requirements of her calf. Similarly Boggs et al. (1980) reported that up to 8 weeks postpartum, dry feed intake had little effect on calf ADG. Therefore, the 44 d milk production evaluation was conducted during the period when a calf's primary source of nutrients was the dam's milk. Butson et al. (1980) studied factors influencing weaning weights of range beef calves and found a 1 kg increase in average daily milk yield was associated with a 7.7 kg increase in weaning weight. Boggs et al. (1980) found that each additional kilogram of daily milk yield by Hereford cows added .34 kg/day of ADG of their calves. The pooled, within group and lactation partial correlation coefficients (Table IV) between 44 d milk production and WW and ADG were .48 ($P<.09$) and 46 ($P<.1$) respectively. Clutter and Nielsen (1987) found the correlation between calf gain to 205 d and milk yield intake was .60 ($P<.01$). These results emphasize the substantial influence of a cow's milk production on calf growth and suggest important differences in maternal ability can be measured as milk production.

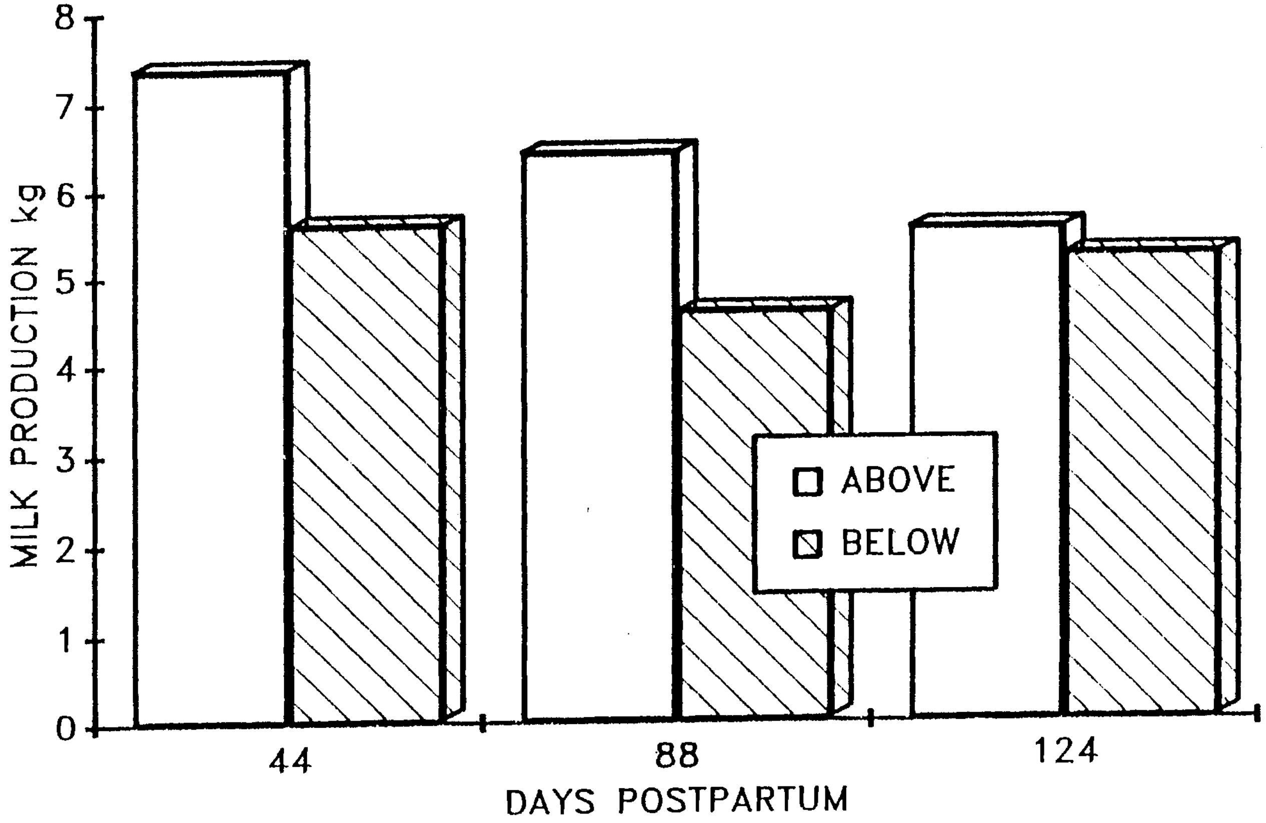

FIGURE 4. ESTIMATES OF 24-h MILK PRODUCTION FOR ABOVE AND BELOW COWS

TABLE IV

RELATIONSHIP BETWEEN PLASMA CONSTITUENTS[a] IN COWS AND CALF GROWTH WITH MILK PRODUCTION[b]

Item	Milk Production[c]
Glucose	.23
Insulin	.11
NEFA	-.28
205-d Weaning Weight	.48 (P<.09)
ADG	.46 (P<.1)

[a] Average of 3-weekly samples.
[b] 44 d postpartum milk production.
[c] Pooled within group and lactation.

Concentrations of plasma constituents were averaged within cow in samples collected the week prior to, during, and following the 44 d milk production trial and are given in Table V. Hart et al. (1975) indicated that peak milk yield of Hereford-cross cows occurred near the sixth week of lactation. Clutter and Nielsen (1987) found that maximum daily milk production for Hereford X Angus cows at day 50 of lactation was 7.04 kg. The cows in the Above group had a similar 24-h milk yield of 7.37 kg at d 44 ± 2.6 of lactation.

Concentrations of glucose in plasma were similar for cows in Above (60.7 ± 1.6 mg%) and Below (62.3 ± 2.1 mg%) groups. Smith et al. (1976) and Jenny et al. (1974) found that concentrations of glucose in plasma of postpartum dairy cows were negatively related to milk production. Although no significant differences were found between Above and Below groups, we can observe that an improvement in milk production was associated with less (P>.10) glucose in the plasma of cows in the Above group. Blum et al. (1983) found significantly reduced concentrations of glucose in the cows with the greatest milk yield. In addition, Herbein et al. (1985) found that cows with above average milk production throughout lactation had reduced glucose concentrations in plasma.

Concentrations of insulin in plasma were similar for cows in Above (0.53 ± 0.09 ng/ml) and Below (0.61 ± 0.21) groups. Concentrations of insulin in plasma are usually

TABLE V

LEAST-SQUARES MEANS (±SE) FOR CONCENTRATION OF PLASMA CONSTITUENTS[a] OF THE 44 D MILK PRODUCTION TRIAL

	Group	
Constituent	Above	Below
NEFA μeq/l	417 ± 150	314 ± 203
Glucose mg%	60.7 ± 1.6	62.3 ± 2.1
Insulin ng/ml	0.53 ± 0.09	0.61 ± 0.21

[a] Average of 3-weekly samples.

inversely related to milk production (Bines and Hart, 1982). Herbein et al. (1985) found that above average milk production was associated with significantly reduced concentrations of insulin in plasma of lactating dairy cows. Etherton and Evock (1986) determined that insulin stimulated lipogenesis in bovine adipose tissue and may oppose the partitioning of energy into milk during lactation (Kennedy et al., 1987). Therefore decreased insulin may allow increased mobilization of lipid from adipose tissue to provide energy substrates for milk production. Hart et al. (1978) compared the mean concentrations of insulin and NEFA in the plasma of high- and low-yielding dairy and beef cows during lactation. The concentrations of insulin were significantly greater in the low-yielding group while the concentrations of NEFA were significantly less compared with high-yielding. Reduced concentrations of insulin in plasma may also reduce the opportunity for insulin to antagonize the utilization of glucose for milk production.

Least-squares means for rebreeding performance and calf growth of Above and Below groups during the second parity are summarized in Table VI. During the second lactation, all cows conceived in the Above and Below groups and had similar postpartum intervals to luteal activity and conception. Weaning weights of calves in the Above group were heavier ($P<.01$) than WW of calves in the Below group, however ADG of calves were similar for both groups.

TABLE VI

LEAST-SQUARES MEANS (±SE) FOR REBREEDING PERFORMANCE AND CALF GROWTH DURING THE SECOND PARITY

	Group	
Trait	Above	Below
Weaning Weight, kg***	216.6 ± 5.3	189.3 ± 6.7
Average Daily Gain, kg	1.02 ± .05	0.92 ± .06
Onset Luteal Activity, d	66.2 ± 7.0	57.5 ± 8.2
Calving To Conception, d	89.9 ± 7.9	104.0 ± 10.7

***P<.01.

Least-squares means for rebreeding performance and calf growth of Above and Below groups during the third parity are summarized in Table VII. Pregnancy rate was 80% for both the Above and Below cows. Cows in the Below group had shorter intervals from calving to conception ($P<.01$), however, the postpartum interval to luteal activity was similar for both groups. No differences were detected between Above and Below groups for calf ADG and weaning weights of the calves.

The production potential of cows must be accurately identified early in life to achieve maximum genetic progress. By evaluating first parity performance to predict the lifetime efficiency of production, beef producers have the opportunity to improve traits which increase productivity. Preweaning growth and weaning weights of calves are influenced by the calf's genotype for growth and the maternal ability of the dam. The influence of maternal effects on weaning weight are of genetic and environmental origin (Cantet et al., 1988). Milk production of the dam influences growth rate of the calf. In this study, selection for average daily gain of calves, based upon first lactation performance, was not repeatable in subsequent lactations (Figure 5). Weaning weights of calves from Above and Below cows were significantly greater ($P<.01$) for lactations 1 and 2, however, WW were similar in lactation 3 (Figure 6). The inclusion of second and third parity data into the evaluation of the lifetime production ability of a

TABLE VII

LEAST-SQUARES MEANS (±SE) FOR REBREEDING PERFORMANCE AND CALF GROWTH DURING THE THIRD PARITY

	Group	
Trait	Above	Below
Weaning Weight, kg	235.1 ± 6.8	227.9 ± 6.8
Average Daily Gain, kg	1.19 ± .06	1.22 ± .06
Onset Luteal Activity, d	56.7 ± 5.6	62.4 ± 5.7
Calving To Conception, d***	104.0 ± 10.5	65.2 ± 10.7

***P<.01.

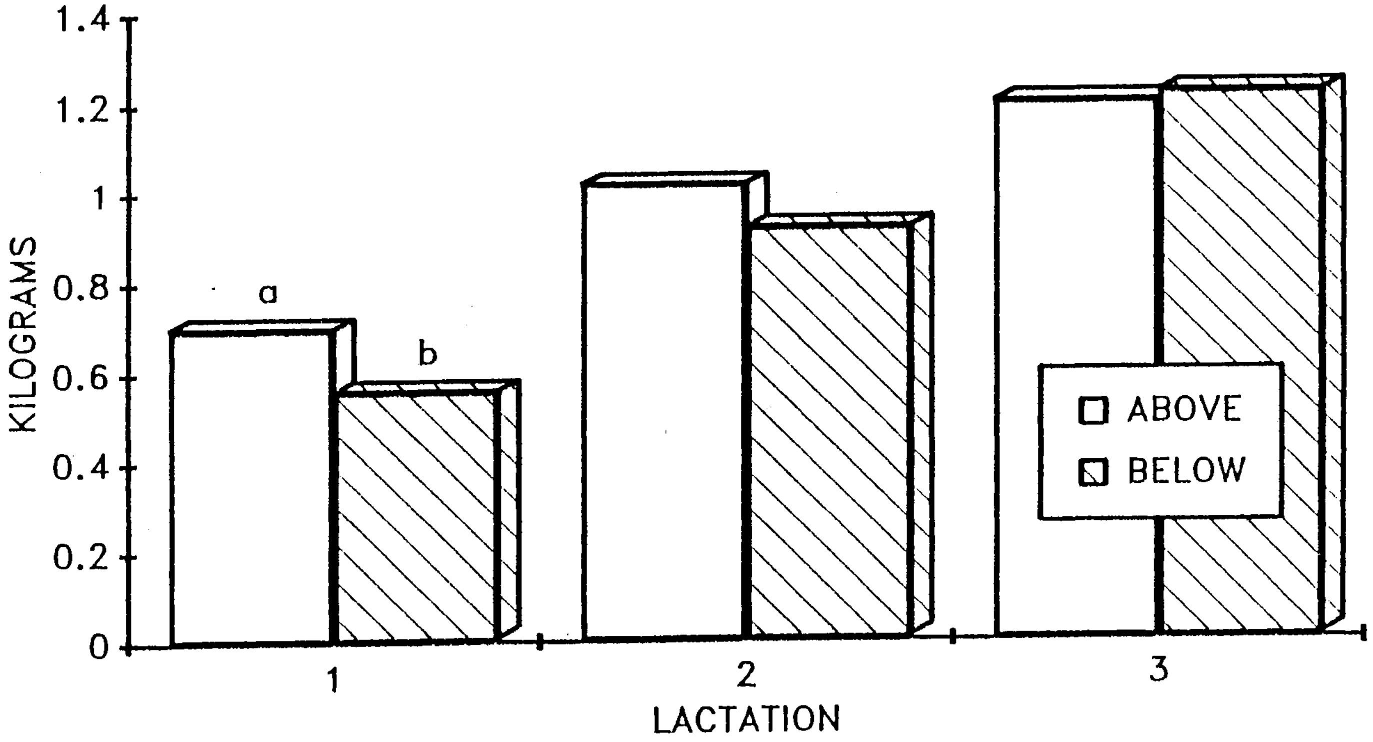

FIGURE 5. AVERAGE DAILY GAIN OF CALVES FROM ABOVE OR BELOW COWS

[a,b]Columns that lack a common superscript differ (P<.06).

beef cow may give a more accurate appraisal of a cow's genetic worth. Davis et al. (1987) determined that multiple regression equations based on first parity dam and calf traits were not of sufficient accuracy ($R^2<.30$) to predict lifecycle efficiency. However by including second and third parity data, life cycle efficiency was predicted with improved accuracy ($R^2\geq.30$). Due to yearly variation in environmental conditions, forage availability, sire selection, and management ability, the inclusion of second and third parity data into the evaluation of the production capabilities of a beef cow may be warranted.

The interval from calving to the onset of luteal activity based upon first lactation performance was not repeatable in subsequent lactations (Figure 7). A similar decrease in the length of the interval from calving to the onset of luteal activity occurred for both Above and Below groups in subsequent lactations. The interval from calving to conception (Figure 8) was shorter for Above than Below cows during lactation 1, ($P<.02$) and greater ($P<.01$) for Above than Below cows during lactation 3. However, the longer interval for the Above cows during lactation 3 may have been caused by the initiation of estrous cycles in three Above cows prior to the beginning of the breeding season. Measures of reproductive efficiency have very small genetic variance and heritabilities near zero (Foote, 1970; Milagres et al., 1979). Azzam and Nielsen (1987) estimated the heritability of the postpartum interval to first estrus

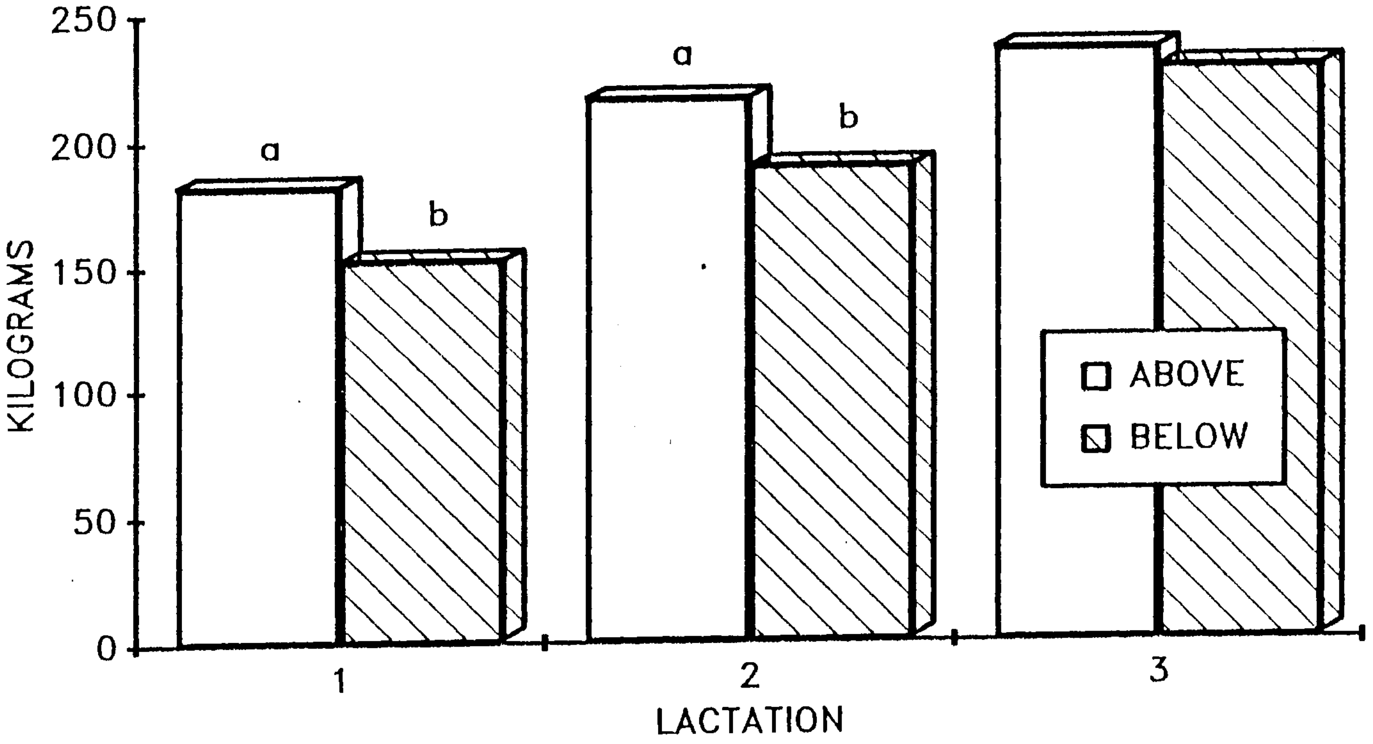

FIGURE 6. 205-DAY WEANING WEIGHT OF CALVES FROM ABOVE OR BELOW COWS

^{a,b}Columns that lack a common superscript differ (P<.01).

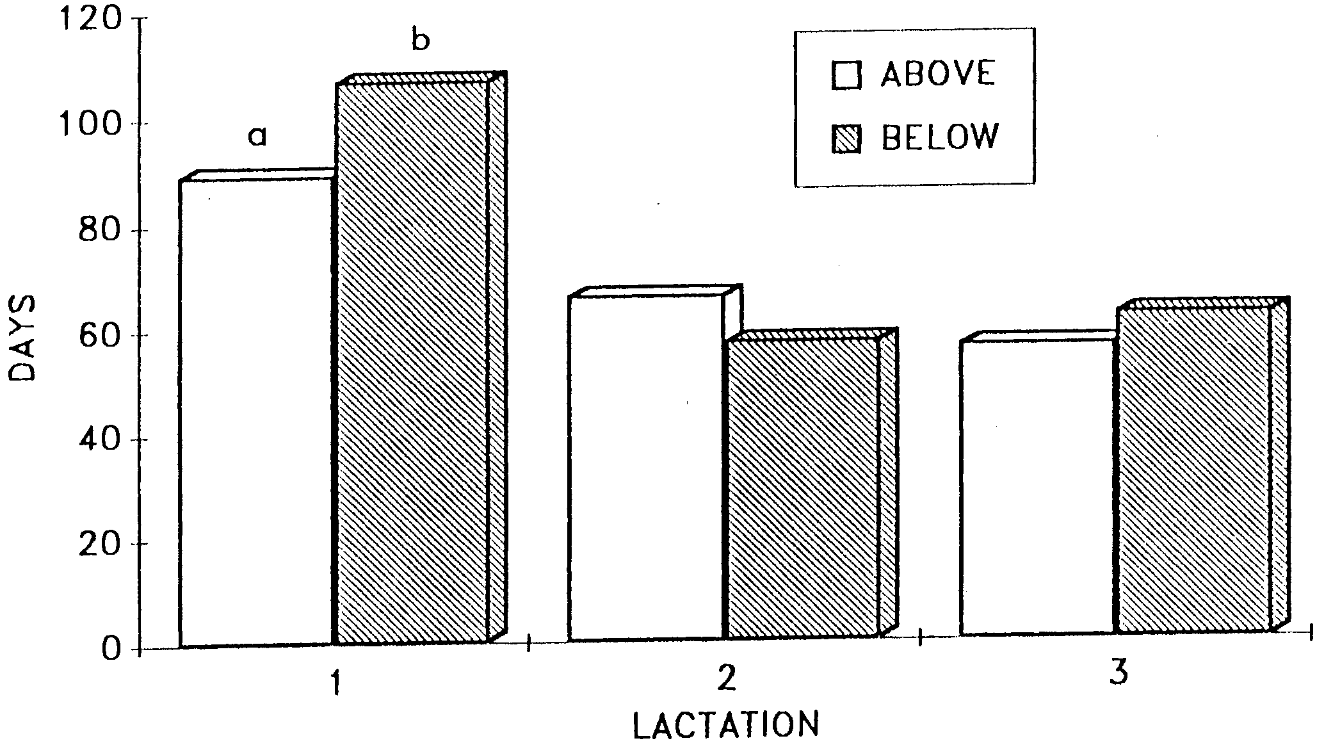

FIGURE 7. INTERVAL FROM CALVING TO ONSET OF LUTEAL ACTIVITY FOR ABOVE AND BELOW COWS

^{a,b}Columns that lack a common superscript differ (P<.01).

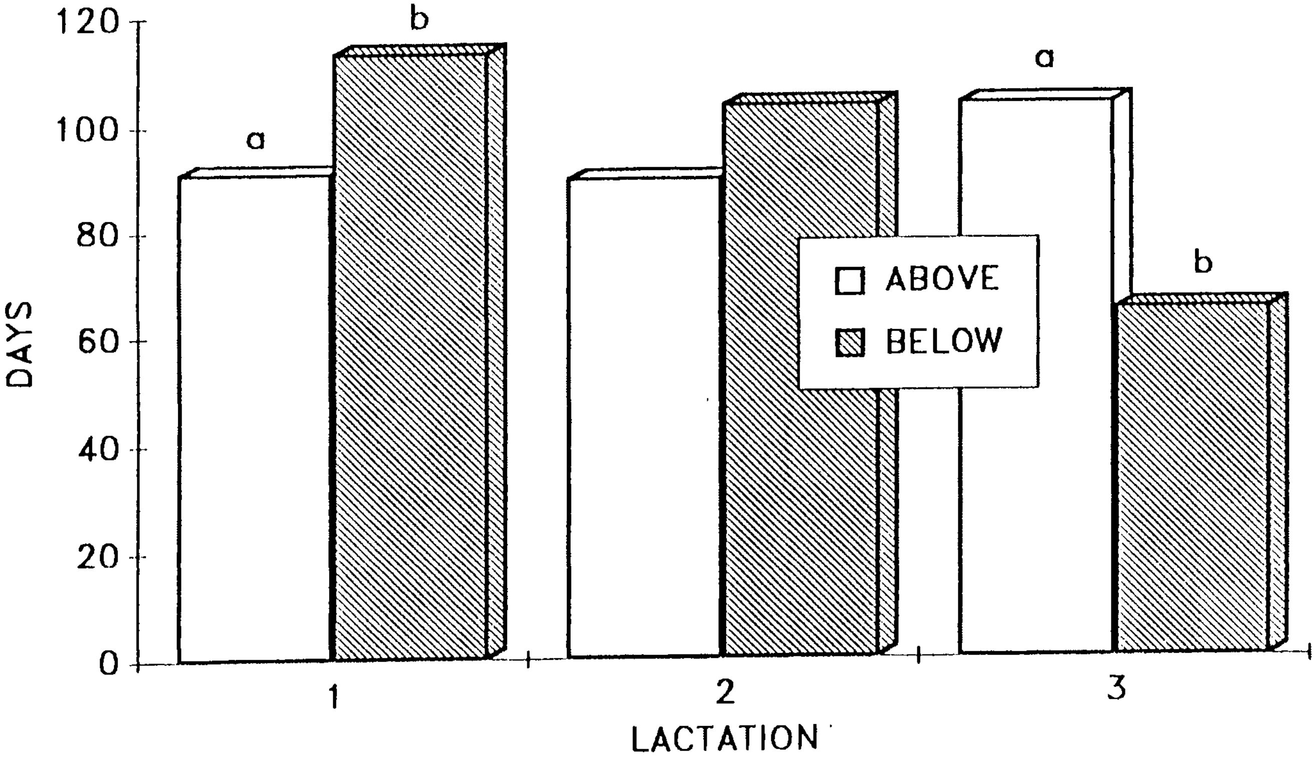

FIGURE 8. INTERVAL FROM CALVING TO CONCEPTION FOR ABOVE AND BELOW COWS

[a,b] Columns that lack a common superscript differ ($P<.02$).

for parity 1 (.05), and parity 2 (.10) and found them to be lowly heritable. Although selection for a decrease in the postpartum interval to LA would improve the efficiency of beef cattle production, the opportunity for such improvements appear limited.

Rapid genetic progress within a beef cow herd requires the evaluation of cow performance to occur early in the productive life of a cow. Results of the study indicate that reproductive and lactational performance during the first lactation was not repeatable. The inclusion of performance during the second or third lactation would more adequately describe the performance of the cow. Concentrations of glucose, insulin and NEFA in weekly samples obtained during the breeding season were not related to rebreeding and calf performance in first lactation cows.

CHAPTER IV

GLUCOSE, INSULIN AND NON-ESTERIFIED FATTY ACIDS IN PLASMA OF BEEF COWS WITH ABOVE OR BELOW AVERAGE PERFORMANCE AFTER TREATMENT WITH EPINEPHRINE AND FASTING

Abstract

Metabolic differences in lactating beef cows were evaluated by quantifying glucose, insulin and nonesterified fatty acids (NEFA) in plasma after treatment of cows with epinephrine and during a 24-h fast. Ten Hereford and Angus X Hereford cows selected during their first lactation based on the ADG of their calves and the interval from calving to the onset of luteal activity were utilized. Cows with performance greater than the average of herdmates were assigned to the Above group (n=5) and cows with performance less than the average of herdmates were assigned to the Below group (n=5). At approximately 60 d post partum, cows were confined to metabolism stalls and fed based on NRC requirements. Calves remained with their dams throughout the trial. All cows were treated intravenously with epinephrine (.7 µg/kg of BW) and frequent plasma samples were obtained via cannulae. Concentrations of glucose, insulin, and NEFA in the plasma of all cows increased following epinephrine (P<.01). Concentrations of glucose in plasma were not different between cow groups. Below cows tended to have greater (P<.10) concentrations of insulin in plasma than Above cows following epinephrine treatment. Cows in the Above group had greater concentrations of NEFA in plasma following epinephrine than cows in the Below group (P<.05). The mean concentrations of NEFA in the plasma of all cows after treatment with epinephrine were correlated with ADG of the calves (r=.89, P<.01) and weaning weight (r=.94, P<.05). Cows in the Above and Below groups were fasted for 24-h, and plasma samples were collected. Removal of feed was associated with a decrease in concentrations of glucose and insulin (P<.01) while concentrations of NEFA in plasma increased (P<.01) in all cows. Concentrations of glucose and insulin in plasma increased following feedings, whereas concentrations of NEFA were reduced. During fasting, cows in the Above group had reduced (P<.06) concentrations of insulin in plasma. Treatment with epinephrine and fasting may be useful to evaluate fat mobilization and plasma concentrations of glucose and insulin in lactating beef cows.

Introduction

To increase the efficiency of a cow-calf operation, beef cows must produce adequate milk and become pregnant within 82 days after calving. To accomplish this, cows must have metabolic and endocrine functions which enhance the partitioning of nutrients to support ovarian function, pregnancy and milk secretion. Concentrations of specific blood constituents under less than optimum conditions could be indicators of the ability of a cow to coordinate the utilization of nutrients and/or the metabolism of body tissues necessary to maintain physiological equilibrium.

The catecholamine, epinephrine (EPI), has a role in the response of animals to stress. Environmental stress such as acute cold exposure in sheep (Thompson et al., 1978) and heat stress in dairy cows (Alvarez and Johnson, 1978) can elicit secretion of EPI. Similarly, physical or emotional stimuli such as electrical shock in cattle (Lefcourt et al., 1986) and handling or transport of bulls (Rulofson et al., 1988) will cause increases in EPI in plasma. Under such situations, EPI may influence the nutrient repartitioning required to make the necessary metabolic adaptations.

Beef cows under range conditions are often subject to variation in the planes of nutrition due to periods of reduced forage availability. A desirable metabolic response to periods of fasting is necessary to maintain an acceptable level of production. During a fast, carbohydrate reserves of ruminant animals are exhausted and concentrations of glucose in plasma decline (Koenig and Boling, 1981; Rule et al., 1985). Therefore, a shift in metabolism involving the reduced utilization of carbohydrates and increased utilization of adipose tissue as an energy yielding substrate occurs (Blum et al., 1982). Cattle adapt to an energy deficit through an increase in the rates of lipolysis and a decrease in triglyceride uptake by adipose tissue (Di Marco et al., 1981). In addition, fasting ruminants adapt by decreasing concentrations of insulin in plasma (Trenkle, 1970; Rule et al., 1985) which favors lipolysis and glycogenolysis (Frohli and Blum, 1988). The objective of this study was to evaluate the effect of epinephrine and fasting on concentrations of glucose insulin and NEFA in the plasma of lactating beef cows with above average or below average calf growth and reproductive performance.

Materials and Methods

Hereford and Hereford X Angus cows (n=42) were evaluated during their first lactation and ranked according to the ADG of their calves and the interval from calving to the onset of luteal activity (LA). Twenty pregnant cows were selected and assigned to either an Above group (A) which had performance greater than the average of herdmates (n=10), for ADG and LA, or a Below group (B) which had performance less than the average of herdmates (n=10). The onset of luteal activity was estimated to occur when concentrations of progesterone in plasma were greater than or equal to 1 ng/ml for two consecutive weeks, followed by concentrations typical for normal estrous cycles or pregnancy. Concentrations of progesterone in plasma were determined by radioimmunoassay (Lusby, et al., 1981). Weight of the calves at weaning was adjusted to 205 d using the equation:

$$\frac{\text{Weaning weight - Birth weight}}{\text{Age}} \text{ X } 205 + \text{Birth weight}$$

Weaning weights of heifer calves were adjusted to steer equivalent: Heifer weight X 1.07 = Steer equivalent weight. Cows were maintained on native range and Bermuda grass pastures as a single herd. During pregnancy, cows were fed a 40% crude protein supplement so that they calved with an average body condition score (BCS; Wagner et al., 1988) of 5.

In this study, five mature lactating cows (third or fourth lactation) from the A group (437 ± 37 kg, 4.6 ± .5 BCS) and five mature cows from the B group (452 ± 36 kg, 4.7 ± .2 BCS) were utilized. Pairs of cows were blocked based on calving date and transported (20 km) at approximately 60 d post partum to the Nutrition Physiology Research Center. Cows were confined to metabolism stalls and calves remained with their dams throughout the trial. Cows were fed a diet of 50% alfalfa pellets and 50% cottonseed hulls free choice, plus 1 kg of soybean meal. Cows were acclimated to the stalls and diet for four days then a jugular polyvinyl cannula[1] was inserted in each cow. Cows were weighed and assigned a BCS at the time of cannulation. Prior to feeding

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[1] Bolab Inc., BB317-85, V/10, inside diameter .157 cm, outside diameter 2.083 cm; Lake Hauasu City, AZ.

on day five, (approximately 15-h after eating) blood samples were collected. All cows were treated with 0.7 µg/kg BW epinephrine[2] i.v. at time 0 (about 0800 h). Blood samples (15 ml) were collected at -30, -15, 0, 5, 10, 15, 20, 25, 30, 45, 60, 75, 90, 120, 150 and 180 minutes. Cows were fed at approximately 1100 h. At 1600 h, all feed was removed and a blood samples was obtained. Additional blood samples were collected at 2400 h and on the next day at 0800, 1200 and 1600 h. Cows were fed at 1600 h (after a 24-h fast). Four hours after feeding the last blood sample was obtained.

Blood samples (15 ml) were collected in tubes containing 32 mg of oxalic acid and cooled immediately to 5 C. Then samples were centrifuged (3200 X g for 20 min) and plasma was decanted and stored at -20 C until quantified for glucose, insulin and non-esterified fatty acids (NEFA).

Concentrations of glucose in plasma samples were quantified by an enzymatic, colormetric procedure[3]. Concentrations of insulin in plasma samples were quantified by the radioimmunoassay described by Selk (1986). Concentrations of insulin-like growth factor I in plasma were determined in plasma samples collected during fasting (Spicer et al., 1988). Concentrations of NEFA in plasma samples were quantified using a colormetric procedure (Patterson, 1963).

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[2] Epinephrine 1 mg/ml, Lot no. 7906; Anpro Pharmaceutical, Arcadia, CA

[3] Sigma Chemical Co., Kit No. 510, St. Louis, MO

Concentrations of glucose, insulin and NEFA in plasma samples were analyzed by analysis of variance. The experimental design was a split plot in which group and block were the main units. Repeated measurements over time were taken on cows, and time sampled was the subplot. When a significant group by time effect existed ($P<.1$), polynomial response curves for concentrations of blood constituents were tested for heterogeneity of regression. Pooled within block and time partial correlation coefficients were calculated to study the association of plasma constituents during fasting and following epinephrine treatment. Pooled within block and group partial correlation coefficients were calculated to study the association of plasma constituents of cows during the epinephrine trial with calf growth and reproductive performance.

Results and Discussion

Least-squares means for calf growth and the postpartum interval to luteal activity of Above and Below cow groups are summarized in Table VIII. Production traits of cows and calves were not significantly influenced by cow group. However, the cows in the Above group tended to wean heavier calves and to initiate ovarian function sooner after calving. Two of the cows in each group had functional corpora lutea during treatment. Three of the Above cows and two of the Below cows had less than 1 ng/ml of progesterone

TABLE VIII

LEAST-SQUARES MEANS (±SE) FOR PRODUCTION TRAITS

	Group	
Trait	Above	Below
Weaning Weight, kg	227.0 ± 13.8	211.3 ± 13.8
Average Daily Gain, kg	1.12 ± 0.11	0.95 ± 0.11
Onset Luteal Activity, d	57.8 ± 9.8	66.6 ± 9.8

during treatment. Progesterone concentrations were not determined for one of the Below cows. Concentrations of insulin and NEFA in plasma were similar for cows in both groups prior to treatment with epinephrine (Table IX) and concentrations of glucose tended to be greater ($P<.1$) in Below cows. Following treatment with EPI, concentrations of glucose, insulin and NEFA in plasma of all cows increased. Time of sampling following epinephrine treatment significantly influenced ($P<.001$) the concentrations of glucose, insulin and NEFA indicating that the dose of epinephrine (0.7 µg/kg of BW) was sufficient to elicit a response.

Concentrations of glucose in plasma reached a maximum at 20 min following EPI treatment in Above cows (86.7 ± 1.4 mg%) and Below cows (83.4 ± 1.4 mg%), representing 29% and 20% increases, respectively, over pre-infusion concentrations (Figure 9). Concentrations of glucose in the plasma of Above and Below cows following EPI treatment were not different ($P>.10$). Epinephrine is a potent hypoglycemic agent in ruminants (Brockman and Laarveld, 1986) and causes an immediate increase in concentrations of glucose in plasma when administered to beef cattle (Blum et al., 1982) and lactating dairy cows (Frohli and Blum, 1988). Increased concentrations of glucose in plasma in response to EPI treatment may reflect enhanced hepatic gluconeogenesis, increased rates of hepatic and muscular glycogenolysis

TABLE IX

LEAST-SQUARES MEANS (±SE) FOR CONCENTRATIONS OF PLASMA CONSTITUENTS PRIOR TO EPINEPHRINE INFUSION

	Group	
Constituent	Above	Below
NEFA μeq/l	466 ± 52	360 ± 52
Glucose mg%*	67.0 ± 0.9	69.7 ± 0.9
Insulin ng/ml	1.15 ± 0.27	1.85 ± 0.27

*$P<.1$.

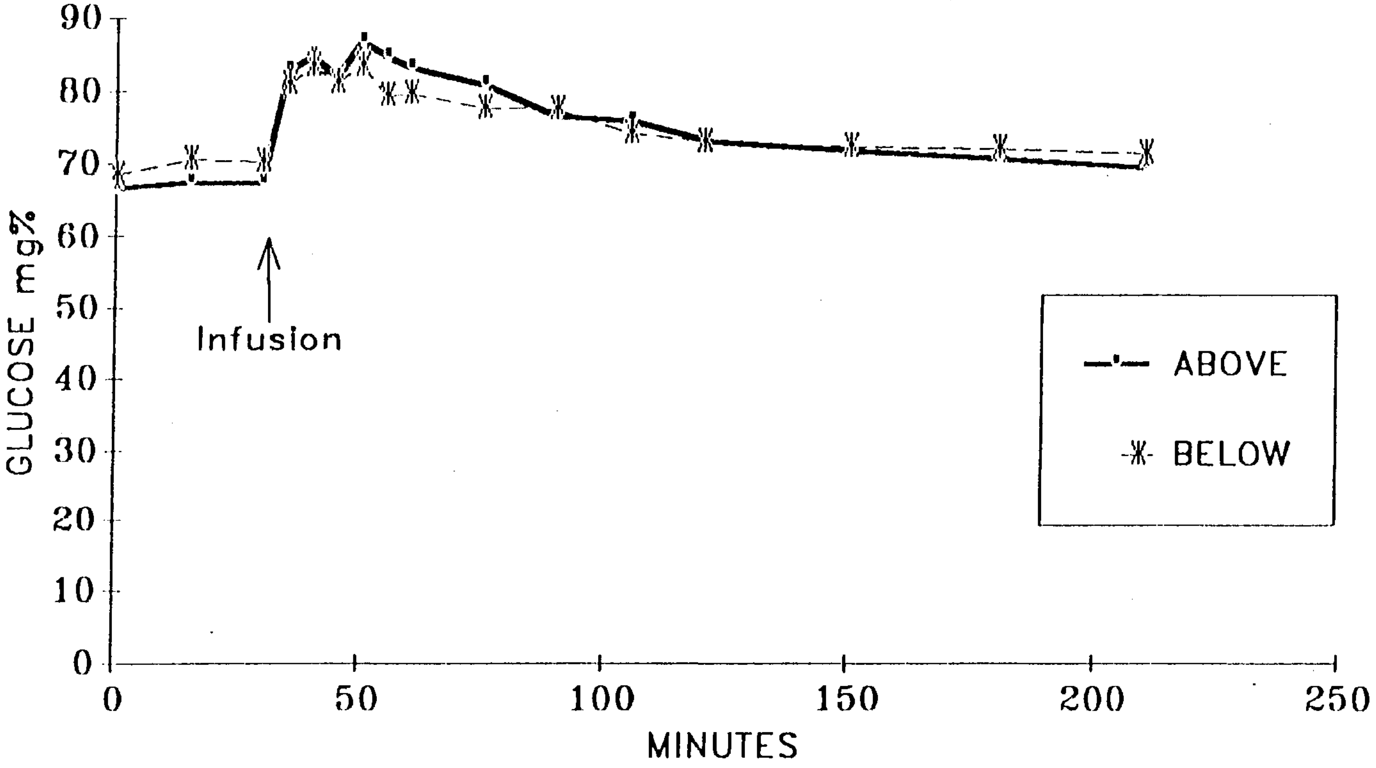

FIGURE 9. CONCENTRATIONS OF GLUCOSE (SE ± 2.11) IN PLASMA OF BEEF COWS AFTER EPINEPHRINE

and/or reduced utilization of glucose by body tissues (McCutcheon and Bauman, 1986).

Concentrations of insulin in plasma samples collected following treatment with EPI were best described by a third-order polynomial regression equation. Analysis of heterogeneity of regression indicate that concentrations of insulin were different ($P<.10$) for A and B cows. Below cows tended to have greater concentrations of insulin in plasma than Above cows ($P<.10$) following EPI treatment. Concentrations of insulin in plasma were maximal at 15 min following EPI treatment in Above cows (2.6 ± .3 ng/ml) and Below cows (4.7 ± .3 ng/ml), representing 136% and 161% increases, respectively, over pre-infusion concentrations (Figure 10). Insulin promotes protein and lipid synthesis, and is the primary hormonal regulator of metabolism in the resting animal (Brockman and Laarveld, 1986). In contrast, EPI allows rapid mobilization of energy stores and is involved with metabolic adaptations to stress rather than regulation of basal metabolism (Brockman and Laarveld, 1986). The reduced concentrations of insulin in plasma of Above cows following EPI indicates differences in the partitioning of nutrients in Above and Below cows. Frohli and Blum (1988) indicate that reduced concentrations of insulin in the blood of lactating dairy cows favors lipolysis and glycogenolysis. A reduced response to EPI by the Above cows, as indicated by lower concentrations of insulin in plasma, may enhance the ability of Above cows to

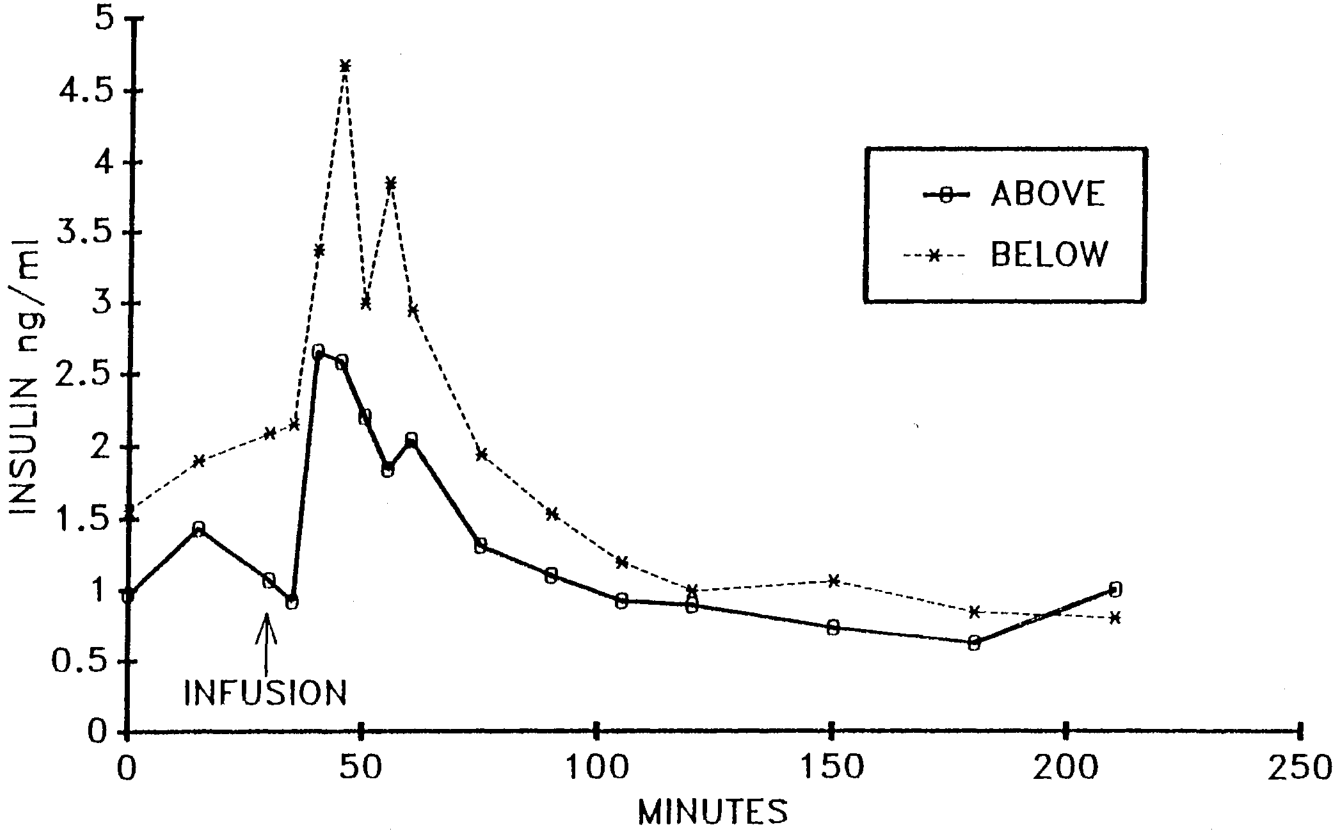

FIGURE 10. CONCENTRATIONS OF INSULIN (SE ± .46) IN PLASMA OF BEEF COWS AFTER EPINEPHRINE

mobilize energy yielding metabolites to meet the high nutrient demands for milk synthesis.

Concentrations of NEFA in plasma were maximal at 15 min following EPI treatment in Above cows (977.1 ± 89.6 μEq/l) and 10 min following EPI treatment in Below cows (648.31 ± 89.6 μEq/l). These concentrations of NEFA in plasma represent 110% and 80% increases, over pre-treatment concentrations in Above and Below cows, respectively (Figure 11). Concentrations of NEFA in plasma samples collected following treatment with EPI were best described by a second-order polynomial regression equation. Analysis of heterogeneity of regression indicates that concentrations of NEFA were different ($P<.05$) for Above and Below cows. Concentrations of NEFA in the plasma of Above cows were greater than those for Below cows ($P<.05$) after treatment with EPI. Increases in NEFA in plasma following the administration of EPI have been reported previously in cattle (Blum et al., 1982; Di Marco et al., 1986; McCutheon and Bauman, 1986; Frohli and Blum, 1988; McNamara, 1988). Epinephrine is the most effective lipolytic agent in ruminants (Basset, 1970). Blum et al. (1982) suggests that β-adrenergic receptors on fat cells mediate the β-adrenergic components of catecholamines which stimulate lipolysis, elevating concentrations of NEFA in the plasma of cattle. Results of the present study indicate that an EPI challenge may be useful to evaluate fat mobilization in lactating beef

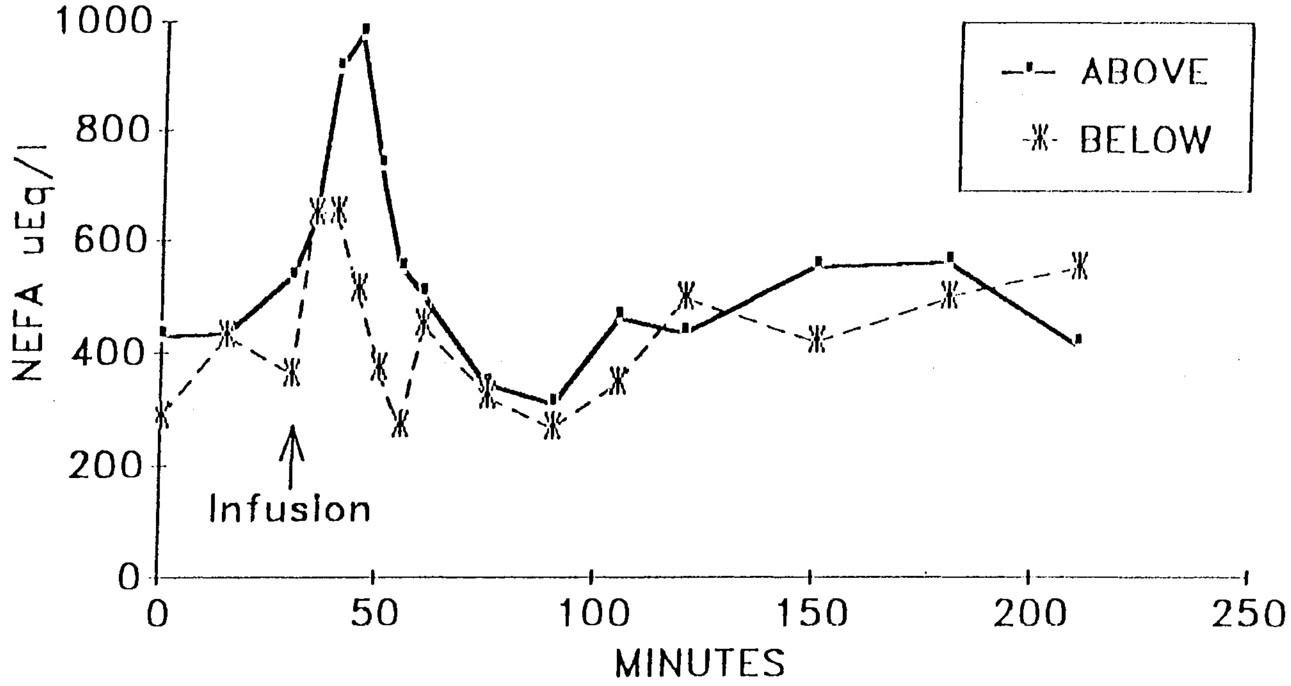

FIGURE 11. CONCENTRATIONS OF NEFA (SE ± 104) IN PLASMA OF BEEF COWS AFTER EPINEPHRINE

cows, and identify those cows with the ability to most efficiently mobilize body fat reserves.

The pooled within block and group partial correlation coefficients between plasma constituents during the EPI challenge and calf performance are listed in Table X. Following treatment with EPI, mean concentrations of NEFA in the plasma of all cows were correlated with ADG r=.94 (P<.05) and weaning weight r=.89 (P<.01). During lactation, adipose tissue undergoes adaptations to meet the requirements of the mammary gland. To support milk synthesis, the uptake of nutrients for lipogenesis is decreased and lipid reserves are mobilized (Bauman and Currie, 1980). In dairy cows, the greatest concentrations of NEFA in plasma were during the period of maximum milk production (Head et al., 1976). Therefore, in lactating cows, the rate of adipose tissue lipolysis varies proportionately with the rate of milk synthesis (Bauman and Currie, 1980; McNamara and Hillers, 1986). Increased milk yield of the dam results in increased ADG (Boggs et al., 1980) and weaning weight of her calf (Butson, 1980). Clutter and Nielson (1987) found a positive correlation (r=.60, P<.01) between milk intake and calf gain to 205 d. Results of this study (Chapter III) indicate the pooled, within group and lactation partial correlation between 44 d milk production and WW and ADG were .48 (P<.09) and .46 (P<.1) respectively. These results indicate that cows with a greater ability to mobilize body stores may have an

TABLE X

PARTIAL CORRELATION COEFFICIENTS AND PROBABILITY LEVELS BETWEEN PLASMA CONSTITUENTS AND CALF PERFORMANCE OR POSTPARTUM INTERVAL

	Plasma Constituents		
Variable	Glucose	Insulin	NEFA
Weaning Weight	-.03	-.32	.89***
Average Daily Gain	-.21	-.21	.94**
Onset Luteal Activity	-.20	-.48	.34

**P<.05, ***P<.01.

increased potential for milk synthesis, which can result in greater ADG and heavier weaning weights of calves.

Feed removal was characterized by a gradual decrease in concentrations of glucose in plasma (P<.01; Figure 12) of all cows indicating a depletion of carbohydrate reserves (muscle and liver glycogen) which are small in comparison to stores of body fat in animals. Within four hours following refeeding, concentrations of glucose in plasma increased, but did not attain pre-fast concentrations. Concentrations of glucose in plasma were not different (P>.10) for cows in the Above and Below groups following feed removal. A decrease in concentrations of glucose in plasma is a well established result of reduced food intake (Blum et al., 1982; Blum et al., 1985; Rule et al., 1985). During periods of fasting an animal may increase the utilization of fat as an energy source and decrease the utilization of carbohydrates. Concentrations of NEFA in plasma were not different (P>.10) for cows in the Above and Below groups following feed removal. Figure 13 indicates a rapid increase (P<.01) in concentrations of NEFA in the plasma of all cows from 8 to 20 h following food removal. This shift in metabolism resulting in increased rates of fat mobilization, may partially compensate for the energy deficit caused by food restriction. The increased concentrations of NEFA in plasma during fasting followed by a rapid decline in concentrations of NEFA during refeeding, indicates that adipose tissue of cattle adapt rapidly to

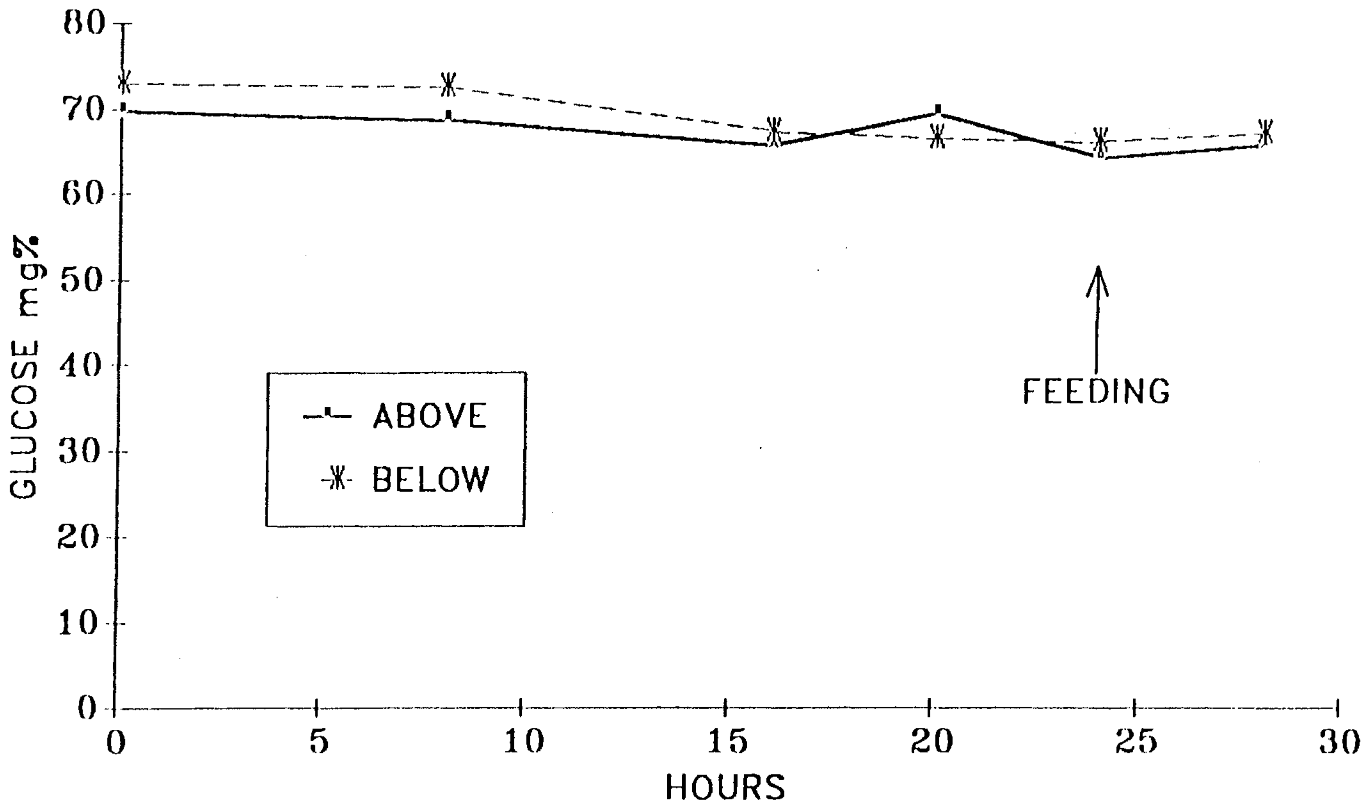

FIGURE 12. CONCENTRATIONS OF GLUCOSE (SE ± 1.7) IN PLASMA OF BEEF COWS DURING A 24-h FAST

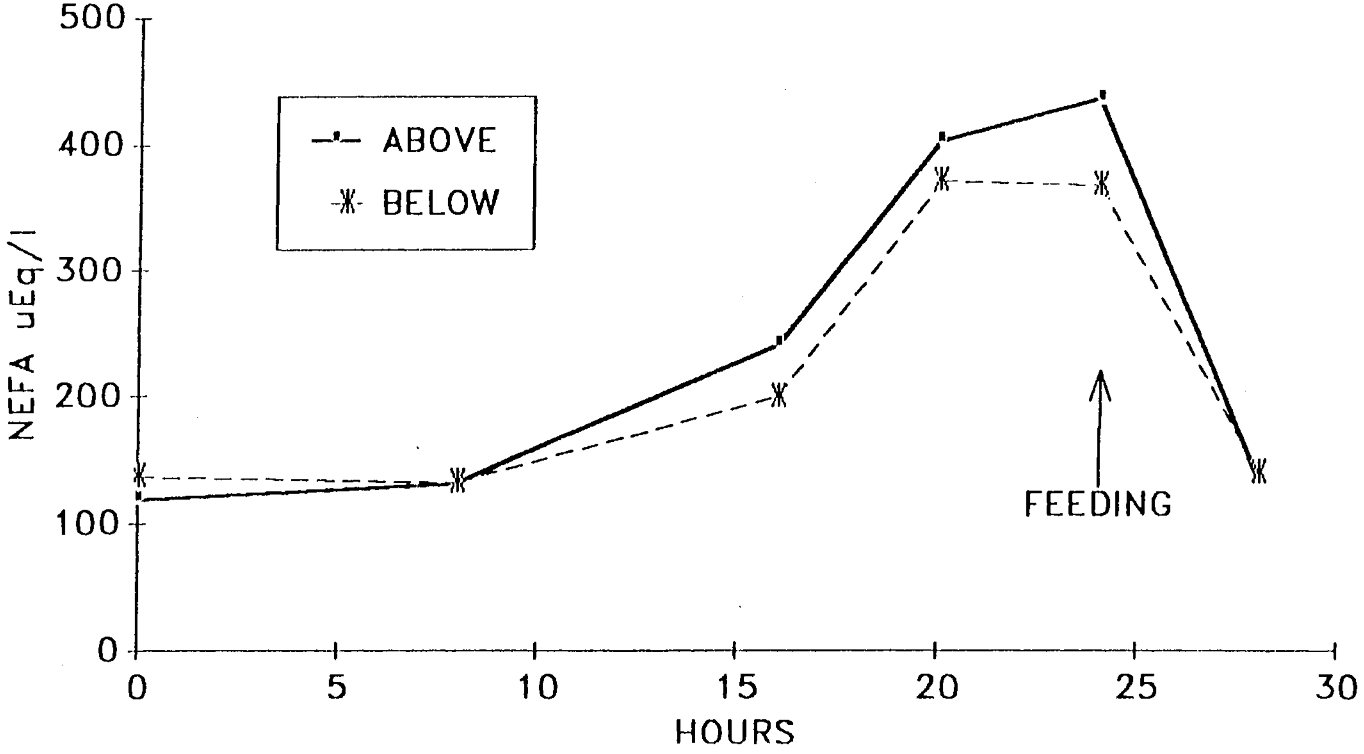

FIGURE 13. CONCENTRATIONS OF NEFA (SE ± 35) IN PLASMA OF BEEF COWS DURING A 24-h FAST

major changes in nutrient intake (Di Marco et al., 1981; Rule et al., 1985; Rutter et al., 1989).

Changes in concentrations of insulin in plasma during fasting are depicted in Figure 14. Following feed removal, concentrations of insulin in plasma decreased (P<.01) in all cows. Within four hours following refeeding, concentrations of insulin in plasma increased. These results are in agreement with the observation that fasting markedly decreased insulin concentrations in plasma (Rule et al., 1985; Frohli and Blum, 1988; Rutter et al., 1989). Following feed removal, cows in the Above group had reduced (P<.06) concentrations of insulin in plasma compared to Below cows. Frohli and Blum (1988) suggested that insulin is important for the regulation of concentrations of NEFA in plasma. Reduced concentrations of insulin in plasma may decrease the antilypolytic effect exerted by this hormone. This allows nutrients to be mobilized from adipose tissue which compensate for the reduction in nutrient absorption from the gut during fasting. Insulin is the primary hormonal regulator of metabolism in ruminants (Brockman and Laarveld, 1986). Concentrations of insulin in plasma were lower (statistically and/or numerically) for cows in the Above group, each time insulin was quantified throughout this research. A greater concentration of insulin in plasma would tend to decrease the rate of fat mobilization and depress the concentration of glucose in plasma by inhibiting gluconeogenesis and glycogenolysis. These differences in

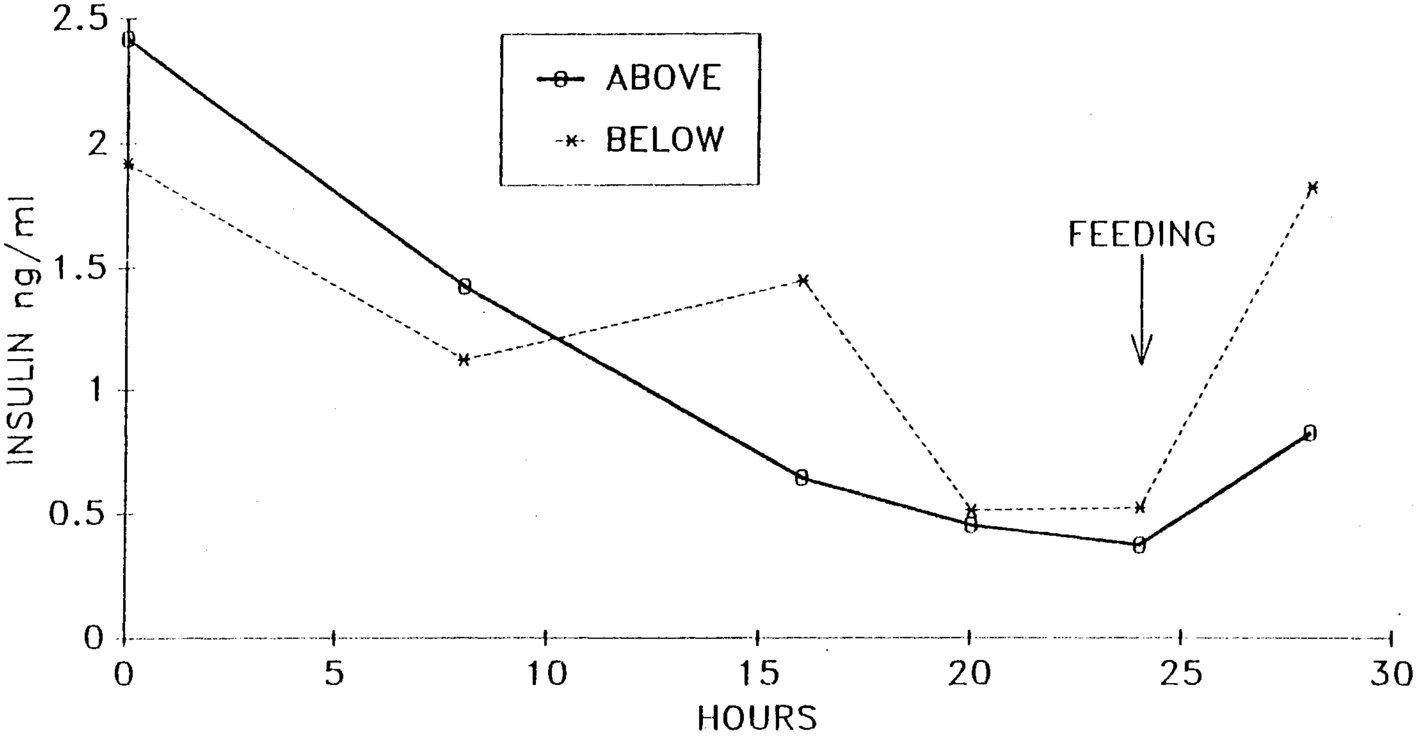

FIGURE 14. CONCENTRATIONS OF INSULIN (SE ± .27) IN PLASMA OF BEEF COWS DURING A 24-h FAST

concentrations of insulin would influence the partitioning of nutrients for milk synthesis and may be a key difference between cows in the Above and Below groups.

Concentrations of insulin-like growth factor I (IGF-I) in plasma were determined for all cows during the 24-h fast. Plasma concentrations of IGF-I were not different (P>.1) in Above cows (45.6 ± 7.8 ng/ml) when compared with cows in the Below group (49.6 ± 7.4 ng/ml). Concentrations of IGF-I tended (P<.01) to decrease during the fast, then increase 4 h following feeding (Figure 15). A decline in plasma concentrations of IGF-I have been reported for short-term (4 d) (Rutter et al., 1989) and extended (41 wk) (Richards et al., 1989) periods of reduced nutrient availability. These results would indicate that IGF-I concentrations are depressed in beef cows under negative energy balance. In addition to level of nutrition, concentrations of energy yielding metabolites and metabolic hormones, IGF-I may influence reproductive function. Richards (1989) indicated that reduced concentrations of IGF-I in serum of beef cows were associated with reduced LH concentrations. Rutter et al. (1989) suggested that IGF-I may be a link between metabolic regulation and reproduction. Further investigation into the relationship between IGF-I and reproductive endocrine function may be warranted.

Coordinated endocrine and metabolic adjustments occur in response to nutrient availability and stage of production, causing concentrations of glucose, insulin and

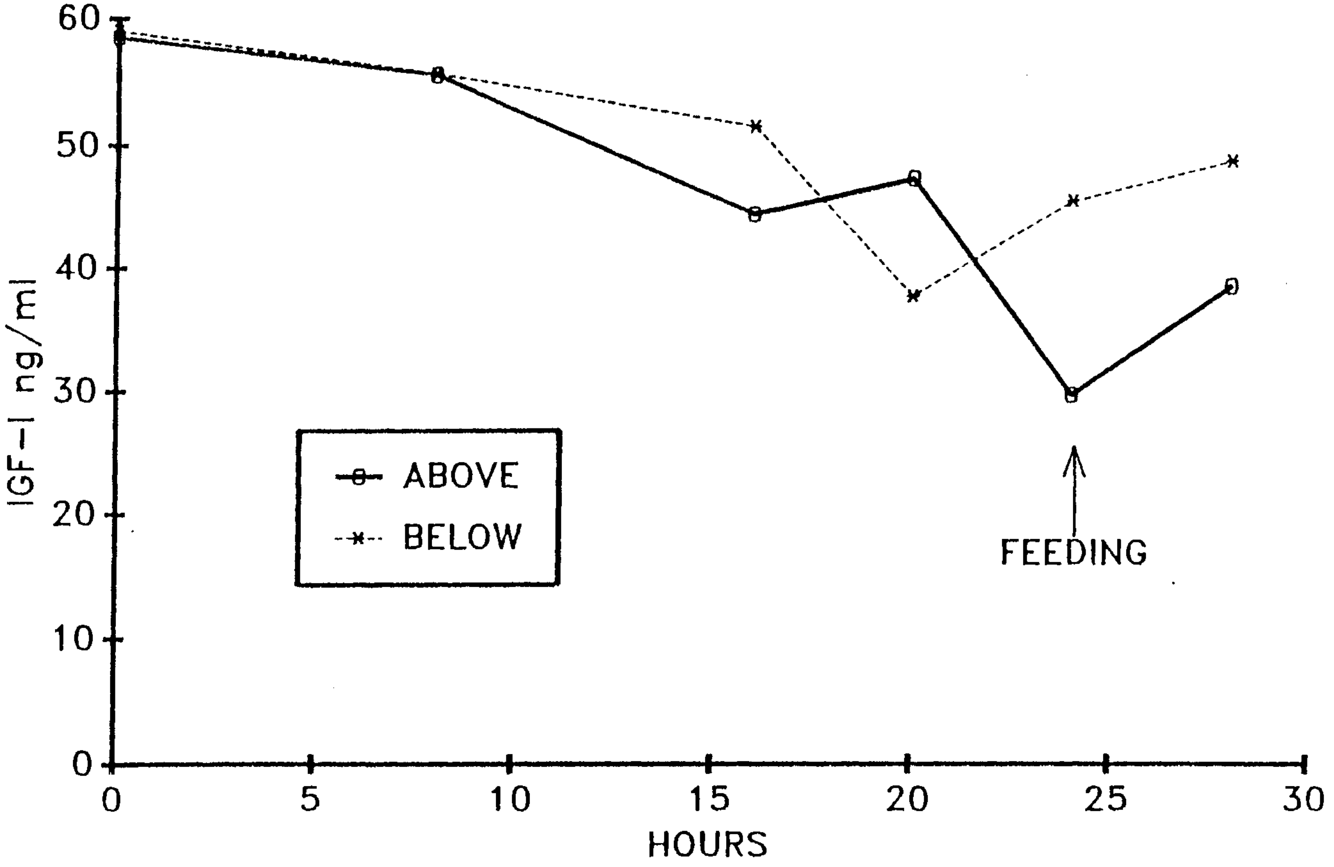

FIGURE 15. CONCENTRATIONS OF IGF-I (SE ± 5.2) IN PLASMA OF BEEF COWS DURING A 24-h FAST

NEFA to change. Beef cows must utilize the ability to adjust their energy metabolism to meet the requirements for reproduction and lactation. The metabolic response of lactating beef cows to an epinephrine challenge and fasting will influence concentrations of glucose, insulin and NEFA in plasma and may be useful to evaluate the potential productivity of cows.

CHAPTER V

SUMMARY AND CONCLUSIONS

Summary

Two important measurements of beef cow production efficiency are the interval from calving to conception and calf weaning weight. Nutrient requirements for reproduction and lactation must be met for cows to be profitable. Within a beef cow herd, certain cows have the ability for superior production with the nutrient availability, environmental conditions and management. Cattlemen must identify and select superior beef cows to achieve maximum genetic progress.

Nutrition has a major influence on reproductive function and lactation. Range beef cows must meet the majority of their nutrient requirements from grazed forage, with a minimum of supplemental feeding. Body energy reserves are often required to make up a deficit in nutrient intake caused by reduced forage availability, environmental conditions or producer interference. Beef cows must coordinate the utilization of food and the metabolism of body tissues to meet the nutritional requirements for reproduction and milk secretion. Therefore, the quantification of glucose, insulin and NEFA in the plasma of beef cows of differing producing ability may identify patterns of metabolic and endocrine function which enhances the ability of superior cows to regulate nutrients to achieve optimum production.

In this study, cows were assigned to Above or Below groups based on performance during the first lactation, as measured by ADG of the calf and the postpartum interval from calving to the onset of luteal activity. The advantages that Above cows had over Below cows in calf ADG, calf 205-d WW and the intervals from calving to the onset of luteal activity and conception were not consistently maintained over subsequent parities. A decision to retain or remove a cow from the herd based on performance during the first lactation would be difficult to make and may be an error. The inclusion of performance during the second or third lactation would have more completely described the ability of the cow, however, the greatest opportunity for rapid genetic improvement would require such decisions to be made following the first lactation. Reproductive performance was more variable in subsequent lactations than was calf performance.

Estimates of 24-h milk production during lactations two or three were not significantly different between groups, however Above cows had numerically greater milk production during each trial. A cow's ability to coordinate the partitioning of nutrients for milk synthesis during peak milk yield is of primary importance. During lactation, cows will mobilize body fat to meet the high metabolic demands of lactation. Adequate body condition will provide cows with a source of energy for milk synthesis. Beef cows must provide milk in quantities to supply calves with sufficient nutrients for growth. Following treatment with epinephrine, the mean concentrations of NEFA in the plasma of all cows were correlated (r=.94, P<.05) with ADG of the calves and weaning weight (r=.89, P<.01). Beef cows with a greater ability to mobilize body stores may have an increased potential for milk production which can result in greater ADG and heavier weaning weights of calves.

Insulin is the primary hormonal regulator of metabolism in ruminants (Brockman and Laarveld, 1986). Insulin is the major regulator of energy substrates (Rule et al., 1985) and may be a key endocrine factor that differs between high and low milk producing cows (Bauman and Currie, 1980). Cows in the Above group had reduced concentrations of insulin in plasma following epinephrine treatment (P<.10) and during fasting (P<.06) compared to Below cows. Reduced concentrations of insulin in plasma would favor lipolysis, indicating that insulin is important for the regulation of NEFA concentrations in plasma (Frohli and Blum, 1988). Cows in the Above group had higher concentrations of NEFA in plasma following epinephrine (P<.05). Reduced concentrations of insulin in plasma allows an increase in fat mobilization, elevating plasma concentrations of NEFA making energy available for milk synthesis which influences calf growth.

Beef cows with a reduced ability to adjust their energy metabolism to meet the requirements for reproduction and lactation are limited in their production capabilities. This study indicates that an epinephrine challenge and fasting influence the concentration of glucose, insulin and NEFA in plasma of lactating beef cows and may aid in the metabolic evaluation to assess the potential productivity of cows.

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APPENDIX

TABLE 1

ANALYSIS OF VARIANCE USED TO TEST FOR HETEROGENEITY OF REGRESSION COEFFICIENTS FOR POLYNOMIAL RESPONSE CURVES FOR CONCENTRATIONS OF GLUCOSE IN PLASMA SAMPLES FOLLOWING EPINEPHRINE

Error	D.F.	S.S.	M.S.	F
Above	62	1775.80		
Below	62	960.75		
Total	124	2736.55	22.06	
Above, Below	127	2830.15		
Difference	3	93.60	31.20	1.41[a]

[a] (P>.10)

TABLE 2

ANALYSIS OF VARIANCE USED TO TEST FOR HETEROGENEITY OF REGRESSION COEFFICIENTS FOR POLYNOMIAL RESPONSE CURVES FOR CONCENTRATIONS OF INSULIN IN PLASMA SAMPLES FOLLOWING EPINEPHRINE

Error	D.F.	S.S.	M.S.	F
Above	62	43.94		
Below	62	83.70		
Total	124	127.64	1.02	
Above, Below	127	134.55		
Difference	3	6.91	2.30	2.24[a]

[a] (P<.10)

TABLE 3

ANALYSIS OF VARIANCE USED TO TEST FOR HETEROGENEITY OF REGRESSION COEFFICIENTS FOR POLYNOMIAL RESPONSE CURVES FOR CONCENTRATIONS OF NEFA IN PLASMA SAMPLES FOLLOWING EPINEPHRINE

Error	D.F.	S.S.	M.S.	F
Above	62	4466743.97		
Below	59	1857551.45		
Total	121	6324295.42	32266.90	
Above, Below	123	6656003.20		
Difference	2	331707.78	165853.89	3.17[a]

[a] $(P<.05)$

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