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RELATIONSHIPS BETWEEN ENERGY STATUS AND REPRODUCTIVE EFFICIENCY IN FIRST-CALF BEEF HEIFERS

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Lipalesa Motjope

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DEDICATION

This dissertation is dedicated to my parents

'M'e 'M'aseeng Mamelo Florence Motjope
&
Ntate Lesenyeho Paseka Jacob Motjope

" Ke ka kholiso, likhothaletso le lerato la lona ke tsebileng ho fihla boemong bona, 'me kea le leboha kese ke le kopela mahlohonolo le ts'ireletso ho Morena Molimo ".

To my brothers, sisters and nieces and to all my friends for their encouragement, love, support and prayers without which this program could not have been successfully completed. Thanks for helping bring this program to a wonderful and joyous closure.

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ABSTRACT

Study 1. Effects of increasing energy intake at breeding on reproductive performance was investigated with 26 first-calf Angus heifers. In separate but comparable pastures, half (lower energy group) were supplemented with 7 kg corn silage·heifer^{-1}·d^{-1}; half (higher energy group) were given 3.5 kg corn grain·heifer^{-1}·d^{-1} in addition to silage. Supplementation period extended from 22 d before to 22 d into breeding. Body weight (BW) and backfat were taken on d 1 and d 44. Blood samples were collected on d 2, 11, 22, 33 and 44 of supplementation. Basal blood samples were analyzed for non-esterified fatty acids (NEFA), progesterone (P_4), luteinizing hormone (LH) and follicle stimulating hormone (FSH). Blood samples collected on d 11 at 0 and 2 h after 10 μg of gonadotropin-releasing hormone (GnRH) were analyzed for LH, FSH and P_4. Postpartum interval (PPI), conception rate, subsequent calving and weaning rates were determined. There were no significant effects of diet on BW, NEFA, P_4, LH, FSH, response to GnRH, reproductive performance, or growth of the current calf. Heifers fed the higher energy diet accumulated more ($P < .05$) fat (1.5 vs .4 mm). Based on these results increasing energy intake during breeding of heifers fed pasture and 7.0 kg·heifer^{-1}·d^{-1} corn silage does not improve and may impair reproductive performance.

Study 2. First-calf Angus heifers (n = 83) were utilized to characterize postpartum nutritional and hormonal status of those that are reproductively efficient or inefficient. A short period (< 17 d) from exposure to the bull to conception (PPI) and delivery of a live calf represented reproductive efficiency. Body condition scores (BCS), BW, BW to hip height (BW:HH) ratio, NEFA, LH, FSH, P_4, E_2 and androstenedione were determined. Hormones released in response to GnRH and estradiol (E_2) were determined. Prolactin (PRL) was determined for indicating stress. Blood collection for hormonal assays was made between 35 d and 63 d postpartum. Heifers with a short PPI had higher ($P < .05$) BW:HH ratio between 35 d and 63 d postpartum, less ($P < .05$) fat and change in BW from beginning to 60 d into breeding, higher ($P < .05$) basal LH, lower ($P < .05$) FSH, lower ($P < .05$) androstenedione, lower ($P < .01$) release of FSH in response to GnRH and higher ($P < .05$) secretion of PRL. These results suggest that a fat body condition may have contributed to a longer PPI, a first-calf Angus heifer gaining less fat and BW during breeding and having more LH and PRL but less FSH and androstenedione is likely to be reproductively efficient.

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CHAPTER I

INTRODUCTION

Beef cattle rank among the top five income-generating agricultural commodities in the United States. Optimum performance of the beef herd is a key to ensuring that beef remains a competitive source of food and income. Reproductive performance dictates the efficiency of the cow-calf enterprise. Estimates of calving rate in beef females indicate that only about 70% exposed to a bull each year deliver a live calf. The low reproductive performance is due mainly to a long postpartum interval, which is defined as the period from parturition to first fertile estrus or conception. Low conception rates and early embryonic mortality are major contributors to an extended postpartum interval. Abortion among those that remain pregnant past the early embryonic mortality stage, and stillbirth also contribute to reduced reproductive efficiency.

Under current beef production systems, heifers are usually first bred at 14 to 15 mo of age to calve at approximately 24 mo of age. Reproductive success is generally high (87%) in heifers exposed for the first time but is low (68%) in first-calf heifers. This is primarily because first-calf heifers are bred for their second

pregnancy when their energy intake is not adequate to satisfy the multiple nutritional requirements of maintenance, lactation, growth and reproduction. Reproduction is believed to have lower priority than the other demands on energy.

Considering all factors that contribute to low reproductive rates, inadequate nutrition, particularly energy deficit, is believed to exert a major effect. A common phenomenon in energy deficient beef cows is a delay to resume estrous activity following parturition. Duration of the postpartum interval is influenced by other factors such as dystocia, parity, suckling stimulus and body condition at calving.

Studies have linked pre- and postpartum dietary energy levels to subsequent reproductive performance in beef cattle. Some studies have shown that reproductive efficiency is improved when beef cattle are fed high energy diets either prepartum, postpartum or both. Conversely, other studies found no reproductive benefit to prepartum and/or postpartum energy supplementation, especially to heifers calving in moderate to good body condition and maintaining this body condition postpartum.

Although studies have linked undernutrition to impaired activity of the hypothalamic-pituitary-ovarian axis, the exact mechanism by which nutrition affects endocrine patterns associated with reproduction has not

been fully elucidated. It is known however, that neuropeptide Y and insulin-like growth factor-1 may mediate the effect of nutrition on reproduction. A search of the literature did not reveal a nutritional and endocrinological characterization of reproductively efficient and inefficient first-calf beef heifers.

Thus, the studies reported herein attempted to examine the effect of varying energy status on reproductive performance of first-calf beef heifers. Emphasis was placed on first-calf heifers because their reproductive performance is usually lower than that of nulliparous and multiparous cows. A literature search revealed a lack of data that relates nutritional status and hormonal status to reproductive performance in first-calf beef heifers. Therefore, another objective was to determine the relationship between estimates of nutritional status with the reproductive success and its estimates of first-calf heifers. Estimates of nutritional status included metabolic body size, change in body weight and condition, serum non-esterified fatty acids and calf growth.

Measures of reproductive success included the length of postpartum interval, conception rate and calving rate. Gonadotropins (luteinizing hormone and follicle stimulating hormone) and ovarian steroids (progesterone, estrogen and androstenedione) served as estimates of reproductive success. In addition, these studies attempted to determine

how limited measurements of gonadotropins and ovarian steroids could predict reproductive competence (potential reproductive success) in first-calf beef heifers. The intent of the hormonal measurements was to test pituitary and ovarian competence by assessing the quantities of gonadotropins and ovarian steroids released in response to exogenous gonadotropin-releasing hormone and estrogen challenges, respectively, and to determine how these were related to reproductive success.

In summary, the objectives of these studies were to 1) evaluate the effects of varying energy status during breeding on reproductive performance of first-calf beef heifers, 2) examine the nutritional and hormonal differences between reproductively successful and unsuccessful first-calf heifers and 3) asses postpartum response of first-calf beef heifers to exogenous gonadotropin-releasing hormone and estrogen in order to determine whether prebreeding hormonal profiles were meaningfully related to nutritional status and reproductive success.

CHAPTER II

LITERATURE REVIEW

Nutritional Status and Reproductive performance

Determinants of Nutritional Status and its Indicators in Beef Females

Data reviewed by Short and Adams (1988) and Short et al. (1990) show that, in general, nutrients in a beef female are partitioned and prioritized for physiological functions in the following order : 1) basal metabolism 2) activity factor 3) growth 4) maintenance of basic energy reserves 5) gestation 6) lactation 7) additions to energy reserves 8) resumption of estrous activity and establishment of another pregnancy and finally 9) fattening.

One precise way of quantifying nutritional status is by calculating energy balance (EB) (Staples et al., 1990; Villa-Godoy et al., 1988, 1990a, 1990b). Energy balance is a sensitive measurement of energy status because it takes into consideration the energy requirements for each of the aforementioned physiological functions; compares the requirements to energy intakes and quantifies energy surplus and deficits (Staples et al., 1990; Villa-Godoy et al., 1988). Staples et al. (1990) define EB in the mature

lactating dairy cow as the difference between net energy intake plus energy derived from endogenous fat and the energy required for maintenance and lactation

i.e EB, Mcal $NE \cdot d^{-1} = NE_I - NE_m - NE_l + NE_{BWL}$

Positive (or Negative) EB therefore, occurs when the energy required by the animal exceeds (or is less than) the animal's intake (Villa-Godoy et al., 1988; 1990a; 1990b Canfield and Butler, 1991). Estimates of EB in beef cows are more difficult to determine because of the difficulties involved in determining feed intake. Beef cows generally graze pastures which are sometimes supplemented with hay, silage and concentrates. Dry matter intake (DMI) is therefore difficult to determine. Also beef cows are not milked and the calves not weaned early as in dairy production, hence it is not easy to determine milk production.

An animal's body condition, or degree of fatness, is often used as an indicator of nutritional status (Fox et al., 1984). When body condition is used in combination with changes in body weight (Houghton et al., 1990; Northcutt et al., 1992), EB (Staples et al., 1990) and concentration of blood metabolites (Trenkle and Kuhlemeir, 1966) and hormones sensitive to nutritional changes (Trenkle, 1971) it provides a reliable estimate of nutritional status.

Body condition scoring (BCS) is a subjective process used to evaluate degree of fatness (Fox et al., 1984;

Northcut et al., 1992). The body is visually appraised and assigned a score depending on the level of fat cover over the whole body, particularly over the ribs and around the pin and the hip bones. Two scoring systems are in common use. One of these uses a 1 to 9 point system (Richards et al., 1986; Rice, 1987), whereby 1 = emaciated and 9 = obese with five to seven designated optimum condition (appendix A). Another system scores body condition on a scale of 1 to 5 (Houghton et al., 1990), whereby 1 = emaciated and 5 = obese with three being the ideal body condition (appendix B).

An objective way of estimating body composition of a live beef cow is by measuring subcutaneous fat with an ultrasound measuring device, thus, it can serve as an indicator of nutritional status (Klosterman et al., 1968; Faulkner et al., 1990; Bullock et al., 1991). The fat thickness is measured on the area between the 12th and 13th rib and approximately 10 cm from the spine area (Faulkner et al., 1990; Bullock et al., 1991)

Other objective methods of estimating body composition include measurements of body weight and hip height and determinations of weight to height ratio (Klosterman et al., 1968; Houghton et al., 1990). Changes in body weight, body condition and back fat are easily determined and can be used by researchers, extension workers and farmers.

Non-esterified fatty acids (NEFA) can also indicate nutritional status (Easdon et al., (1985); Wettemann et al., 1986; Canfield and Butler, 1991). Plasma NEFA levels reflect the degree to which stored fat is mobilized from adipose tissue. Nonesterified fatty acids can be mobilized in response to hormones associated with sympathetic nervous stimulation induced by stress (epinephrine). However, if stress (handling, venipuncture etc.) is reduced at the time of blood sample collection, NEFA provide a reliable indicator of nutritional status (Dunshea et al., 1990; Rutter and Manns, 1991). Plasma NEFA levels have been shown to increase in fasted (Heitmann et al., 1986; Patterson, 1963; Trenkle and Kuhlemeir, 1966) or insulin-induced hypoglycemic ruminants (Trenkle and Kuhlemeir, 1966). In their study Dunshea et al. (1990) demonstrated a significant negative correlation between plasma NEFA concentration and EB in goats during early lactation. They also observed that NEFA entry rate into the circulation as measured from the carotid artery, the jugular vein and the right ventricle significantly decreased as days of lactation increased, indicating that the rate of lipolysis declined.

Indicators of nutritional status include both metabolic hormones and blood metabolites. Decreasing nutritional status is accompanied by decreasing plasma concentrations of growth hormone (GH) (Trenkle, 1971;

Villa-Godoy et al., 1990a, 1990b), insulin (Canfield and Butler, 1991) and/or glucagon, the ratio of which also decreases (Bassett, 1974). Blood glucose becomes low during nutrient deficiency or fasting but volatile fatty acids (Trenkle, 1971) or ketone bodies increase due to mobilization of endogenous fat (Heitmann et al., 1986; Kaufman and Bergman, 1971).

Nutritional Status During Early Lactation. Energy requirement increases during the last trimester of gestation due to the rapidly developing fetus and is highest during early lactation because of the high energy demand for milk production and repair of body tissues from parturition. Therefore, during early lactation the order in which the animal prioritizes the aforementioned physiological functions is altered such that after basic maintenance, activity and growth the mammary gland gets first priority (Short and Adams, 1988; Short et al., 1990). The demand for nutrients during early lactation in first-calf beef heifers is added to that required for growth, therefore, one might expect that they too will experience a negative EB (Short et al, 1990). In an attempt to meet the high demand for energy, cows will increase their intake or mobilize their adipose tissue or both (Moe et al., 1971).

Staples et al. (1990) examined the energy status of dairy cows during the first 63 d of lactation. They observed that during early lactation cows were in negative

EB (- 5.6 Mcal·cow^{-1}·d^{-1}). Positive EB was attained by 56 d postpartum.

Determinants of Reproductive Success and Fertility Indicators in Beef Females

Ideally, a beef female of the British breeds is considered reproductively successful if she reaches puberty by 14 mo of age or earlier and become pregnant at first service. It is also ideal for the said heifer to carry the fetus to term, deliver a healthy calf and return to a fertile estrus within 60 d of calving. An ability to sustaining a second pregnancy, but still wean a healthy calf with an average weaning weight characteristic of the heifer's age and breed also represents reproductive success. Thus, a heifer that can consistently maintain this reproductive performance (that is, a short postpartum interval (PPI), conception at first service, delivering a life calf each year, etc.) throughout it's life would be considered reproductively successful.

Ideally, an efficient beef production operation aims at producing a calf from each cow each year. This goal is achieved if a PPI of ≤ 80 d (assuming a gestation length that ranges from 282 to 287 d), is maintained (Holness et al., 1978; Dunn and Kaltenbach, 1980; Gauthier et al., 1982; Montgomery et al., 1982; Hanzen, 1986). As defined earlier, PPI represents the period from parturition to the first fertile estrus and conception (Acosta et al., 1983;

Short et al., 1990). The length of the PPI is affected by the level of pre and/or postpartum nutrition (Beal et al., 1978; Dunn and Kaltenbach, 1980; Imakawa et al., 1986; Nolan et al., 1988; Short and Adams, 1988; Short et al., 1990), body condition at calving (Dunn et al., 1969; Richards et al., 1986), suckling (Short et al., 1972, 1979; Kesler et al., 1980; LaVoie et al., 1981; Acosta et al., 1983; Hanzen, 1986), the genotype of the cow (Hansen et al., 1982; Hansen and Hauser, 1983), parity and calving difficulty (Doornbos et al., 1984; Laster et al., 1973) and season of calving (Bellows and Short, 1978).

First-calf heifers experience a longer (by 15 to 20 d) PPI than older cows (Wiltbank, 1970; Dziuk and Bellows, 1983). A long PPI may lead to calves being conceived late in a given breeding season, thus, these calves will be born late in the calving season and subsequently they will be younger and probably lighter at weaning (Corah et al., 1975; Bellows and Short, 1978). A long PPI also results in cows having long (> 365 d) calving interval, thus, affecting the efficiency of the whole herd.

Conception rate (the number of services it takes for each cow to become pregnant) is another criterion in judging reproductive success or failure of the cow herd. One service per conception should be ideal for any production system. However it has been observed that sometimes the first ovulation following parturition yields

a corpus luteum (CL) which is short lived (6 to 12 d) or produces a progesterone (P_4) level not sufficient (< .5 $ng \cdot ml^{-1}$) to sustain the CL hence conception fails to occur due to early regression of the CL (Short et al., 1972; LaVoie et al., 1981; Lishman and Inskeep, 1991). This infertile postpartum estrus/estruses necessitates several services for conception, thus affecting reproductive success of the cow herd.

Calving rate (the number of calves born alive and healthy to all cows exposed to the bull) is another indicator of reproductive success of the cow herd. So is the weaning rate of the cow-calf operation.

Postpartum luteinizing hormone (LH) pulse frequency is a reliable indicator of fertility. Parturition in beef females is followed by a period of anestrus (Nett, 1987; Short et al., 1990; Lishman and Inskeep, 1991). A major factor causing anestrus is that pulsatile release of LH is not sufficient (< .25 $pulses \cdot h^{-1}$) to induce follicular maturity hence ovulation (Nett, 1987). A CL lasting longer than 16 d and producing P_4 levels $\geq$ 1 $ng \cdot ml^{-1}$ for two consecutive days indicates ovarian activity, thus fertility (Short et al., 1972; Lishman et al., 1979; Canfield and Butler, 1991; Lishman and Inskeep, 1991).

In order to describe how nutrition may affect reproductive success a summary of events that culminate in postpartum anestrus is needed.

Regulation of Postpartum Estrous Cycle. During gestation, placental estrogen (E_2) and P_4 inhibit hypothalamic synthesis and release of gonadotropin releasing hormone (GnRH) (Nett, 1987; Short et al., 1990). As a result, GnRH pulse frequency is low, (< .25 pulses·h^{-1}) (Hanzen, 1986). Gonadotropin-releasing hormone induces synthesis and release of gonadotropins (LH and FSH). Therefore, a low serum level of GnRH is not sufficient to induce adequate pituitary synthesis and release of LH. Thus, at parturition, the pituitary store of LH is almost depleted (Nett, 1987). Following parturition, hypothalamic activity is still inhibited due to residual negative effect of low E_2 and P_4 (Walters et al., 1982b; Acosta et al.; 1983 Nett, 1987; Short et al., 1990) and the inhibitory effects of endogenous opioids released as a result of the suckling stimulus (Garcia-Winder et al., 1984; Acosta et al., 1986; Malven et al., 1986; Whisnat et al., 1986; Rice, 1987; Williams, 1990). As a result, GnRH secretion is still not sufficient to increase the frequency of LH pulses (Carter et al., 1980) beyond 1.25 pulses·h^{-1} (Short et al., 1990). Follicular growth is inhibited as a result of low LH pulse frequency (Nett, 1987) resulting in insufficient E_2. High concentration of E_2 is required to stimulate the hypothalamus to produce GnRH which leads to the pituitary preovulatory LH surge.

Initiation of Postpartum Estrous Cycle. The quantity of LH secreted as well as the frequency of LH pulses are critical to the reestablishment of the estrous cycle. The resumption of the estrous cycle begins with removal of the residual inhibitory effects of the gestational steroids (P_4 and E_2) on the hypothalamus and pituitary. Consequently, GnRH pulse frequency increases to about .25 pulse$\cdot h^{-1}$ (Nett, 1987). This stimulates some LH synthesis, but, since the GnRH pulses are infrequent, little LH is released so pituitary LH stores are replenished. Following this, an increase in GnRH pulse frequency leads to sufficient LH secretion to stimulate ovarian follicular growth. The growing follicles produce sufficient E_2 to cause estrus and ovulation (Kesler et al., 1980; Nett, 1987). Estrogen in high amounts leads to GnRH pulse frequencies of about 1.25 pulses$\cdot h^{-1}$ (Gauthier et al., 1982; Hanzen, 1986). This leads to preovulatory LH surge, (LH pulses frequencies of about 1 to 2 pulses$\cdot h^{-1}$) (Carruthers et al., 1980; Gauthier et al., 1982; Walters et al., 1982a), in turn leading to follicular maturation and ovulation.

Serum concentrations of follicle stimulating hormone (FSH) may increase slightly during the early postpartum period but generally are affected neither by the residual effects of P_4 and low E_2 following gestation (Gauthier et al., 1982; Manns et al., 1983; Nett, 1988) nor by suckling (Walters et al., 1982b; Cross et al., 1987). Therefore, FSH

is apparently not limiting to the recovery of the hypothalamic-pituitary-ovarian axis.

Recovery of the hypothalamic-pituitary-ovarian axis starts as early as 2 wk postpartum in nonsuckled beef cows (Rice, 1987; Nett, 1987) or cows calving in adequate to good body condition (Body condition score, BCS ≥ 5, Dunn et al., 1980; Richards et al., 1986; Warren et al ., 1988) and varies from 30 d to 6 mo in suckled beef cows (Rice, 1987) or those with a BCS ≤ 5 at calving (Whitman et al., 1975; Richards et al., 1986).

Nutritional Effect on Fertility in Beef Females

Prepartum Nutritional Effect on Fertility. This review will focus on the effect of prepartum nutrition on PPI and conception rate in beef cattle. Nutrition, particularly energy, is a major factor that greatly affects the length of the PPI in beef cattle (Wiltbank et al., 1962, 1964; Clanton and Zimmerman, 1970; Bellows and Short, 1978; Bartle et al. 1984; Short et al., 1990). Clanton and Zimmerman (1970) fed 32 bred yearling Hereford heifers four diets varying in protein and energy levels for 140 d prior to anticipated calving date. Percentage of 1963 NRC recommendations of protein and energy provided were 50% in maintenance ("low") and 75% in 1.5 times maintenance diets ("high"). Following calving the heifers were fed a common ration. Duration of postpartum anestrus in the low protein-low energy, low protein-high energy, high protein-low

energy and high protein-high energy diets was 142, 54, 148 and 51 d, respectively, with conception rates of 67, 38, 50 and 83%, respectively. Prepartum energy restriction resulted in a longer PPI (142 and 148 d) and lower conception rates (50 and 67%). Where protein was limiting and energy level was high, PPI was shorter (54 d) but conception rates were also low (38%). The data show that energy deficit greatly reduces reproductive performance. The heifers fed the high energy rations performed best. However, when protein was limiting conception was greatly reduced despite the high level of energy intake. This is because at this stage of their productive life, the heifers (2 yr old) require protein for growth and reproduction simultaneously and growth takes precedence over reproduction (Short and Adams, 1988; Short et al., 1990).

Bellows and Short (1978) also fed two groups of yearling bred beef heifers diets designed to provide 3.4 or 6.3 kg TDN·heifer^{-1}·d^{-1} according to the 1976 NRC recommendations for 90 d prepartum. They also observed that restricting prepartum energy intake increased PPI 21 d (87 vs 66 d) and reduced percentage of heifers showing estrus (47 vs 79%) before onset of the breeding season. These results further indicate that restricting nutrient intake prepartum impairs subsequent reproductive performance by extending PPI and reducing conception rates.

Wiltbank (1968) and Dunn et al., (1969) showed that some beef females can experience nutrient shortages and loss of body weight and condition prepartum but when adequately fed postpartum, their conception rate becomes similar to those unrestricted in nutrient intake prepartum. However, they will be calving late in the breeding season. These contradicting results could be due to differences in the amount of energy supplementation and the duration of the supplementation in addition to differences in the extent to which the cows had lost their body condition.

Postpartum Nutritional Effect on Fertility. An extended PPI (100 vs 76 d) (Wettemann et al., 1986) and lower conception rates (50 vs 90%) (Selk et al., 1988; Wettemann and Lusby, 1987) have been demonstrated in beef cattle fed energy intakes resulting in calving BCS $\leq$ 4 compared to $\geq$ 5. In a recent review on factors that control postpartum anestrus or PPI in beef cattle, Short et al., (1990) also concluded that body condition at calving is a major factor that affects PPI. This is because body condition at calving and PPI are linearly related, that is, theoretically an animal will have a longer PPI even if postpartum nutrition is adequate if that animal calved in a $\leq$ 4 BCS (9 point system). On the other hand there is little benefit on PPI that can be derived from increasing postpartum nutrient intake of cows that calve in BCS of $\geq$ 5 and maintain their body condition postpartum. A similar

conclusion was drawn by Dunn and Kaltenbach (1980) in their review of the effects of nutrition on PPI.

Dunn et al., (1969) fed two groups of nulliparous heifers diets that provided a daily intake of either 8.7 (low, L) or 17.3 (high, H) Mcal $DE_m \cdot heifer^{-1}$ of the 1963 NRC recommendations for approximately 137 d prepartum. Following calving, the L group was divided into two groups and fed diets that provided a daily energy intake of either 27.3 or 48.2 Mcal $DE_m \cdot heifer^{-1}$, designated low-moderate (L-M) and low-high (L-H) respectively. The H group was divided into three groups and fed diets that provided daily energy intake of 14.2, 27.3 and 48.2 Mcal $DE_m \cdot heifer^{-1}$, designated high-low (H-L), high-moderate (H-M) and high-high (H-H) respectively. Postpartum feeding period lasted 120 d. By 80 d postpartum 54% of the H-M heifers were pregnant compared to 32% of the L-M heifers. However, by 120 d postpartum pregnancy rate of the H-M and L-M heifers was similar (71 and 73% respectively). Conception rate of the L-H heifers was lower than that of the H-H group (51 vs 56%) at 80 d postpartum. But by 120 d postpartum the L-H heifers had also outperformed the H-H group (90 vs 83%). Only 33% of the H-L heifers were pregnant by 80 d postpartum and 64% by 120 d. These results suggest that restricting energy intake postpartum could be more detrimental to subsequent reproductive performance than restricting it prepartum, especially if an animal calved in an adequate body

condition but lost weight and condition during the postpartum period (as was the case with the H-L heifers). The results also show that precalving energy restriction extended PPI as indicated by conception rates of the H-L group being low early in the breeding season. When nutrient intake was increased postpartum the heifers recovered fast enough to be bred before the breeding season was over. However, it is possible that some heifers failed to be bred during the breeding season. Because of late conception some heifers will calve late and their calves will be smaller at weaning (Wiltbank, 1968; Dunn et al., 1969).

Wiltbank (1968) noted that first-calf beef heifers restricted in energy intake prepartum (2.0 vs 3.6 kg TDN) but adequately fed postpartum (5.9 kg TDN for both groups) had lower conception rates (32 vs 54%) during the first 20 d of the 60 d breeding season but by the end of the breeding season their conception rate was similar (73 vs 71%) to that of the group not restricted in energy intake prepartum. In the same study mature beef cows were also restricted in energy intake prepartum (2.1 vs 4.1 kg TDN) and both groups were fed 7.3 kg TDN postpartum. Pregnancy rate of the restricted cows during the first 20 d of the breeding season was lower (46 vs 60%) but by the end of the 60 d breeding season their conception rate was the same (95%) as in the group that was not restricted in energy intake prepartum. It seems that a heifer/cow loosing body

weight prepartum but gaining it postpartum is likely to conceive later in the breeding season, thus, affecting reproductive performance. However, this will depend on the extent of the prepartum weight loss. Whitman et al., (1975) also reported that body condition at calving is a major factor influencing occurrence of estrus between 60 and 90 d postpartum.

Richards et al., (1986) fed four groups of mature beef females starting at 3 d postpartum up to 30 d into the breeding season. Daily energy allowances were 25.8, 20.7 and 14.7 Mcal ME·cow^{-1}·d^{-1} for the high (H), moderate (M) and low (L) diets, respectively. The fourth group of cows, the low-flush (L-F), was fed 14.7 Mcal ME·cow^{-1}·d^{-1} from 3 d postpartum to 14 d before initiation of the breeding season whereby their energy intake was increased to 36 Mcal ME·cow^{-1}·d. Cows were also classified according to whether they calved in BCS of ≤ 4 or ≥ 5. Postpartum nutrition or flushing had no effect on the time from parturition to the first sign of estrus activity, days to pregnancy and pregnancy rates within beef cows of the same BCS at calving. However, cows calving in body condition score of ≥ 5 had a significantly shorter PPI (84 vs 90 d) than those calving in BCS ≤ 4. Fewer of the cows in BCS ≤ 4 and fed a low diet conceived to the first service (54 vs 69%) and had overall the lowest pregnancy rate (68 vs 88%). By the end of the 60 d breeding season the flushed (L-F) group

performed equally and sometimes better than the H and M groups. Whereas, the L group performed poorer on all reproductive parameters. These results indicate that energy intake, in relation to conception rate, may be more crucial at breeding than soon after calving because cows that showed better reproductive performance had an increase in energy intake shortly prior to breeding.

Warren et al., (1988) conducted a study similar to that of Richards et al., (1986) but observed no significant effect of postpartum energy intake on reproductive performance, which is in agreement with Richards et al., (1986) results for cows calving in BCS ≥ 5. All cows in Warren et al., (1988) study had calved in BCS ≥ 5. Rutter and Randel (1984) also found that cows that lost body condition (by 1.5 points) during 42 d following parturition had longer PPI (60 vs 32 d) and fewer exhibited standing estrus (35% vs 88%) when compared to cows that maintained body weight. These results further strengthen the importance of body condition at calving as it relates to subsequent reproductive performance. They show that cows maintaining good body condition (BCS ≥ 5) after calving have enhanced reproductive performance compared to those losing body condition.

Nutritional Effect on Postpartum Reproductive Hormone Profiles. During gestation, high levels of P_4 and E_2 exert a negative effect on the hypothalamic-pituitary axis.

Release of GnRH from the GnRH neurone is inhibited; thus there is reduced synthesis and release of LH from the gonadotrophs. Because of insufficient LH (< 1 pulse·4 h^{-1}) follicular maturity does not occur, thus E_2 production is not high enough to induce preovulatory LH surge (Nett, 1987; 1988). Initiation and maintenance of normal estrous cycles is a function of the coordinated activities of the hypothalamus, the pituitary and the ovaries (Nett, 1987; Griffin and Ojeda, 1988). Therefore, a cow's delay to resume normal estrous activity following parturition (Short et al., 1990) could result from the malfunction of any or all of the components of the axis.

The relationship between nutrition and reproductive hormones has been reviewed by Short and Adams, 1988; Short et al., 1990; Dunn and Moss, 1992). They concluded that restricting energy intake either pre- and/or postpartum has a more suppressive effect on postpartum activity of the hypothalamic-pituitary axis than the residual effects of fetal-placental steroids (P_4 and E_2) (Walters et al., 1982b; Acosta et al., 1983) and suckling-induced opioids (Garcia-Winder et al., 1984; Acosta et al., 1986). Energy deficiency increases the hypothalamic-pituitary axis' response to the negative effects of P_4 and E_2; thus negatively affecting events leading to the preovulatory LH surge.

Rutter and Randel (1984) found that cows that lost body condition (by 1.5 points) after calving had significantly lower levels of plasma LH (.61 vs .83 $ng \cdot ml^{-1}$) at 21 d postpartum than those maintaining body condition. The authors concluded that cows maintaining body condition have enhanced LH production compared to those loosing body condition. Apgar et al., (1975) also observed that basal plasma LH concentration in heifers restricted in intake (60 vs 100% of Morrison's (1956) TDN recommendations) for approximately 63 d postpartum was significantly reduced (1.7 vs 4.1 $ng \cdot ml^{-1}$). They concluded that the decrease in LH may have been due to increased sensitivity of the hypothalamus to the negative effects of P_4.

Gauthier et al. (1983) observed that beef cows restricted in energy intake (10.38 vs 15.57 $Mcal \cdot d^{-1}$ NE_m) from parturition to 45 d postpartum had lower mean plasma LH (1.9 vs 2.4 $ng \cdot ml^{-1}$) and FSH (86 vs 101 $ng \cdot ml^{-1}$) concentrations during 30 d postpartum than did cows not restricted in energy intake. These authors concluded that the high level of P_4 (5.7 vs 4.6 $ng \cdot ml^{-1}$) seen in underfed cows may have resulted in reduced plasma LH and FSH shortly following parturition.

The cows in the Gauthier et al. (1983) study had been restricted in energy intake (7.7 vs 12.11 $Mcal \cdot d^{-1}$ NE_m) for the 70 d preceding parturition. At 14 d prior to

parturition cows that were restricted in energy intake had significantly higher (5.7 vs 4.6 $ng \cdot ml^{-1}$) P_4 concentrations in their peripheral blood than did cows not restricted in energy intake. None of the cows on a restricted diet had resumed cyclicity by 30 d postpartum, whereas 50% of the cows not restricted in energy intake had ovulated. Corpus luteum (CL) of the first ovulation had a short lifespan (5 to 10 d) and plasma P_4 content was low (< 1 vs ≥ 3 $ng \cdot ml^{-1}$). They concluded that the low levels of LH and FSH delayed the onset of estrus.

In contrast, Apgar et al., (1975) observed that although the CL of heifers restricted in intake were significantly smaller (4.4 vs 6.4 g), P_4 production was not affected by diet. These authors concluded that the decrease in the size of the CL may have been due to reduced LH secretion. A lack of dietary effect on P_4 plasma concentration was attributed to the fact that designed dietary variation did not yield variation in body condition of experimental cows. That is, cows restricted in intake did not become nutritionally stressed.

Boyd et al., (1987) noted that cows fed a low-energy diet (Coastal bermuda grass hay and pasture) for 50 d preceding parturition had higher (6.9 vs 4.9 $ng \cdot ml^{-1}$) levels of P_4 at 10 d prior to parturition than cows fed a high-energy diet (Coastal bermuda grass hay, pasture and 2.7 kg ground $corn \cdot head^{-1} \cdot d^{-1}$). Estrone ($E_1$) levels in the

peripheral circulation of cows fed a low-energy diet were higher (.65 vs .43 $ng \cdot ml^{-1}$) at 30 d before parturition than in cows fed a high-energy diet. By 10 d prepartum serum estrone sulfate (E_1SO_4) and E_1 concentrations for the low-energy fed cows were 9.8 and 1.5 $ng \cdot ml^{-1}$ respectively, and for the high-energy fed cows these values were 7.9 and 1.3 $ng \cdot ml^{-1}$ respectively. These authors suggested that because E_2 increases uterine blood flow and facilitates nutrient transfer to the fetus, higher levels of E_2 observed in cows fed a low-energy diet may reflect increased ovarian steroid production in an attempt to increase nutrient extraction efficiency by the feto-placental unit. In contrast, concentrations of E_2 may be lower in cows fed a high energy diet because less uterine blood flow may be required for the development and maintenance of the fetus.

Insulin-like growth factor-1 (IGF-1) has been suggested as a potential regulator of ovarian activity during early lactation in dairy cows (Spicer et al., 1990) and in nonlactating beef cows (Richards et al., 1991). Serum IGF-1 concentration increases with increasing EB (Spicer et al., 1990; Richards et al., 1991). Rutter et al., (1989) noted that IGF-1 was higher (168 vs 115 $ng \cdot ml^{-1}$) in beef cows infused with 4 $mg \cdot kg^{-75} \cdot min^{-1}$ of glucose for 6 d starting from 26 d following parturition compared to cows infused with saline solution. They concluded that serum concentration of IGF-1 is influenced by energy

availability. Concentration of IGF-1 is high in follicular fluid (Mondschein et al., 1989; Richards et al., 1991) and E_2 has been found to induce IGF-1 production (Richards et al., 1991), (E_2 is in turn induced by FSH and LH). Mondschein et al., (1989) demonstrated that IGF-1 may be involved as a mediator of the stimulatory effects of FSH, E_2 and GH on P_4 production by the granulosa cells of swine.

Spicer et al., (1990) studied the relationships between EB, ovarian activity and IGF-1 in dairy cows from parturition to 85 d following parturition. They observed that cows in a positive EB (3.4 $Mcal \cdot d^{-1}$) had significantly higher serum IGF-1 (102.5 vs 78.8 $ng \cdot ml^{-1}$) at 35 d after parturition compared to those in a negative EB (-1.69 $Mcal \cdot d^{-1}$). These authors also observed that peaks in P_4 secretion were higher (13.1 vs 6.4 $ng \cdot ml^{-1}$) in cows in a positive EB than those in a negative EB. Eighty percent of cows in a positive EB ovulated by 56 d postpartum compared to 67% of cows in a negative EB. They suggested that because EB is positively correlated to IGF-1, and high levels of IGF-1 stimulates P_4 production by the luteal cells in cows, IGF-1 may mediate the effects of EB on luteal function. These authors further suggest that expression of ovarian activity during early lactation could be suppressed because of reduced production of E_2 by ovarian follicles and that E_2 production could be reduced by IGF-1.

Recently the possibility that the neurotransmitter, neuropeptide-Y (NPY) may be a link between nutrition and reproduction has been raised (McShane et al., 1992; Miner, 1992). Hunger or undernutrition increases levels of NPY in the brain (Miner, 1992). The Hypothalamus and other parts of the brain of anorexic women, rats and sheep restricted in intake have been found to contain high levels of NPY (Miner, 1992) and NPY has been found to decrease pulsatile LH release (McShane et al., 1992). McShane et al., (1992) suggest that undernutrition may affect reproduction by diminishing GnRH release and that this effect may be mediated by NPY.

Effect of Nutritional Status on the response of Beef Heifers to Exogenous Gonadotropin-Releasing Hormone. The competency of the hypothalamic-pituitary-ovarian axis to resume activity following parturition can be evaluated with exogenous hormonal challenges (Lishman et al., 1979; Killen et al., 1989). Challenge means testing the response of an organ to a specific exogenous substance. Gonadotropin releasing hormone stimulates the gonadotrophs of the pituitary to release the gonadotropins LH and FSH (Griffin and Ojeda, 1988). Available LH and FSH in the gonadotrophs is released in response to a GnRH challenge (Nett et al., 1988; Dunn and Moss, 1992). A large single dose of GnRH causes the release of the store of LH and FSH. Thus, it provides a direct index of pituitary competence and an

indirect competence of hypothalamic competence in that E_2 produced in response to released LH and FSH will stimulate GnRH synthesis and release, ultimately leading to preovulatory LH surge. Exogenous GnRH can also provide an evaluation of ovarian function because E_2 production from granulosa cells of follicles will increase in response to LH and FSH. Injections of E_2 provide another means of evaluating hypothalamic and pituitary function. High quantities of E_2 during the follicular phase of the estrus cycle (Lishman et al., 1979) induce an increase in the pulsatile release of GnRH from the GnRH neuron. The GnRH released stimulates LH synthesis and release from the gonadotrophs. It is the occurrence of GnRH release and increased LH pulse frequency that culminates in the preovulatory LH surge which stimulates follicular maturity and ovulation. Follicle stimulating hormone stimulates follicular growth and the production of E_2, thus exogenous FSH can also provide a means of evaluating ovarian function (Lishman et al., 1979).

Killen et al., (1989) studied the effect of nutrition on response to GnRH challenge in 52 crossbred 2-yr old heifers. From 90 d prior to anticipated calving date to parturition, heifers were fed at either 2%, 1.5% or 1% of their body weights of a 1.9 Mcal ME$\cdot$kg^{-1} diet. These diets were intended to cause either gain, maintenance or loss of body weight, respectively. The heifers were challenged with

a single dose of 100 μg GnRH i.m. The challenge was administered at 14 d pre and 14 d and 21 d postpartum. Serum LH concentration was quantified from blood samples taken 30 min prior to each GnRH injection and every 30 min for 4 h following the injection. Prepartum GnRH-induced LH peak concentrations were higher in heifers either loosing or maintaining body weight than in heifers maintaining or gaining body weight (74.4 vs 64.9 vs 29.6 $ng \cdot ml^{-1}$ respectively). The authors concluded that the high amount of LH released prepartum reflects the releasable form available from the pituitary but whose release is being inhibited by gestational steroids compounded by nutritional stress. They also suggest that nutritional stress during gestation may suppress pulsatile release of GnRH and LH thus increasing pituitary LH content. However, mean GnRH-induced LH peak concentration in the heifers during both postpartum challenge periods was higher in those gaining body weight than in those loosing or maintaining body condition (31.7 vs 18.4 vs 14.6 $ng \cdot ml^{-1}$ respectively). The authors suggested that nutritional stress during gestation may lead to postpartum reduction of pituitary LH stores. Hence, heifers that lost body weight during gestation had the lowest postpartum pituitary LH content. Rutter and Randel (1984) also observed that in response to a 100 μg GnRH injection given 21 d postpartum, cows gaining body condition released more LH (45 vs 33 $ng \cdot ml^{-1}$) than those

maintaining body condition. Thus, they concluded that an increase of nutrient intake in cows that maintain body condition enhances pituitary function.

To study the effect of nutrition on pituitary response to GnRH Lishman et al., (1979) fed heifers at either 115% or 60% of the 1970 NRC energy requirements from 30 d prepartum to 48 d postpartum. On 34 d postpartum the heifers were injected with 300 μg of GnRH and blood samples taken every 30 min. for 7 h for LH analysis. The LH released did not differ significantly between the dietary groups in response to GnRH treatment. However, the LH released by heifers fed the high plane of nutrition peaked 30 min earlier than in heifers that were fed the low plane of nutrition. Lishman et al., (1979) speculated that the delay in response to GnRH observed in underfed heifers may have been due to deficient pituitary LH stores.

Gautheir and Mauleon (1983) studied two groups of multiparous cows that were fed to either lose (310 $g \cdot cow^{-1} \cdot d^{-1}$) or gain (70 $g \cdot cow^{-1} \cdot d^{-1}$) body weight during the interval of 45 d prepartum to 45 d postpartum. At 5, 15 and 30 d postpartum the cows were injected with 55 μg GnRH and serial blood samples were taken starting at 15 min prior to each injection to 4 h after the injection. Plasma LH concentration of cows loosing body weight was significantly higher (192.6 vs 83.2 $ng \cdot ml^{-1}$) than in cows gaining body weight. They concluded that undernutrition reduces the

hypothalamic content of GnRH and that the pituitary of underfed cows contains more LH in a releasable form. Gautheir and Mauleon (1983) further noticed that the CL formed as a result of the GnRH-induced ovulations were of short duration (< 15 d) with a P_4 content of < 1 $ng \cdot ml^{-1}$ for both dietary groups.

The results of Rutter and Randel (1984) and Killen et al., (1989) show a tendency towards a negative correlation between nutritional status and LH production in response to GnRH challenge during the postpartum period in beef cows. The data further suggest that increasing nutrient intake during early lactation enhances hypothalamic, pituitary and ovarian function.

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CHAPTER III

EFFECT OF ENERGY LEVEL ON REPRODUCTIVE EFFICIENCY OF FIRST-CALF BEEF HEIFERS

Abstract

First-calf Angus heifers (n = 26) were utilized to study the effect of increased energy intake during breeding on reproductive performance. One half of the heifers was fed corn silage at 7.0 kg·heifer^{-1}·d^{-1} and pasture (lower energy group) the other half (higher energy group) was supplemented with 3.5 kg corn grain·heifer^{-1}·d^{-1} in addition to silage and pasture. The supplementation period extended from 22 d before the beginning of the breeding season to 22 d into the breeding season. Body weights (BW) and backfat were determined at the beginning and end of the supplementation period. The estrous cycle was synchronized with prostanglandin and synchromate-B. The competence of the hypothalamic-pituitary axis was assessed by measuring luteinizing hormone (LH) and follicle stimulating hormone (FSH) in blood samples collected 0 and 2 h after the heifers were injecting with a bolus of gonadotropin-releasing hormone (GnRH). Ovarian activity was assessed by quantifying progesterone (P_4). Basal samples were analyzed for non-esterified fatty acids (NEFA). Reproductive traits evaluated included duration of the postpartum interval (PPI),

conception rate, calving rate and weaning rate. There was no significant effect of diet on BW gain, NEFA, P_4, LH, FSH, response to GnRH, reproductive performance or performance of the first calf. Heifers fed the higher energy diet accumulated more backfat (1.5 vs .4 mm) ($P < .05$) than those fed the lower energy diet. Serum NEFA concentrations tended to be higher for heifers fed the lower energy diet. During the last 22 days of supplementation heifers fed the higher energy diet tended to have lower serum P_4 and higher LH concentration. Heifers fed the higher energy diet tended to have longer PPI and lower conception rate at first service. Based on these results increasing the energy intake for approximately three weeks prior to and three weeks during the breeding season of heifers fed 7.0 $kg \cdot d^{-1}$ corn silage and pasture does not improve reproductive performance.

Key Words: Heifers, Energy Intake, Body Condition, GnRH, Postpartum Interval, Conception

Introduction

Replacement heifers are often first bred at 14 to 16 mo to calve at 23 to 25 mo of age (Dziuk and Bellows, 1983). Conception rate following the first parturition is usually low (Dziuk and Bellows, 1983), because rebreeding occurs when energy demands for lactation and growth exceed energy intake. Cows and heifers in negative energy balance are

generally anestrous (Short and Adams, 1988; Short et al., 1990).

Therefore, first-calf heifers generally experience a prolonged postpartum interval (PPI), a period from parturition to first successful conception (Wiltbank, 1970; Dziuk and Bellows, 1983) or fail to become pregnant during a fixed breeding period. Heifers with a long PPI calve late in the season and thus have a calving interval longer than 365 d. Calves born late will be younger and/or lighter at weaning (Corah et al., 1975; Bellows and Short, 1978; Dunn and Kaltenbach, 1980), thus, a method that reduces the PPI is highly desirable.

Some studies have shown that increasing the energy intake of first-calf beef heifers shortly before or early in the breeding season increases ovulation rate and enhances conception rate (Dunn et al., 1969; Richards et al, 1986). But in other studies no effect on reproductive performance was found (Spitzer et al., 1978; Warren et al., 1988). Inconsistent results could be due to variation in the heifers' nutritional status and/or condition at calving and at breeding. Duration or level of energy supplementation could also be a factor.

The objective of this study was to examine the effects of varying energy intakes at breeding on the reproductive performance of first-calf beef heifers challenged with exogenous gonadotropin releasing hormone (GnRH).

Materials and Methods

Animals, Diets and Management

Twenty-six spring calving first-calf Angus heifers (24 to 29 mo old) were used in this experiment. Pre-experimental diets consisted of corn silage fed at approximately 7 $kg \cdot heifer^{-1} \cdot d^{-1}$. Hay, pasture and mineral mix were available free choice. All heifers were managed the same until 23 d before the initiation of breeding. At this time they were divided into two groups based on sire, age and age of calf. Both groups were kept on separate but similar pastures of mainly tall fescue and some orchard grass until the end of supplementation (d 44). Dietary treatments were (Table 1) : 1) lower energy, corn silage fed at approximately 7 $kg \cdot heifer^{-1} \cdot d^{-1}$ 2) higher energy, corn silage as in treatment 1 plus a supplement of 3.5 kg cracked $corn \cdot heifer^{-1} \cdot d^{-1}$.

Nutritional and Calf Measurements

Feed offered and refused was recorded. Duplicate feed and pasture samples were taken every ten days. The day following assignment to treatments (d 2, Appendix C), heifers were weighed and thickness of subcutaneous fat was determined by Sonaray in the area between the 12th and 13th rib. This procedure was repeated on the last day of feed supplementation (d 44).

Table 1. Intake of first-calf Angus heifers during breeding

Item	Diet[a]	
	Low energy	High energy
Number of animals	13	13
Feed intake, kg·heifer^{-1}·d^{-1}		
Corn silage	7.0	7.0
Corn grain	--	3.5
Pasture	free choice	free choice

[a]Dry matter basis.

GnRH Challenge, Blood Collection and Breeding

On d 2 heifers were injected with 5 mg of prostaglandin F2 alpha ($PGF_{2\alpha}$, Lutalyse, The Upjohn Co, Kalamazoo, MI) to induce regression of the corpus luteum (CL) and thereby effect a degree of estrous synchronization. A blood sample was taken from the non-catheterized jugular vein for P_4 analysis. A progesterone (P_4) concentration of > 1 $ng \cdot ml^{-1}$ signals the presence of an active CL.

On d 10, heifers were injected with $PGF_{2\alpha}$ to complete synchronization of the estrous cycle. On d 11, heifers were injected with 10 μg of a GnRH analogue (des-gly^{10},[D-Ala^6]-GnRH-ethylamide, Sigma Co., St. Louis, MO). Blood was collected at 0 h and 2 h after the injection and assayed for P_4 LH and FSH.

During collection of the last blood sample, a synthetic progestin, norgestomet or Synchromate-B (CEVA laboratories, Inc. Overland Park, KS) was administered. Synchromate-B implantation was coupled with an injection of 2 mg 17ß-estradiol-3-Benzoate (E_2, Sigma Co, St. Louis, MO). Nine days following implantation (d 20) the Synchromate-B was removed. Forty-eight hours later (d 22) the heifers were artificially inseminated (AI) and a blood sample was collected for characterization of hormonal profiles at this stage.

Eleven days following AI (d 33) a blood sample was collected for a determination of ovulation rate and as an early indicator of incidence of pregnancy. A final blood

sample was collected on the last day of supplementation (d 44 or 22 d after AI) for pregnancy determination. Thirty days following AI (d 52) heifers were placed with a bull. Sixty days following the end of the 90 d breeding season heifers were rectally palpated for pregnancy determination.

Reproductive Determinants

Breeding to conception interval was calculated as the period from AI for the second breeding to the second calving minus gestation. This calculation is equivalent to the period from the first parturition to the second parturition minus gestation minus the period from first parturition to AI. This postpartum interval was designated PPI-1. This calculation is biased against heifers that calve late because they may be exposed for breeding before resuming postpartum estrus activity. Thus, heifers calving late may appear to have a longer breeding to conception interval when compared to heifers that calved early.

Postpartum interval was calculated as the period from the date of the first calving to the second minus gestation. This PPI is artificially extended and was designated PPI-2. The heifers were managed such that breeding commenced at a set period (April), thus heifers who calved early (January to February) appeared to have a longer calving interval than those who calved late. Gestation length was estimated to be 281 d which is the observed average for first-calf heifers of the Angus breed.

The number of estrous cycles required for conception from the time of AI to conception was back-calculated from the second calving date (assuming 281 d of gestation and 21 d per estrous cycle). Other criteria defining reproductive efficiency included calving rate and weaning rate.

Chemical Analysis

Samples of feed, pasture and refused feed were oven dried at 60 C and ground to pass through a 1 mm screen of a Willey mill. Chemical analysis included dry matter (DM), crude protein (CP) and gross energy (GE) according to A.O.A.C. (1984), and neutral detergent fiber (NDF), acid detergent fiber (ADF) and lignin according to Goering and Van Soest, (1970).

Blood samples were immediately placed on ice, transported to the laboratory for centrifugation at 1764 X g for 20 min. Serum was harvested and stored at - 20 C until analyzed for non-esterified fatty acids (NEFA), or subjected to radioimmunoassays (RIA) to quantify P4, LH and FSH.

Concentrations of NEFA were determined in serum with a "Wako NEFA C test kit", (Wako Pure Chemicals Industries, Dallas, TX). The procedure allows an enzymatic colorimetric determination of NEFA in plasma or serum.

Radioimmunoassays

Progesterone was quantified according to the method of Surve et al. (1976). The antibody for P_4 (#332) was provided by Dr. Ali H. Surve (Sandoz Research Institute, Hanover, NJ). The P_4 used in the reference curve, came from Sigma

(Sigma Co., St. Louis, MO) and tritiated P_4 came from Amersham (Amershan Co., Arlington Height, Il). The sensitivity of the assay was 10 pg·tube^{-1} and intra- and interassay coefficients of variation (CV) were 5% and 9%, respectively for five assays of a serum pool.

Concentrations of LH were determined using a double antibody RIA described by Niswender et al. (1969) and modified by Bolt et al. (1981). The antibody for LH (# 15 antiovine LH) was provided by Dr. G. Niswender (Colorado State University, Fort Collins, CO). Purified LH (LER-1072-2, provided by Dr. L. E. Reichert, Albany, NY), was used as the iodinated tracer; whereas, USDA-bLH-B-5 (provided by Dr. D. G. Bolt, USDA, Beltsville, MD) was used for the reference curve. Assay sensitivity was 31.3 ng·tube^{-1}. The intra- and interassay CV were < 5% and < 8%, respectively.

For the FSH analysis the procedure used was that of Bolt and Rollins (1983). The antibody used was USDA-5-0122. USDA-bFSH-1 and USDA-bFSH-I-2 were used for the reference curve and iodination, respectively. All products were supplied by Dr. D. J. Bolt (USDA, Beltsville, MD). The sensitivity of the assay was .12 ng·tube^{-1}. The intra- and interassay CV were < 5% and < 9% respectively.

Statistical Analysis

Data were analyzed as a completely randomized design (CRD) using the GLM procedure of Statistical Analysis System (SAS) (1989). Least Significant Difference (LSD) procedure

was used to separate significant treatment means. The model statement was:

$$Y_{ij} = \mu + \tau_i + \epsilon_{ij}$$

Where:

Y = Change in body weight
Or Change in backfat
Or Non-esterified fatty acid concentration
Or Postpartum interval
Or Hormonal Concentrations (LH, FSH & P_4)
Or Services·Conception^{-1}
i = Number of treatments (n = 2)
j = Number of animals within a treatment (n = 13)
μ = Grand mean
τ = Treatment (lower & Higher Energy)

ϵ = Experimental error

Pearson correlations were run among nutritional and reproductive performance traits, NEFA and reproductive hormone concentrations using SAS (1989) procedures.

Results

Chemical composition of experimental diets is shown in Table 2 and changes in body characteristics of the heifers during the 43 d of supplementation is shown in Table 3. Body weight increase, although not significant (P > .10) was 7% for heifers fed the higher energy diet and 5% for those fed the lower energy diet. Backfat measurements of heifers fed the higher energy diet were significantly higher (1.5 vs .4 mm) than those of heifers fed the lower energy diet. Despite the designed differences in dietary composition for the two groups, there was no significant difference in PPI,

Table 2. Chemical composition of diets, %[a]

Item	Diet		
	Pasture	Corn silage	Corn grain
Crude protein,	23.5	8.4	7.6
Detergent fiber,			
Neutral	48.7	59.0	24.2
Acid	24.3	35.6	5.1
Lignin	2.8	4.8	1.3

[a]Dry matter basis.

Table 3. Effect of lower and higher energy diets during breeding on body characteristics of first-calf Angus heifers

Item	Diet[a]		
	Lower energy	Higher energy	SE
Number of animals	13	13	
Body weights, kg[b]			
Initial	420.8	402.1	8.4
Final	444.7	431.8	8.7
Change	23.9	29.7	2.8
Average daily gain, $kg \cdot d^{-1}$	0.6	0.7	
Backfat estimates, mm[b]			
Initial	3.0	2.8	0.137
Final	3.4[c]	4.3[d]	0.169
Change	0.4[c]	1.5[d]	0.197

[a]Lower represents heifers not supplemented with corn grain.
Higher, high energy intake, these heifers were supplemented with corn grain at 3.5 $kg \cdot heifer^{-1} \cdot d^{-1}$ for 44 d.
[b]During 44 d of supplementation.
[cd]Means within a row with different superscript differ ($P < .05$).
SE = Standard error of the pooled mean.

number of estrous cycles per conception, calving rate or weaning rate due to treatment (Table 4).

Serum NEFA concentrations (Table 5) for d 2 and d 44 were excluded from the analysis due to inconsistency of the relationship between NEFA and body condition. Heifers fed the higher energy diet had lower ($P = .07$) serum NEFA (278 vs 318 $\mu m \cdot ml^{-1}$) during the supplementation period than those fed the lower energy.

The effects of diet on basal concentrations of reproductive hormones are shown in Table 6. One heifer from the higher energy group and two from the lower energy group had serum P_4 concentrations higher than 1 $ng \cdot ml^{-1}$ at the beginning of supplementation indicating the presence of a functional CL, thus, their P_4 data for this period was excluded from the analysis. Overall, there was no significant effect of diet on basal serum P_4, LH and FSH concentrations. Heifers fed the higher energy diet tended to have lower levels of basal P_4 and higher levels of basal LH and FSH compared to heifers fed the lower energy diet (Table 6). On d 2 the basal serum LH of heifers assigned to the higher energy diet was higher ($P < .01$) than in heifers designated to be fed the lower energy diet. However, 11 d into the supplementation period heifers fed the lower energy diet had serum LH concentration higher ($P < .05$) than in heifers fed the higher energy diet (Table 7). On d 22 of supplementation heifers, fed the high energy diet had

Table 4. Reproductive performance of first-calf Angus heifers as affected by diet during breeding

Item	Diet[a]		
	Lower energy	Higher energy	SE
Number of animals	12	12	
Postpartum interval-1, d[b]	24	38	5.1
Postpartum interval-2, d[c]	93	100	5.6
Estrous cycles·conception^{-d}	1.8	2.4	0.2
Calving rate, %	92	92	
Weaning rate, %	92	92	

[a]Lower represents heifers not supplemented with corn grain.
Higher, high energy intake, these heifers were supplemented with corn grain at 3.5 kg·heifer^{-1}·d^{-1} for 44 d.
[b]Postpartum Interval-1 = Period from birth of the first calf to birth of the second calf - 281 - the period from first calving to AI.
[c]Postpartum Interval-2 = Period from birth of the first calf to birth of the second - 281 d
No statistical significance was detected between treatments ($P > .10$).
SE = Standard error of the pooled mean.

Table 5. Changes in concentration of non-esterified fatty acids during breeding, $\mu m \cdot l^{-1}$

Day[b]	Event[c]	Diet[a] Lower energy	Higher energy	SE
	Number of animals	13	13	
2	$PGF_{2\alpha}$	306[e]	201[f]	19
11	GnRH, T=0	258	222	13
22	AI	387	338	21
33	11 days post AI	311	275	12
44	22 days post AI	172[e]	220[f]	11
	Overall Mean[d]	287[e]	251[f]	19

[a]Lower represents heifers not supplemented with corn grain.
Higher, high energy intake, these heifers were supplemented with corn grain at 3.5 $kg \cdot heifer^{-1} \cdot d^{-1}$ for 44 d.
[b]Day of corn supplementation.
[c]Event, represents what was performed on the heifers $PGF_{2\alpha}$ = Prostanglandin-F-2-alpha, 5 mg i.m.
GnRH = Gonadotrophin releasing hormone, 10 μg i.m. T = 0, basal blood sample.
AI = Artificial insemination.
[d]Mean for d 11 d 22 and d 33 only.
[ef]Means within a row with different superscript differ (P = .07).
SE = Standard error of the pooled mean.

Table 6. Means of basal reproductive hormones of first-calf Angus heifers during breeding

Day[a]	2	11	22	33	44	
Event[b]	$PGF_{2\alpha}$	GnRH T=0	AI	11 d post AI	22 d post AI	Overall Mean
Diet[c]						
	---------progesterone, $ng \cdot ml^{-1}$----------					
Lower	.53	.29	.46	1.58	.98	.77
Higher	.52	.33	.35	1.32	.80	.67
SE	.04	.01	.06	.14	.12	.06
	---Luteinizing hormone, $ng \cdot ml^{-1}$----------					
Lower	.56[d]	.88[d]	.78	.60	.62	.69
Higher	.79[e]	.54[e]	.70	.74	.81	.72
SE	.05	.055	.05	.07	.08	.03
	--Follicle stimulating hormone, $ng \cdot ml^{-1}$--					
Lower	1.85	2.13	1.49[f]	1.64	1.56	1.73
Higher	1.92	2.04	1.70[g]	1.65	1.65	1.79
SE	.05	.10	.06	.06	0.90	0.04

[a]Day of corn supplementation, (44 d).
[b]Event, represents what was performed on the heifers.
$PGF_{2\alpha}$ = Prostanglandin-F-2-alpha, 5 mg i.m., d 2 & d 10
GnRH = Gonadotrophin releasing hormone, 10 μg i. m.
T = 0, basal blood sample.
AI = Artificial insemination.
[c]Lower represents heifers not supplemented with corn grain, n = 13.
Higher, high energy intake, these heifers were supplemented with corn grain at 3.5 $kg \cdot heifer^{-1} \cdot d^{-1}$, n = 13.
[de]Means within a column with different superscripts differ ($P < .01$) and ($P < .05$) respectively.
[fg]Means within a column with different superscripts differ ($P < .10$).
SE = Standard error of the pooled mean.

significantly higher levels of FSH than heifers fed the lower energy diet.

The hormonal response to GnRH is shown in Table 7 (d 11 T=0 and T=1). Heifers fed the higher energy diet had numerically greater concentrations of P_4 at the time of GnRH injection compared to those fed the lower energy diet (.33 vs .29 $ng \cdot ml^{-1}$). The magnitude of P_4 increase in response to GnRH was twice as high in heifers fed the higher energy diet (.33 to .49 vs .29 to .36 $ng \cdot ml^{-1}$). However, the magnitude of the P_4 response to GnRH was small (.12 $pg \cdot ml^{-1}$) for both dietary groups. Concentration of GnRH-induced LH increased from .54 to 4.20 $ng \cdot ml^{-1}$, (a 7.8 fold increase) for heifers fed the higher energy diet compared to an increase from .88 to 4.68, (a 5.3 fold increase) for heifers fed the lower energy diet. Release of FSH in response to GnRH was greatest in heifers fed the higher energy diet (2.04 to 2.87 vs 2.13 to 2.50 $ng \cdot ml^{-1}$). The magnitude of FSH response to GnRH was small (.6 $ng \cdot ml^{-1}$) for the two dietary groups.

The number of heifers with a functional CL at various times during supplementation is shown in Table 8. Results at d 2 do not represent the effect of diet. Between d 2 and d 22 of supplementation one heifer and three heifers from the higher and lower energy diets respectively had basal serum P_4 content > 1 $ng \cdot ml^{-1}$ indicating the presence of a functional CL. By d 33 of supplementation the number of heifers with a functional CL had increased to 9 and 11 in the high and low energy groups, respectively. By the end of

Table 7. Means of reproductive hormone levels of first-calf Angus heifers during breeding

Day[a]	2	11	11	22	33	44	
Event[b]	$PGF_{2\alpha}$	GnRH T=0	GnRH T=1	AI	11 d post AI	22 d post AI	Overall Mean
Diet[c]							
	----------progesterone, $ng \cdot ml^{-1}$----------						
Lower	.53	.29	.36	.46	1.58	.98	.72
Higher	.52	.33	.49	.35	1.32	.80	.64
SE	.04	.01	.06	.06	.14	.12	.05
	----------Luteinizing hormone, $ng \cdot ml^{-1}$-------						
Lower	.56[d]	.88[d]	4.68	.78	.60	.62	1.35
Higher	.79[e]	.54[e]	4.20	.70	.74	.81	1.30
SE	.05	.05	.40	.05	.07	.08	.13
	----Follicle stimulating hormone, $ng \cdot ml^{-1}$----						
Lower	1.85	2.13	2.50	1.49[f]	1.64	1.56	1.85
Higher	1.92	2.04	2.87	1.70[g]	1.65	1.65	1.97
SE	.05	.10	.13	.06	.06	.09	.05

[a]Day of corn supplementation, (44 d).
[b]Event, represents what was performed to the heifers.
$PGF_{2\alpha}$ = Prostanglandin-F-2-alpha, 5 mg i.m., d 2 & d 10.
GnRH = Gonadotrophin releasing hormone, 10 μg i. m.
T = 0, basal blood sample.
T = 1, 2 h post- GnRH blood sample.
AI = Artificial insemination.
[c]Lower represents heifers not supplemented with corn grain. Higher, high energy intake, these heifers were supplemented with corn grain at 3.5 $kg \cdot heifer^{-1} \cdot d^{-1}$.
[de]Means within a column with different superscripts differ ($P < .01$) and ($P < .05$) respectively.
[fg]Means within a column with different superscripts differ ($P = .07$).
SE = Standard error of the pooled mean.

Table 8. Number of first-calf Angus heifers with serum progesterone content greater than 1 $ng \cdot ml^{-1}$ during breeding[a]

Day[c]	Event[d]	Diet[b] Lower energy	Higher energy
	Number of animals	13	13
2	$PGF_{2\alpha}$	1	2
11	GnRH, T=0	1	1
22	AI	2	0
33	11 days post AI	11	9
44	22 days post AI	7	7

[a]AI = Artificial insemination, April 9.
Natural breeding period : May 2 to July 5.
[b]Lower represents heifers not supplemented with corn grain.
Higher, high energy intake, these heifers were supplemented with corn grain at 3.5 $kg \cdot heifer^{-1} \cdot d^{-1}$ for 44 d.
[c]Day of corn supplementation.
[d]Event, represents what was performed to the heifers $PGF_{2\alpha}$ = Prostanglandin-F-2-alpha, 10 mg i.m., d 2 & d 10.
GnRH = Gonadotrophin releasing hormone, 10 μg i. m.
T = 0, basal blood sample.

supplementation an equal number (7) from each group had a functional CL and were therefore, presumed to be pregnant.

Calving performance of the heifers is shown in Table 9. Two of the heifers fed the higher energy diet conceived to AI compared to five of the heifers fed the lower energy diet. More of the heifers fed the higher energy diet conceived late in the breeding season than those fed the lower energy diet. Only one heifer from each dietary group failed to become pregnant.

A comparison of the nutritional status of fertile versus infertile heifers is shown in Table 10. Although not significant heifers that failed to become pregnant were heavier at birth (36 vs 32 kg), 52 d prior to being bred for the first time (287 vs 273 kg) and approximately 30 d prior to calving for the first time (487 vs 458 kg) when compared to those that became pregnant. Heifers that failed to become pregnant gained less BW (18 vs 28 kg) during the 43 d supplementation period than heifers that became pregnant. Estimates of back fat of heifers that failed to become pregnant was similar to that of heifers fed the high energy diet but was significantly greater than that of heifers fed the low energy diet.

All heifers were weaned at a similar age (212 d) but the two heifers that failed to become pregnant for their second calving had conceived late ($P < .05$) when bred for their first calving (508 vs 447 d), thus they calved late (789 vs 728 d) ($P < .05$) and their calves were younger

Table 9. Calving performance of first-calf Angus heifers supplemented at breeding[a]

Birth month second calf	Diet[b] Lower energy	Higher energy
Number of animals	13	13
January	5	2
February	5	5
March	2	4
April	0	1
Not pregnant	1	1
Postpartum interval-1, d[c]	24	38
Postpartum interval-2, d[d]	93	100

[a]Artificial insemination date : April 9.
Natural breeding period : May 2 to July 5.
[b]Lower represents heifers not supplemented with corn grain.
Higher, high energy intake, these heifers were supplemented with corn grain at 3.5 $kg \cdot heifer^{-1} \cdot d^{-1}$. for 44 d.
[c]Postpartum interval-1 was calculated as calving interval minus 281 d gestation minus the period from first calving to AI.
[d]Postpartum interval-2 was calculated as calving interval minus 281 d gestation.

Table 10. Performance of first-calf Angus heifers that were reproductively successful and unsuccessful as affected by diet during breeding

Item	Diet[a] Lower energy	Higher energy	Not pregnant	SE
Number of animals	12	12	2	
Heifer performance[b]:				
Birth weight, kg	31.90	31.10	35.80	1.02
Weaning ADG, $kg \cdot d^{-1}$	1.07	1.02	1.11	0.01
Weaning BW:HH, $kg \cdot cm^{-1}$	2.27	2.21	2.35	0.03
52 d prior to First breeding BW, kg	273	272	289	5.52
30 d prior to First calving BW, kg	463	452	487	8.68
Second breeding BW, kg	435	365	431	
At Supplementation,[c]				
Initial BW, kg	422	400	422	8.50
Final BW, kg	447	430	440	8.80
Change BW, kg	25	30	18	2.87
ADG, $kg \cdot d^{-1}$	.58	.70	.42	0.07
Initial backfat, mm	3.1	2.8	2.5	0.14
Final backfat, mm	3.4	4.3	3.5	0.17
Change, mm	0.3^{d}	1.5^{e}	1.0^{de}	0.20
Heifer age, d				
Weaning	209	218	209	4.30
First breeding	447^{f}	447^{f}	508^{g}	7.00
First calving	728^{f}	728^{f}	789^{g}	7.00
Second breeding	801^{f}	800^{f}	$852+^{g}$	5.96
First calf performance,				
Birth weight, kg	30.0	28.0	27.9	0.62
Age when dam was bred, d	73	72	63	3.29
Weaning ADG, $kg \cdot d^{-1}$	1.11	1.14	1.16	0.03

[a]Lower represents heifers not supplemented with corn grain. Higher, high energy intake, these heifers were supplemented with corn grain at 3.5 $kg \cdot heifer^{-1} \cdot d^{-1}$.

[b]ADG = Average daily gain, adjusted to 205 d.
BW = Body weight, HH = Hip height.
Second breeding weight = (Initial BW + final BW)/2, heifers were bred on d 22 of supplementation.

[c]Supplementation period = 44 d.

[de]Means within a row with different superscripts differ ($P < .05$).

[fg]Means within a column with different superscripts differ ($P < .05$).

SE = Standard error of the pooled mean.

(63 vs 73 d) when they were bred for the second time.

Birth weights of the first calves and their performance from birth to weaning (Table 10) was similar for all heifers and did not affect second breeding reproductive performance of the heifers.

Hormonal data (Table 11) showed that the heifers that failed to become pregnant overall had lower levels of basal serum P_4 and LH (.63 vs .69 $ng \cdot ml^{-1}$ and 1.10 vs 1.34 $ng \cdot ml^{-1}$ respectively) but higher concentrations of basal FSH (2.11 vs 1.90 $ng \cdot ml^{-1}$). At the beginning of supplementation heifers that failed to become pregnant had numerically higher basal serum P_4 (.66 vs .51 $ng \cdot ml^{-1}$) and lower FSH (1.60 vs 1.92 $ng \cdot ml^{-1}$) but LH was greater than in heifers fed the lower energy diet but smaller than in those fed the higher energy diet (.56 vs .62 vs .80 $ng \cdot ml^{-1}$). Release of P_4 and LH in response to exogenous GnRH was lowest in heifers that were not pregnant (.28 to .34 vs .32 to .43 $ng \cdot ml^{-1}$ and .60 to 3.32 vs .72 to 4.54 $ng \cdot ml^{-1}$ respectively) when compared to those that fell pregnant. However, FSH release in response to GnRH was highest ($P < .05$) in heifers that did not become pregnant (2.44 to 4.44 vs 2.05 to 2.63 $ng \cdot ml^{-1}$) compared to those that became pregnant. Nonpregnant heifers also had the highest ($P < .05$) serum P_4 (99 vs 35 $ng \cdot ml^{-1}$) and FSH (1.74 vs 1.58 ng·ml-1) content during AI and lowest ($P < .05$) serum P_4 (.41 vs 1.54 $ng \cdot ml^{-1}$) 11 d following AI than heifers that became pregnant.

The concentration of NEFA was lowest in heifers fed the

Table 11. Means of reproductive hormones and non-esterified fatty acids levels of reproductively successful and unsuccessful first-calf Angus heifers supplemented at breeding

Day[a]		2	11	11	22	33	44	
Event[b]		$PGF_{2\alpha}$	GnRH T=0	GnRH T=1	AI	11 d post AI	22 d post AI	Overall Mean
Diet[c]	Animal[d]							
		----------progesterone, $ng \cdot ml^{-1}$----------						
Lower	All	.51	.30	.37	.35[e]	1.67[e]	0.90	.70
Higher	All	.51	.33	.49	.35[e]	1.40[e]	.84	.67
Not pregnant		.66	.28	.34	.99[f]	.41[f]	1.12	.63
SE		.04	.01	.06	.04	.13	.12	.05
		----------Luteinizing hormone, $ng \cdot ml^{-1}$-------						
Lower	All	.56	.89	4.79	.80	.58	.62	1.37
Higher	All	.80	.54	4.28	.70	.73	.82	1.31
Not pregnant		.62	.60	3.32	.60	.80	.67	1.10
SE		.05	.05	.40	.05	.07	.08	0.13
		----Follicle stimulating hormone, $ng \cdot ml^{-1}$----						
Lower	All	1.89	2.08	2.50[e]	1.46	1.64	1.49	1.84
Higher	All	1.94	2.01	2.74[e]	1.70	1.65	1.66	1.95
Not pregnant		1.60	2.44	4.44[f]	1.74	1.66	1.96	2.11
SEM		.05	.10	.11	.06	.06	.09	.05
		-------Non-esterified fatty acids, $\mu m \cdot l^{-1}$-----						
Lower	All		252		394	314		320
Higher	All		221		346	271		279
Not pregnant			281		274	297		284
SE			14		22	13		11

[a]Day of the 44 d corn supplementation period.
[b]Event, represents what was performed to the heifers.
$PGF_{2\alpha}$ = Prostanglandin-F-2-alpha, 5 mg i.m.
GnRH = Gonadotrophin releasing hormone, 10 μg i. m.
T = 0, basal blood sample.
T = 1, 2 h post-GnRH blood sample.
AI = Artificial insemination.
[c]Lower represents heifers not supplemented with corn grain. Higher, heifers supplemented with corn grain at 3.5 $kg \cdot heifer^{-1} \cdot d^{-1}$.
[d]12 heifers in each dietary group and two not pregnant.
[ef]Means within a column with different superscripts differ ($P < .05$).
SE = Standard error of the pooled mean.

higher energy diet (Table 11), intermediate in heifers that failed to become pregnant and highest in heifers fed the lower energy diet (279 vs 284 vs 320 $\mu m \cdot ml^{-1}$).

Because diet had no significant effect on reproductive performance, data for all pregnant heifers were pooled for correlation determinations (Table 12). The length of time from exposure to the bull to conception (PPI-1), PPI-2 and the number of estrous cycles per conception were negatively correlated to the heifer's ADG and BW to hip height ratio at weaning. Artificially extended PPI (PPI-2) was negatively correlated to heifer BW and age when bred for the first time ($r = -.42$, $P < .05$ and $r = -.39$, $P = .06$ respectively), BW when calving for the first time ($r = -.39$, $P = .06$), BW ($r = -.41$, $P < .05$) and basal P_4 ($r = -.46$, $P < .05$) during second breeding. The relationship between other nutritional measurements and reproductive variables of the heifer during second breeding was found to be nonsignificant ($P > .10$). Growth performance of the first calf was also not significantly correlated to second breeding performance of the heifer ($P > .10$).

Due to a lack of dietary effect on reproductive performance, heifers were classified according to whether they took a short time or a long time to become pregnant from the time they were exposed to breeding until conception (PPI-1). A short PPI-1 extended from 0 d to 26 d, whereas a long PPI-1 extended from 31 to 91 d. A comparison of heifers

Table 12. Significant Pearson correlation coefficients between physical and reproductive variables of first-calf heifers

Independent variables[b]	Dependent variables[a]		
	PPI-1	PPI-2	Estrous cycles
ADGW, kg	-.39[b]	-.54**	
WW:HT, $kg \cdot cm^{-1}$	-.51**	-.64***	-.45*
FBrW, kg		-.42*	
FCvW, kg		-.396%	
SBrW, kg		-.41*	
FBrA, d		-.396%	
P_4, $ng \cdot ml^{-1}$		-.46*	

[a]PPI-1, Postpartum Interval = from birth of the first calf to birth of the second calf - 281 d - the period from first calving to AI.
PPI-2, Postpartum Interval = from birth of the first calf to birth of the second calf - 281 d.
Estrous cycles elapsing from AI to conception
ADGW = Heifer ADG at weaning.
WW:HT = Heifer weaning weight to hip height ratio.
FBrW = Heifer first breeding weight.
FCvW = Heifer first calving weight.
SBrW = Heifer second breeding weight.
FBrA = Heifer first breeding age.
P_4 = Progesterone, $ng \cdot ml^{-1}$.
*** $P < .001$.
** $P < .01$.
* $P < .05$.
[b](P = .06)

with a short PPI-1 or a long PPI-1 and those that did not become pregnant is shown in Table 13. Birth weight of heifers with a short PPI-1 and those that did not calve was similar, but numerically heavier than that of heifers with a long PPI-1 (35 vs 29 kg). All heifers were similar at weaning. Heifers with a short PPI-1 were numerically lighter in weight 52 d prior to being bred for their first parity (228 vs 266 kg) when compared to heifers with a long PPI-1 or those that did not calve (228 vs 289 kg). However, about 30 d prior to first parturition heifers with a short PPI-1 were heavier than those with a long PPI-1 (468 vs 449 kg), but lighter than the nonpregnant heifers (468 vs 487 kg). The age when heifers were first bred was back-calculated from the calving date. Age at first breeding (or calving) was not a factor that contributed to whether heifers had a short PPI-1 or a long PPI-2. However, the two heifers that did not become pregnant when bred for a second pregnancy conceived late during the first breeding season. Performance of the first calves for all three groups was similar and did not affect subsequent reproductive performance of the dam.

Overall heifers with a short PPI-1 had numerically higher basal serum P_4 (.80 vs .62 $ng \cdot ml^{-1}$) when compared to heifers with a long PPI-1 or those that did not become pregnant (Table 14). Heifers with a short PPI-1 had numerically less basal LH (1.29 vs .1.39 $ng \cdot ml^{-1}$) when compared to heifers with a long PPI-1, but more LH when compared to heifers that did not become pregnant (1.29 vs

Table 13. Performance of first-calf Angus heifers with a varying length of period from exposure to the bull to conception

Item	Short PPI-1[a]	Long PPI-1[b]	Not pregnant	SE
Number of animals	11	13	2	
Heifer performance[c] :				
Birth weight, kg	34.30[d,e]	29.20[e]	35.80[d]	0.89
Weaning ADG, $kg \cdot d^{-1}$	1.07	1.02	1.08	0.03
Weaning BW:HH, $kg \cdot cm^{-1}$	2.32[d,e]	2.22[e]	2.35[d]	0.04
52 d prior to First breeding BW, kg	280	266	289	5.36
30 d prior to First calving BW, kg	468	449	487	8.57
Second breeding BW, kg	435	424	431	8.65
Second breeding BFM, mm	3.64	3.32	3.00	0.16
Heifer age, d				
Weaning	210	216	209	4.35
First breeding	449[d]	445[d]	508[e]	6.99
First calving	730[d]	726[d]	789[e]	6.99
Second breeding	803[d]	798[d]	852+[e]	5.94
First calf performance,				
Birth weight, kg	29.48	28.61	27.90	0.64
Age when dam was bred, d	73	72	63	3.30
Weaning ADG, $kg \cdot d^{-1}$	1.10	1.17	1.06	0.03

[a]Short PPI-1 = Short postpartum interval, 0 to 26 d.
[b]Long PPI-1 = Long postpartum interval, 31 to 91 d.
PPI-1 = Period from exposure to the bull to conception.
[c]ADG = Average daily gain, adjusted to 205 d.
BW = Body weight.
HH = Hip height.
Second breeding weight = (Initial BW + final BW)/2,
Heifers were bred on d 22 of supplementation.
Second breeding BFM = Backfat measure = (Initial BFM + Final BFM)/2.
[de]Means within a row with different superscripts differ ($P < .05$).
SE = Standard error of the pooled mean.

Table 14. Means of reproductive hormones and non-esterified fatty acids of first-calf Angus heifers with a varied interval from exposure to the bull to conception

Day[a] Event[b]	2 $PGF_{2\alpha}$	11 GnRH T=0	11 GnRH T=1	22 AI	33 11 d post AI	44 22 d post AI	Overall Mean
Animal[c]							
	----------progesterone, $ng \cdot ml^{-1}$----------						
Short PPI-1	.46	.31	.38	.34[d]	1.78[d]	1.19[d]	.80
Long PPI-1	.55	.32	.46	.35[d]	1.32[d]	.60[e]	.60
Not pregnant	.66	.28	.34	.99[e]	.41[e]	1.12[d]	.63
SE	.03	.01	.06	.04	.12	.11	.05
	----------Luteinizing hormone, $ng \cdot ml^{-1}$-------						
Short PPI-1	.73	.73	4.39	.65	.63	.58	1.29
Long PPI-1	.64	.71	4.65	.84	.67	.84	1.39
Not pregnant	.62	.60	3.32	.60	.80	.67	1.10
SEM	.06	.06	.40	.05	.08	.08	.13
	----Follicle stimulating hormone, $ng \cdot ml^{-1}$----						
Short PPI-1	1.90	2.06	2.51[d]	1.64	1.64	1.59	1.89
Long PPI-1	1.92	2.04	2.71[d]	1.53	1.65	1.56	1.90
Not pregnant	1.60	2.44	4.44[e]	1.74	1.66	1.96	2.11
SEM	.05	.10	.11	.06	.06	.09	.05
	-------Non-esterified fatty acids, $\mu m \cdot l^{-1}$-----						
Short PPI-1		228		359	282		290
Long PPI-1		243		378	301		307
Not pregnant		281		274	297		284
SEM		14		22	14		11

[a]Day of the 43 d corn supplementation period.
[b]Event, represents what was performed to the heifers.
$PGF_{2\alpha}$ = Prostanglandin-F-2-alpha, 5 mg i.m.
GnRH = Gonadotrophin releasing hormone, 10 μg i. m.
T = 0, basal blood sample.
T = 1, 2 h post-GnRH blood sample.
AI = Artificial insemination.
[c]PPI-1 = Postpartum interval, from exposure to the bull to conception, Short = 0 to 26 d Long PPI-1 = 31 to 91 d.
[de]Means within a column with different superscripts differ ($P < .05$).
SEM = Standard error of the mean.

1.10 $ng \cdot ml^{-1}$). Basal FSH was the same for heifers with either a short or a long PPI-1 but numerically lower than in heifers that did not calve (1.90 vs 2.11 $ng \cdot ml^{-1}$). Heifers with either a short or a long PPI-1 had less P_4 ($P < .05$) during AI (d 22) when compared to nonpregnant heifers. Eleven days following AI (d 33) pregnant heifers had more basal P_4 ($P < .05$) when compared to heifers that did not calve. However, 22 d following AI (d 44) heifers with a short PPI-1 had serum P_4 concentration similar to that of nonpregnant heifers but greater ($P < .05$) than that of heifers with a long PPI-1. Although statistically insignificant release of LH in response to GnRH for heifers with a short PPI-1 was lower (.73 to 4.39 vs .71 to 4.65 $ng \cdot ml^{-1}$) than in heifers with a long PPI-1, but greater than in heifers that did not become pregnant (.37 to 4.39 vs .60 to 3.32 $ng \cdot ml^{-1}$). Similarly, GnRH-induced FSH in pregnant heifers was less (2.05 to 2.61 vs 2.44 to 4.44 $ng \cdot ml^{-1}$) than in heifers that did not calve ($P < .05$).

The NEFA concentration (Table 14) of heifers with a short PPI-1 was numerically similar to that of heifers that did not calve and lower than that of heifers with a long PPI-1 (287 vs 307 $\mu m \cdot ml^{-1}$).

Discussion

The study was conducted to determine whether reproductive performance of first-calf Angus heifers can be

improved by increasing energy intake during breeding. The magnitude of BW gain was the same for both dietary groups (Table 3) (1.06 fold). However, body fat increase was significantly (.43 fold) greater for heifers fed the higher energy diet, indicating that heifers fed the higher energy diet accumulated more fat than muscle when compared to those fed the lower energy diet.

Heifers fed the higher energy diet had a longer PPI (34 vs 24 d or 100 d vs 93 d, Table 4), fewer had a functional CL (P_4 content > 1 $ng \cdot ml^{-1}$, Table 8) and fewer became pregnant at first service (15% vs 38%, Table 9) when compared to those fed the lower energy diet. In contrast, studies have shown that heifers that lose body condition postpartum or during breeding, experience a longer PPI and lower conception rates (Dunn et al., 1969; Rutter and Randel, 1984; Richards et al., 1986). A possible explanation of why the heifers in this study that gained less body fat had better reproductive performance than those that were fed the higher energy diet could be that heifers fed the higher energy diet became overconditioned and the excess fat interfered with reproductive performance (Houghton et al., 1990). It is also possible that the heifers calved with a BCS ≥ 5 (9 point system, appendix A) and maintained it postpartum. Richards et al., (1986) and Warren et al., (1988) have shown that beef cattle that calve in a BCS ≥ 5 and maintain it postpartum have shorter PPI and higher conception rates when compared to those that calve in a BCS

< 5. It could also be that at the time of supplementation, (which commenced approximately 50 d postpartum), the heifers had already recovered from the negative energy balance which they may have experienced during early lactation (Short et al., 1990), thus, the supplemental energy merely increased body fat. Data on body condition of the heifers at calving or shortly thereafter was not available.

Non-esterified fatty acids are the transport form of fat and serum NEFA concentration is known to be negatively correlated to body condition (Easdon et al., 1985; Villa-Godoy, 1990; Canfield and Butler, 1991). At the beginning of supplementation (d 2) heifers that were assigned to the lower energy diet had significantly higher concentration of serum NEFA (Table 5) and their mean BW was also numerically higher (Table 3) than those assigned to the higher energy diet. On the final day of supplementation (d 44) heifers on the higher energy diet had significantly higher levels of serum NEFA and they had also gained more weight and body fat compared to those receiving the lower energy diet. Based on these observations serum NEFA levels for d 2 and d 44 could not be used as a reliable indicator of nutritional status. The variation in NEFA concentration among heifers on d 2 and d 44 was thought to be due to stress induced by handling because on those days the heifers were handled more than at other times during the supplementation period (Appendix C). Stress of any kind increases serum levels of epinephrine and epinephrine stimulates lipolysis. Heifers in both dietary

groups gained BW and body fat and had increased levels of NEFA.

Serum P_4 concentrations have been found to be lower in heifers restricted in energy intake (Hill et al., 1970; Beal et al., 1978; Imakawa, 1983; Williams, 1989). Progesterone is required to sustain pregnancy. The heifers fed the higher energy diet tended to have lower basal serum P_4 (Table 6) concentration following AI and fewer had a functional CL by the end of supplementation. However, the heifers used in this study were not nutritionally stressed because they actually gained BW and body fat. Therefore, a lower P_4 concentration could have been due to factors other than nutritional stress.

Basal concentration of gonadotropins (Table 6) tended to be higher in heifers fed the higher energy diet. This is in agreement with studies that have shown a decrease in pituitary and serum LH (Tatman et al., 1990; Kile et al., 1991) and FSH (Kile et al., 1991) in underfed ovariectomized ewes, as well as a reduction of LH in underfed beef cattle (Rutter and Randel, 1984; Rutter and Manns, 1987). It is hypothesized that depressed gonadotropins secretion and to some extent synthesis is the result of impaired release of GnRH (Gauthier and Mauleon, 1983; Tatman et al., 1990; Kile et al., 1991). On d 11 heifers fed the lower energy diet had lower concentration of serum P_4 as a result their LH concentration was higher ($P < .05$) when compared to heifers fed the higher energy diet.

Luteinizing hormone released in response to exogenous GnRH has been found to be higher in heifers deficient in energy (Beal et al., 1978; Gauthier and Mauleon, 1983). In this study a higher response to GnRH (Table 7) was found in heifers fed the higher energy diet than those fed the lower energy diet (7.8 vs 5.6 fold LH increase), similarly Rutter and Randel (1984) observed higher LH released in response to GnRH in heifers gaining BW. Lishman et al., (1979) also observed that LH released in response to GNRH peaked 30 min earlier in heifers fed a high energy diet.

Heifers fed a higher energy diet had low reproductive performance when compared to heifers fed the lower energy diet (Table 9), this suggests that the heifers were overconditioned (BCS ≥ 8) and the body fat interfered with reproductive performance (Houghton et al., 1990).

The heifers that failed to become pregnant when bred for the second parity were heavier at birth, when bred for the first time and when they calved for the first time (Table 10). However, results of the analysis of correlation suggest that heifers that are in good body condition at weaning, first breeding, first calving and second breeding are more likely to have a short PPI. The contradiction may have been due to a small sample size of heifers that failed to become pregnant (2). It can be assumed that had there been more heifers with body conditions similar to the ones that did not become pregnant, the correlation between BW at

birth, first breeding and first calving to PPI-1, PPI-2 and estrous cycles per conception may have been positive.

The nonpregnant heifers had also conceived later for their first parity than heifers that became pregnant (age of first calf when dam was bred for the second parity was 63 vs 73 d). It is possible that when bred for their second parity the heifers that had calved late had not resumed estrous activity. Custer et al., (1990) observed a PPI of 73 d to 77 d in first-calf beef heifers not exposed to a bull shortly after calving. Similarly, Doornbos et al., (1984) reported PPI of 61 d to 64 d in first-calf heifers that experienced a normal and a prolonged parturition labor, respectively.

The hormonal profiles of heifers that did not become pregnant (Table 11) showed low levels of basal P_4, normal LH but high FSH. Thus, it can be inferred that the ovarian follicles in these heifers were beginning to grow. Because of low level of follicular development inhibin production was probably not high enough to inhibit FSH production. This further suggests that these heifers may not have resumed postpartum estrus activity.

Heifers with a short PPI-1 were heavier (Table 13) than those with a long PPI-1 during their first calving and when bred for their second parity. However, for these times heifers that did not become pregnant were heavier than those with a short PPI-1. This suggests that the heifers with a short PPI-1 had optimum body condition for reproductive performance. During breeding for the second parity, BW as

well as Serum NEFA were lower in heifers with a short PPI-1 than in those with a long PPI-1, suggesting that heifers with a long PPI-1 mobilized their body fat in an attempt to meet their energy requirements. Based on this observation it can be suggested that a BW range of 460 to 480 kg of Angus females during breeding for second parity is ideal for reproductive success. Whereas, BW < 450 kg may result in heifers conceiving late, and that > 480 kg may lead to reproductive failure.

Hormonal profiles of heifers with a short PPI-1 (Table 14) indicated higher levels of P_4 but lower levels of LH when compared to those that had a long PPI-1. High P_4 was indicative of a functional CL.

A search of the literature did not reveal the effect of excessive body conditioning on reproduction in first-calf heifers. This is understandable because under most farm conditions it is unlikely that first-calf heifers will become fat because they are bred for their second pregnancy when they are both nursing a calf and growing.

Implications

Results of this study indicate that a reduction in reproductive performance observed in first-calf heifers compared to nulliparous or multiparous heifers may in some cases be due to factors other than an energy deficit prior to and during breeding. The results also indicate that

reproductive performance may be impaired by excessive body fat. Because of the knowledge that reproductive performance of first-calf heifers is often low, and because it is known that nutrient deficit greatly influences reproduction, it is possible that nutritional needs of first-calf heifers may be exceeded to a point that infertility may result from excessive body condition. It can be concluded that there are factors that influence the physiological changes that occur in first-calf beef heifers during the postpartum interval or around breeding, and in order to understand the favorable relationship between body condition and reproductive success a more quantifiable characterization of nutritional status such as energy balance, of first-calf heifers at this stage is needed.

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CHAPTER IV

NUTRITIONAL AND ENDOCRINOLOGICAL CHARACTERIZATION OF REPRODUCTIVELY EFFICIENT FIRST-CALF BEEF HEIFERS

Abstract

First-calf spring-calving Angus heifers (n = 83) were utilized during two production years to characterize postpartum nutritional and hormonal status of those that were reproductively efficient or inefficient. A short period (< 17 d) from exposure to the bull to conception (PPI) and delivery of a live calf represented reproductive success. Body condition scores (BCS), body weights (BW) and serum concentration of non-esterified fatty acids (NEFA) were used as indicators of nutritional status. Luteinizing hormone (LH), Follicle stimulating hormone (FSH) and gonadotropin-releasing hormone (GnRH)-induced and estradiol(E_2)-induced LH and FSH were used as indicators of hypothalamic and pituitary competence. Progesterone (P_4), E_2 and androstenedione were used as indicators of ovarian competence to resume postpartum cyclicity. Prolactin (PRL) was used as an indicator of stress. Blood collection for hormonal assays was made between 35 d and 63 d postpartum. Heifers with a short PPI had higher BW, backfat and BCS and

low concentration of NEFA between 35 d and 63 d postpartum. However, heifers with either a long PPI or that were nonpregnant rapidly gained BW and fat from the beginning to the end of the breeding season. When compared to heifers with a long PPI heifers with a short PPI had higher ($P < .05$) basal LH, lower ($P < .05$) FSH, lower ($P < .05$) androstenedione, numerically lower P_4 and E_2. Release of FSH in response to GnRH was lower ($P < .01$) in heifers with a short PPI than in heifers with a longer PPI. Release of LH and E_2 in response to GnRH was numerically lower in heifers with a short PPI, whereas, P_4 and androstenedione release was numerically higher. Heifers with a short PPI released numerically more LH and less FSH in response to exogenous E_2 when compared to heifers with a long PPI. Overall, heifers with a short PPI had numerically higher LH, lower ($P < .05$) FSH, numerically higher P_4, but low E_2 and androstenedione. Secretion of PRL was consistently higher ($P < .05$) in heifers with a short PPI. Based on the results of this study a fleshy body condition appeared to have contributed to a longer PPI and heifers that were reproductively successful had higher levels of LH and P_4 but lower levels of FSH, E_2 and androstenedione. Based on these results, a heifer that is likely to be reproductively efficient is characterized by a BCS of 5.5 to 5.6 at approximately 35 d postpartum to the beginning of breeding, basal concentrations of .80 vs .57 or .90 $ng \cdot ml^{-1}$ for LH,

2.10 vs 2.47 $ng \cdot ml^{-1}$ for FSH, 107.41 vs 125.08 for androstenedione and release of 6.74 vs 8.58 $ng \cdot ml^{-1}$ FSH in response to GnRH and PRL secretion of 77.4 vs 54.08 $ng \cdot ml^{-1}$.

Key words : Postpartum interval, Nutritional status, Reproductive hormones, GnRH and E_2 challenges, Beef cattle

Introduction

Characteristically, a suckled beef cow has suppressed ovarian activity following parturition (Garcia-Winder et al., 1984; Walters et al., 1982a; Williams, 1990). This suppressed activity can be extended by insufficient energy intake (Connor et al., 1990; Dunn and Kaltenbach, 1980; Short et al., 1990), poor body condition (Houghton et al., 1990; Richards et al., 1986) and fleshy body condition (Houghton et al., 1990). A slow resumption of ovarian activity following parturition extends the postpartum interval (PPI), the period from calving to the first fertile estrus (Lishman and Inskeep, 1991; Short et al., 19990), and leads to cows conceiving late in the breeding season or not at all. A characteristic endocrinological state associated with postpartum anestrus is a chronic suppression of luteinizing hormone (LH) release, which is a reflection of suppressed gonadotropin-releasing hormone

(GnRH) release (Hanzen, 1986; Nett, 1987). Progesterone (P_4) and low levels of circulating estrogen (E_2) inhibit the GnRH pulse generator of the hypothalamus, thus inhibiting GnRH release (Nett, 1987; Walters et al., 1982b). Reproductive success is realized when cows can resume estrous activity within 60 d of calving and wean a healthy calf with a weaning weight characteristic of it's breed.

In the following study heifers were classified according to the length of time it took them to become pregnant. This time extended from the day they were exposed to the bull to the day they became pregnant. Date of conception was determined by subtracting 281 d from the calves birth date. Postpartum interval was also classified as the length of time from birth of the first calf to conception.

Under both classifications the heifers' performance was related to her nutritional status and hormonal profile. Estimates of nutritional status included subjective body condition, changes in body weight (BW), changes in body fat, BW to hip height (HH) ratio, serum non-esterified fatty acids (NEFA) and changes in the calf's body weight from birth to weaning. Reproductive hormones assayed included LH, follicle stimulating hormone (FSH), P_4, E_2 and androstenedione. The quantity and degree of release of these hormones in response to exogenous GnRH and E_2 was

also examined. Prolactin (PRL) secretion was determined and used as an index of stress. The objective of this study was to relate nutritional status to reproductive performance and hormonal profiles of first-calf Angus heifers.

Materials and Methods

Animals and their Management

A two-year study was conducted involving 83 first-calf Angus heifers (23 to 30 mo old). During the first year, 53 heifers with body weight ranging from 356 to 533 kg were divided into two groups according to calving date. The first group consisted of 30 heifers that had calved from January 8 to February 6. The second group consisted of 23 heifers that had calved between February 7 and March 5. The following year, 30 heifers that calved between January 6 and February 21 were used. Heifers selected for use in the second year had similar physical characteristics as those used in the first year. The heifers were managed the same and had been reared on pasture and fed corn silage, mineral mix and water, free choice.

Diets and their Determination

Silage Intake. A known quantity of fresh silage was fed and replenished when that previously fed had been consumed. Daily DM intake of corn silage was estimated as the proportion of each heifer's metabolic BW ($BW^{.75}$)

multiplied by the amount of silage fed and divided by the number of days the silage was fed. Feeding of silage was discontinued at the beginning of the 90 d breeding season. Duplicate silage samples were taken for analysis every 28 d.

Pasture Intake. Pasture DMI was estimated using the Ratio Technique similar to that of Harris (1970). Thus, pasture DMI, $kg \cdot d^{-1}$ = {(fecal DM output, $(kg \cdot d^{-1})$ * IADF in feces, (%)) - (silage DM intake, $(kg \cdot d^{-1})$ * IADF in silage, (%))} ÷ IADF in pasture, (%). Fecal DM output (FDMO) was determined using intraruminal controlled release capsules containing chromic oxide (Cr_2O_3, Captec Chrome, Captec Nufarm, Auckland, New Zealand). Thus, FDMO, $kg \cdot d^{-1}$ = (Cr_2O_3 release rate, $mg \cdot d^{-1}$) ÷ Cr concentration in the feces, $mg \cdot g^{-1}$ (Barlow et al., 1988). Due to the high cost of the capsules and the amount of work involved in sample collection not all heifers were dosed, but a representative sample of 6 heifers from each group was selected according to calving date, weight of heifer and sex of the calf within group during the first year. The following year 10 heifers were dosed. Body weights of heifers used for determination of pasture DMI starting at approximately 35 d postpartum to the beginning of breeding ranged from 369.7 kg to 555.7 kg (mean 467.3 kg). Whereas, at 60 d into the breeding season BW ranged from 416.4 kg to 605.5 kg (mean of 483.3 kg). Fecal DM output estimations were made over

two periods each year, the first period started 35 d postpartum (appendix D and E) and the second was towards the middle of the breeding season. At the beginning of the FDMO determination period the heifers were orally dosed with the Cr_2O_3 bolus and a fecal sample collected via the rectum. The marker was allowed about 10 d to stabilize to conditions of the rumen after which fecal grab samples were taken on d 11, 14, 15, 22, 24 and 25 post-dosing for the first period and on d 3, 9, 12 and 17 for the second period. Nutrient content of the pasture was determined from duplicate samples clipped from random areas every 28 d until the end of the 90 d breeding season for the first year. During the second year, fecal sample collection was on d 7, 9, 10, 18, and 21 following dosing for period one and on d 8, 14, 24 and 29 following dosing for period two. Silage and pasture samples were frozen prior to analysis.

Evaluation of the Heifers' Nutritional Status

Body condition, body weights and hip heights were determined for all heifers at approximately 35 d following parturition (Appendix D and E). All measurements, except those for hip height were subsequently made at 213 d and postpartum in yr 1 63, 123 and 181 d postpartum in yr 2.

Body condition was determined by sonaray measurements of the thickness of subcutaneous fat in the area of the back between the 12th and 13th rib. Heifers were also assigned a visual body condition score (BCS) at the time

when backfat estimates and live weight measurements were made. A BCS scale of 1 to 15 was used, but was later converted to a 1 to 9 scale (Appendix A) by dividing 9 by 15 and multiplying each of the 1 to 15 scale points by .6.

First-born calves were weighed every time their dams were weighed. Data for the first-born calves including date of birth, birth weight, sex, weaning weight and weaning age were obtained from farm records.

Challenges with GnRH and Estradiol, Blood Collection and Breeding

Evaluation of the hypothalamic-pituitary-ovarian axis of all heifers commenced 35 d postpartum (Appendix D). On d 1, heifers were injected with 5 mg of prostaglandin-F2-alpha ($PGF_{2\alpha}$, Lutalyse, The Upjohn Co, Kalamazoo, MI) to induce CL regression and 10 μg of a GnRH analogue (des-gly^{10}, [D-Ala^{6}]-luteinizing hormone, Sigma Co., St Louis, MO) to induce release of LH and FSH and possibly ovulation. Blood samples were taken from the non-catheterized jugular veins at 0, 1.5 and 3 h after GnRH injection. On d 10, the heifers were again injected with 5 cc $PGF_{2\alpha}$ to complete synchronization of estrus and blood samples were collected at 0 and 1 h. On d 13, the heifers were injected with 1 mg of 17ß-estradiol-3-benzoate (E_2, Sigma Co., St. Louis, MO) at 18:00 h, to cause a preovulatory LH surge. Starting at 16 h following the E_2 injection (d 14), three blood samples were collected at two hour intervals.

Events of d 1, 13 and 14 (previous paragraph) were repeated on the now synchronized heifers at d 24, 27 and 28, respectively, after which the 90 d breeding season was initiated. The purpose of the second GnRH injection (d 24) was to assess both pituitary and luteal function. Pituitary function was reflected by the amounts of LH, and FSH released. These gonadotropins indicate the gonadotrophs' response to GnRH. Luteal and to a degree, follicular function was assessed by the amount of P_4 secreted. Assays of E_2 and androstenedione were used to indicate the degree of follicular development and function.

Rectal palpation to detect pregnancy was performed 60 d after the end of the breeding season in the first year. During the second year, ultrasound was used 28 d following the end of the breeding season to determine pregnancy. A blood sample for P_4 analysis was collected to complement the results of the ultrasound. Conception dates were estimated from the actual calving date minus 281 d. A gestation length of 281 d has been found to be the mean for first-year Angus heifers.

Reproductive Determinants

Length of the PPI was calculated as the period from exposure to the bull for the second pregnancy to the day of conception (PPI-1). Date of conception was estimated by subtracting 281 d from the birth of the second calf. This calculation is biased against heifers that calve early

because heifers that calve early in the year probably were cycling before exposure to the bull and therefore might have had a shorter PPI. The calculation is also biased against heifers that calve late because heifers that calf late in the year may be exposed to breeding before the ovary becomes fully functional, thus a longer PPI and PPI in these heifers may not be due to a physiological deficiency. Heifers that became pregnant within the first estrous cycle following exposure to the bull were designated short PPI-1 (0 to 17 d). Heifers that required more than one estrous cycle to become pregnant were designated long PPI-1 (18 to 83 d).

The PPI was also calculated as the period from birth of the first calf to birth of the second calf minus gestation length (281 d), this calculation was designated PPI-2. The heifers were managed such that the breeding period commenced at a set period (April), thus heifers calving early (January to February) would likely have a longer interval between calves than those that calved late in the year. The PPI-2, therefore, represents an artificially extended PPI. Heifers were divided into two groups depending on their PPI-2. Short PPI-2 extended from 52 to 82 d and a long PPI-2 extended from 83 to 125 d.

At the time of exposure to the bull the estrous cycles of all the heifers had been synchronized. Therefore, conception rate-1 was back-calculated from the second

calving date as the number of estrous cycles from exposure to the bull to conception (assuming 281 d of gestation and 21 d per estrous cycle). Conception rate-2 was calculated as the period from first calving to the second calving minus gestation divided by 21 days of the estrous cycle. Conception rate-2 determination corresponds to artificially extended number of estrous cycles elapsing before conception occurs.

Chemical Analysis of Feed and Feces

Corn silage, pasture and fecal samples were oven dried at 50 C, ground to pass through a 1-mm screen of a Willey mill. Pasture and silage were assayed for dry matter (DM), crude protein (CP) and gross energy (GE) according to A.O.A.C. (1984), and neutral detergent fiber (NDF), acid detergent fiber (ADF) and lignin according to Goering and Van Soest, (1970). In vitro dry matter digestibility (IVDMD) was determined using the Tilley and Terry (1963) procedure. Indigestible acid detergent fiber (IADF) was used as an internal marker. Indigestible acid detergent fiber was determined as ADF remaining after the Tilley and Terry in vitro digestion procedure followed by reinoculation with rumen fluid and McDougalls buffer (McDougall, 1948) for a 96 h incubation period as described by Waller et al., (1980) and Nelson et al., (1990).

Ground fecal samples for each heifer for each period were composited across the first three days and the last

three days of period one. Whereas, for period two the first two days and the last two days were composited, yielding two samples per animal per group per period for two years. Day one fecal samples were used as correction blanks.

Feces were analyzed for DM, ash, GE, IVDMD and IADF using the same procedures used for feed analysis. Fecal samples were also analyzed for Cr_2O_3 using an atomic absorption spectrophotometer according to Williams et al., (1962).

Blood Sample Processing

For hormonal and NEFA assays blood samples were immediately placed on ice, transported to the laboratory for immediate centrifugation at 1764 X g for 20 min. Serum was harvested and stored at - 20 C until subjected to radioimmunoassays (RIA) to quantify P_4, E_2, androstenedione, LH, FSH and prolactin (PRL).

Analysis for NEFA. Serum concentration of NEFA was determined in blood samples taken during the second year. Quantification of NEFA was made with the "Wako NEFA C test kit", (NEFA, Wako Pure Chemicals Industries, Dallas, TX). The procedure is an in vitro enzymatic calometric determination of NEFA in plasma or serum.

Radioimmunoassays. Day one blood samples were analyzed for P_4 and E_2. Progesterone Concentration of > 1 $ng \cdot ml^{-1}$ was used as indicator of the presence of a corpus luteum (CL). All blood samples were analyzed for LH, FSH and PRL

to assess hypothalamic and pituitary function. Ovarian steroids P_4, E_2 and androstenedione were determined in blood samples collected on d 1, 10, 21 to assess the degree of follicular development. Progesterone was also determined on d 14 and d 24 basal blood to assess the presence and the quality of the CL. Prolactin was used as an indicator of stress.

Ovarian steroids, P_4, E_2 and androstenedione were quantified in 200 μl of serum. All steroids used in the reference curves came from Sigma (Sigma Co., St. Louis, MO).

Progesterone quantification was done according to Surve et al. (1976). The antibody for P_4 (#332) was provided by Dr. Ali H. Surve (Sandoz Research Institute, Hanover, NJ). The sensitivity of the assay was 10 pg·tube^{-1} and intra- and interassay coefficients of variation (CV) were 5% and 9%, respectively.

Concentration of serum E_2 was determined utilizing the procedure of Cox et al., (1987) as modified by Britt (1990). The antibody was provided by Dr. Norman Mason (Lilly Research Laboratories, Indianapolis, IN). The sensitivity of the assay was .15 pg·tube^{-1} and intra- and interassay CV were 6% and 10%, respectively.

Androstenedione concentration was determined using a procedure described by Babalola and Shapiro (1988). The antibody (X - 322) was purchased from by Dr. P. N. Rao

(Southwest Foundation for Biomedical Research, San Antonio, TX). The sensitivity of the assay was 2.5 pg·tube^{-1} and intra- and interassay CV were 5% and 8%, respectively.

Concentrations of LH were determined in 100 µl of serum using a double antibody RIA described by Niswender et al.,(1969) and modified by Bolt et al., 1981. The antibody for LH (# 15 antiovine LH) was provided by Dr. G. Niswender (Colorado State University, Fort Collins, CO). The purified LH (LER-1072-2) used as iodinated tracer and the LH (USDA-bLH-B-5) used as a reference curve were provided by Dr. L. E. Reichert, Albany, NY). Assay sensitivity was 31.3 ng·tube^{-1}. The intra- and interassay CV were < 5% and < 8%, respectively.

The FSH was assayed in 250 µl of serum using the procedure of Bolt and Rollins (1983). The antibody used was USDA-5-0122, whereas, USDA-bFSH-I-2 was used in the construction of the reference curve and for iodination. All products were supplied by Dr. D. J. Bolt (USDA, Beltsville, MD). The sensitivity of the assay was .25 ng·tube^{-1}. The intra- and interassay CV were < 5% and < 9%, respectively.

Prolactin concentrations were determined in 50 µl of serum utilizing a procedure similar to that of Forrest et al. (1990). The antibody for PRL, the PRL for the reference curve and iodinating were provided by Dr. D. J. Bolt (USDA, Beltsville, MD). The sensitivity of the assay was .05

$ng \cdot tube^{-1}$. The intra- and interassay CV were < 5% and < 9%, respectively.

Statistical Analysis

Data were analyzed using GLM procedure of Statistical Analysis System (SAS, 1989). Least square difference (LSD) procedure was used to separate significant treatment means. The model statement was :

$$Y_{ij} = \mu + \tau_i + \delta_j + \epsilon_{ij}$$

where :

Y = Nutritional status

or Reproductive hormones

i = Number of treatments

j = Number of animals

τ = Treatments

δ = Sex of the first calf

ϵ_{ij} = Experimental error

Pearsons correlations were run among heifer nutritional and reproductive performance traits, NEFA and reproductive hormones concentrations.

Multiple regression procedure (PROC REG) of SAS (1989) was used on various models using biological meaningful independent variables to determine variables that accounted for the most variation in PPI-1 (as well as the number of services required per conception), PPI-2 and basal NEFA. Based on the stepwise regression, the following models resulted in the highest R^2:

Model 1

$$Y = b_0 + b_1CALFAGE + b_2IBCS + b_3IBFM + b_4BASALFSH + b_5MIDBRBCS + E$$

Where :

Y = Postpartum interval-1 (PPI-1), d.

b_0 = The Y intercept.

b_1 to b_8 = Regression coefficients.

CALFAGE = Age of the first calf when the dam was evaluated for postpartum reproductive competency, d.

IBCS = Heifer body condition score at 35 d postpartum.

IBFM = Heifer backfat at about 35 d postpartum, mm.

BASALFSH = Basal follicle stimulating hormone, $ng \cdot ml^{-1}$.

MIDBRBCS = Heifer body condition score at 60 d into the 90 d breeding season.

E = Error

Model 2

$$Y = b_0 + b_1IBFM + b_2CBCS + b_3FBCS + E$$

Where :

Y = Postpartum interval-2 (PPI-2), d.

b_0 = The Y intercept.

b_1 to b_8 = Regression coefficients.

IBFM = Backfat measure at 35 d postpartum, mm.

CBCS = Change in the heifer's BCS from 35 d to 63 d postpartum.

FBCS = Body condition score at about 63 d postpartum.

E = Error.

Model 3

$$Y = b_0 + b_1CCALFBW + E$$

Where :

Y = Non-esterified fatty acid, $\mu m \cdot l^{-1}$.

b_0 = Y intercept

b_1 = Regression coefficient

CCALFBW = Change in the calf's BW from 35 d to 63 d

postpartum, kg.
E = Error.

Results

Heifer distribution between postpartum intervals

Postpartum interval-1. The mean number of days postpartum when dams were exposed to the bull for the second parity and the number of dams either becoming pregnant or not is shown in Table 1. Thirty-five heifers were classified as having a short PPI-1 (0 to 17 d), about one estrous cycle), 13 of these 35 heifers were nursing bull calves and 22 were nursing female calves. Thirty-seven heifers were classified as having a long PPI-1 (18 to 83 d, more than one estrous cycle), 26 of which were nursing bull calves and 11 were nursing female calves. Twenty-three of the heifers from the short PPI-1 group calved early (≥ 65 d, from birth of the first calf to date of exposure to the bull) and 12 calved late (≤ 64 d, from birth of the first calf to exposure to the bull). Fifteen of the 37 heifers from the long PPI-1 group calved early and 22 calved late. A total of 11 heifers did not produce a calf when exposed to the bull for their second parity. Four of the 11 nonpregnant heifers were nursing bull calves and seven had female calves. Four had calved early in the first-calving season and seven had calved late.

Table 1. Number of days postpartum when dams were exposed to the bull for their second parity

Days[c] postpartum	Number of heifers pregnant									
	PPI-1[a]				PPI-2[b]					
	Short		Long		Short		Long		Number of heifers not pregnant	
	M	F	M	F	M	F	M	F	M	F
30	0	1	0	0	0	0	0	0	0	0
38 -40	0	0	1	1	1	0	0	0	0	0
41 - 50	3	0	6	4	9	6	4	0	0	1
51 - 60	2	2	7	1	7	4	2	0	2	4
61 - 64	1	3	2	0	0	3	1	0	0	0
65 - 70	1	4	0	0	0	0	0	0	0	0
71 - 80	4	7	4	1	0	3	9	10	1	0
81 - 90	2	5	6	4	2	0	4	5	1	2
91	0	0	0	0	0	0	1	0	0	0
Total	13	22	26	11	18	18	21	15	4	7

[a]Postpartum interval-1 = Days from exposure to the bull to conception.
Short PPI-1 = 0 to 16 d.
Long PPI-1 = 18 to 83 d.
[b]Postpartum interval-2 = Days from the birth of the first calf to birth of the second calf minus 281 d of gestation.
Short PPI-2 = 52 to 82 d.
Long PPI-2 = 83 to 125 d.
[c]Early calving = 65 to 91 d postpartum.
Late calving = 38 to 64 d postpartum.
Sex of the first calf, M = Male.
F = Female.

Postpartum interval-2. When heifers were reclassified according to the length of time from birth of the first calf to birth of the second calf minus 281 d of gestation (PPI-2), 36 heifers had either a short PPI-2 (52 to 82 d) or a long PPI-2 (83 to 125 d). Of the 36 heifers classified as having a short PPI-2 an equal number (18) were nursing either bull or female calves. Only five of the 36 heifers with a short PPI-2 calved early, whereas, 31 calved late. Twenty-one of the 36 heifers with a long PPI-2 were nursing bull calves and 15 were nursing female calves. Twenty-nine heifers calved early and seven calved late. In summary a total of 38 heifers calved early, 23 became pregnant within the first estrous cycle following exposure to the bull, 15 required more than one estrous cycle to become pregnant. A total of 34 heifers calved late, only 12 became pregnant within the first estrous cycle, whereas 22 required more than one estrous cycle to become pregnant.

Composition of diet and intake

Table 2 shows chemical composition of the diet. Dietary composition for both years was similar, thus the data were pooled. Mean DMI of silage was 4.88 $kg \cdot d^{-1}$ (range 3.59 to 6.51 $kg \cdot d^{-1}$). Pasture DMI could not be accurately estimated because of the overestimation of fecal output which was in turn due to low recovery of Cr_2O_3 in feces. Because of the low recovery rate of Cr_2O_3 individual, instead of composite fecal samples were analyzed. The

Table 2. Chemical composition of diets[a]

Item	Diet		
	Silage	Pasture	Pasture[b]
Gross energy, Kcal·g^{-1}	5.1	4.7	5.0
Crude protein, %	10.1	27.6	21.1
Detergent fiber, %			
Neutral	56.2	45.5	54.8
Acid	30.8	21.6	28.0
Lignin	3.4	2.0	1.7
Indigestible acid	13.6	6.1	8.9
In vitro dry matter digestibility, %	70.3	77.2	73.5

[a]Dry matter basis.
[b]Determined 60 d into the breeding season (June - July).

manufacturer's release rate of Cr_2O_3 from the boluses used in the first and second years was 1.74 $g \cdot d^{-1}$ (1.191 $g \cdot d^{-1}$ of Cr) and 1.58 $g \cdot d^{-1}$ (1.081 $g \cdot d^{-1}$ of Cr), respectively. During period one, the pattern of Cr recovered in fecal samples was uniform for all heifers. Fecal grab samples taken on d 10, 13 and 14 post dosing had the highest mean concentration of Cr (.210 $mg \cdot g^{-1}$), fecal IADF was 34.69%. Fecal grab samples taken on d 24, 27 and 28 post dosing had the least concentration (.081 $mg \cdot d^{-1}$), fecal IADF was 33.44%. However, the .210 $mg \cdot g^{-1}$ concentration of Cr resulted in mean fecal dry matter output (FDMO) of 8.286 $kg \cdot d^{-1}$, an amount that was too high in relation to IVDM digestibility (Table 2) of the diet and the heifers BW.

NRC (1984) estimates that a two-year old heifer weighing 450 kg and nursing a calf requires 9.4 $kg \cdot d^{-1}$ DMI during the first three to four months following parturition. Thus the heaviest heifer (555.7 kg) used for DMI determination would require about 12 $kg \cdot d^{-1}$ and assuming intake of 3% of BW, consumption of about 17 $kg \cdot d^{-1}$ would be expected. However, using the recovery rate of Cr for period one resulted in a DMI that was greater than 38 $kg \cdot d^{-1}$. Conflicting results with regard to estimation of fecal output using the controlled-release Cr_2O_3 boluses have been reported. Barlow et al. (1988), Lee et al. (1988) and Parker et al. (1989) reported the bolus to be accurate in estimating fecal output. In contrast, Brandberry et al.

(1991) and Buntnix et al. (1992) reported an overestimation of fecal output by the Cr_2O_3 boluses. During the second period (60 d of breeding and no silage feeding) Cr recovered in fecal grab samples averaged .337 $g \cdot d^{-1}$ for d 8 and 14 post-dosing, thus, resulting in DMI estimates greater than 20 $kg \cdot d^{-1}$. Fecal output estimates were higher when heifers were supplemented with corn silage. Hatfield et al. (1991) also noted that the accuracy of the Cr_2O_3 boluses was affected when wethers were supplemented with barley.

Due to the low recovery of Cr in fecal grab samples FDMO was overestimated, hence DMI was also overestimated. As a result DMI was not included as a variable in all the analysis of this study.

Performance of Heifers and their first-born calves (PPI-1)

Table 3 shows performance of the first-calf Angus heifers with either a short or a long PPI-1. Heifers with either a short or a long PPI-1 had similar BW at birth (34.2 kg), whereas those that did not become pregnant were slightly heavier at birth (35.8 kg). Weaning weight was numerically lower (260.6 vs 268.9 kg) for heifers with a short PPI-1 than those with a long PPI-1, whereas, heifers that did not become pregnant had intermediate weaning BW (264.9 kg). Similarly weaning body weight to hip height (BW:HH) ratio as well as average daily gain (ADG) were numerically lower (2.31 vs 2.37 $kg \cdot cm^{-1}$ and 1.097 vs 1.145

Table 3. Performance of first-calf Angus heifers with either a short or a long postpartum interval from 35 d postpartum to the beginning of breeding

	PPI-1[a]			
	Short	Long	Not pregnant	SE
Number of animals	35	37	11	
Body weights, kg				
Birth	34.3	34.1	35.8	0.6
Weaning	260.6	268.9	264.9	2.6
Weaning BW:HH,[b] $kg \cdot cm^{-1}$	2.31	2.37	2.35	0.02
Weaning ADG,[c] $kg \cdot d^{-1}$	1.10	1.15	1.14	0.01
Age, d				
Weaning	221	215	213	2.00
First breeding	457	453	447	4.00
First calving	738	734	728	4.00
Second breeding	805	797	793	4.00

[a]Postpartum interval-1 = days from exposure to the bull to conception.
Short PPI-1 = 0 to 16 d.
Long PPI-1 = 18 to 83 d.
[b]Body weight to hip height ratio.
[c]Average daily gain.
No significant difference detected between groups ($P > .10$).
SE = standard error of the pooled mean.

$kg \cdot d^{-1}$) for heifers that had a short PPI-1 when compared to those that had a long PPI-1. However, nonpregnant heifers were intermediate (3.5 $kg \cdot cm^{-1}$ and 0.11 $kg \cdot d^{-1}$, respectively). When weaned, heifers that had a short PPI-1 were 7 d older than heifers that had a long PPI-1 or did not become pregnant. Thus, the heifers with a short PPI-1 were older when bred for the first time, when they calved for the first time and when bred for their second parity.

Table 4 shows the performance of first-calf Angus heifers of varying PPI-1 starting from 35 d postpartum to the end of the 90 d breeding. At approximately 35 d postpartum heifers with a short PPI-1 were numerically heavier (460.4 vs 435.3 kg) than those with a long PPI-1 and significantly heavier than those that did not become pregnant (460.4 vs 432.2 kg). From the beginning (approximately 63 d postpartum) to the end of the breeding season heifers with a short PPI-1 were numerically heavier (484.6 vs 465.5 kg) than those with a long PPI-1, whereas, the nonpregnant heifers, had intermediate BW (477.9 kg). Average daily gain from 35 d to 63 d postpartum was numerically smaller (.28 $kg \cdot d^{-1}$) for heifers with a short PPI-1 than for heifers with a long PPI-1 (.46 $kg \cdot d^{-1}$) or those that did not become pregnant (.73 $kg \cdot d^{-1}$). Although at 60 d into the breeding season heifers with a short PPI still had numerically higher BW (475.7 vs 470.9 kg) than those that had a long PPI-1 their BW gain was smaller ($P <$

Table 4. Performance of first-calf Angus heifers with either a short or a long postpartum interval

	PPI-1[a]			
	Short	Long	Not pregnant	SE
No. of animals	35	37	11	
Body weights, kg[b]				
35 d postpartum	460.4[c]	435.3[c,d]	432.2[d]	5.0
63 d postpartum	468.1	448.2	452.8	4.8
123 d postpartum	475.7	470.9	465.2	4.8
181 d postpartum	510.0 (8)	477.4 (17)	515.7 (5)	9.3
213 d postpartum	487.5[c] (27)	496.5[c] (19)	447.3[d] (6)	4.8
35 d postpartum BW:HH, $kg \cdot cm^{-1}$	3.608[c]	3.381[d]	3.361[d]	0.038
Backfat estimates, mm[b]				
35 d postpartum	4.63	4.30	4.46	0.12
63 d postpartum	4.63	4.30	4.82	0.10
123 d postpartum	4.29[c]	4.62[c,d]	5.09[d]	0.13
181 d postpartum	4.88 (8)	4.94 (17)	5.60 (5)	0.16
213 d postpartum	4.82 (27)	5.60 (19)	4.67 (6)	0.15
Body condition score[b]				
35 d postpartum	5.49	5.22	5.13	0.07
63 d postpartum	5.64[c,d]	5.38[d]	5.85[c]	0.06
125 d postpartum	5.21	5.25	5.24	0.07
181 d postpartum	5.18 (8)	5.33 (17)	5.40 (5)	0.09
213 d postpartum	5.71 (27)	5.85 (19)	5.40 (6)	0.07
Mean PPI-1, d	8[c]	28[d]		1.00
Estrous cycles per conception	1[c]	2[d]	4+[e]	0.07

[a]Postpartum interval-1 = days from exposure to the bull to conception.
Short PPI-1 = 0 to 16 d.
Long PPI-1 = 18 to 83 d.

[b]63 d postpartum = beginning of breeding.
181 d postpartum = 28 d post-breeding (yr 2).
213 d postpartum = 60 d post-breeding (yr 1).
Numbers in brackets represent different sample size.

[cd]Means within a row with different superscript differ ($P < .05$).
SE = standard error of the pooled mean.

.05) (7.6 vs 22.7 kg) than that of heifers with a long PPI-1. Nonpregnant heifers had intermediate BW gain (12.4 kg). Thus, from 35 d to 123 d postpartum ADG was numerically smaller (.17 $kg \cdot d^{-1}$) for heifers with a short than those with a long PPI-1 (.41 $kg \cdot d^{-1}$) or those that did not become pregnant (.38 $kg \cdot d^{-1}$). Body measurements taken 28 d following the end of the breeding season were only made during the second year of the study. Of the 30 heifers measured eight had a short PPI-1, 17 had a long PPI-1 and five did not become pregnant. Heifers with a short PPI-1 had a numerically greater BW (510.0 vs 477.4 kg) than those with a long PPI-1. Heifers that did not become pregnant had the highest BW (515.7 kg). During the first year of the study body measurements were taken 60 d following the end of the breeding season. Twenty seven heifers had a short PPI-1, 19 (initially 20, one was sold) had a long PPI-1 and 6 did not become pregnant. Heifers with a short PPI-1 were numerically lighter in BW (487.5 vs 496.5 kg) than those with a long PPI-1 and nonpregnant heifers were the lightest (447.3 kg). Body weight to HH ratio at 35 d postpartum was greater ($P < .05$) for heifers with a short PPI-1 than for either heifers with either a long PPI-1 or those that did not become pregnant.

Backfat estimates and BCS from 35 d postpartum to the beginning of the breeding season were of a pattern similar to that of BW in that heifers with a short PPI-1 had the

higher backfat and BCS than those that had a long PPI-1. Backfat and BCS at 35 d postpartum were negatively correlated ($r = -.20$, $P = .08$ and $r = -.19$, $P = .10$, respectively) to PPI-1. At the beginning of the breeding season, backfat estimates and BCS for heifers with a short PPI-1 were numerically higher (4.6 vs 4.3 mm and 5.64 vs 5.38, respectively) than for heifers with a long PPI-1. However, heifers that did not become pregnant had the most backfat (4.8 mm) and BCS (5.85). This shows that heifers that did not become pregnant were fatter even before the breeding season commenced. Sixty days into the breeding season heifers with a short PPI-1 had numerically less body fat (4.29 vs 4.62 mm) when compared to heifers that had a long PPI-1 or heifers that did not become pregnant ($P < .05$). By the end of the 90-d breeding season heifers with a short PPI-1 were still heavier (510.0 vs 477.4 kg) than those with a long PPI-1 but their backfat and BCS were similar (4.9 and 4.8 mm, respectively). Heifers that did not become pregnant were the heaviest (515.7 kg) and had the most backfat (5.6 mm) and a BCS of 5.4.

Table 5 shows the performance of the first-born calves of heifers with either a short or a long PPI-1. Birth weight of the calves was similar for all groups (29.7 kg). At 35 d, 63 d (when dams were exposed to the bull) and 221 d of age (weaning) calves of heifers with a short PPI-1 had numerically greater BW than calves belonging to heifers

Table 5. Performance of first-born calves of Angus heifers with varying postpartum interval

	PPI-1[a]			
	Short	Long	Not pregnant	SE
Number of calves[b]	22F 13M	11F 26M	7F 4M	
Body weights, kg				
Birth	29.6	29.7	29.8	0.4
35 d postpartum	66.9	62.0	60.8	1.6
63 d postpartum	79.7	75.6	74.2	1.8
123 d postpartum	160.4	154.8	158.6	2.8
181 d postpartum	183.7(8)	181.8(16)	198.1(5)	4.3
Weaning	247.8	245.6	242.2	3.6
Weaning ADG,[c] $kg \cdot d^{-1}$	1.078	1.097	1.074	0.016
Weaning BW:HH[d], $kg \cdot cm^{-1}$	2.195	2.139	2.151	0.027
Weaning age, d	225	219	219	2.000

[a]Postpartum interval-1 = days from exposure to the bull to conception.
Short PPI-1 = 0 to 16 d.
Long PPI-1 = 18 to 83 d.
[b]F = Female·
M = Male.
[c]Average daily gain.
[d]Body weight to hip height ratio.
Numbers in brackets represent different sample size.
No significant difference detected between groups ($P > .10$).
SE = standard error of the pooled mean.

with a long PPI-1, whereas those of heifers that failed to become pregnant were the lightest. At about age 123 d calves whose dams had a short PPI-1 were still numerically heavier (160.4 vs 154.8 kg) than those whose dams had a long PPI-1 and calves from dams that failed to become pregnant had intermediate BW (158.6 kg). This was because calves of nonpregnant heifers gained more BW (84.4 vs 80.0 kg) than heifers from the other two groups during the first 62 d of the dams' breeding season. Calves whose dams had a short PPI-1 were 6 d older when weaned, notably the dams had themselves been 7 d older when weaned. A heifer whose first calf was a bull tended to have longer PPI-1 ($r = .39$, $P < .01$) than a heifer whose first calf was a female.

Serum concentration of NEFA of heifers with varying PPI-1 is shown in Table 6. Although not statistically different heifers with the shortest PPI-1 had the lowest concentration of serum NEFA at all times except on d 45 postpartum (d 10 of the reproductive axis evaluation) when their serum NEFA concentration was greater (472.04 vs 435.68 $\mu m \cdot l^{-1}$) than that of heifers with a long PPI-1. Overall mean serum NEFA concentration between 35 d and 63 d postpartum (d 28 of the reproductive axis evaluation) was numerically lower (364.42 vs 377.22 $\mu m \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1. Heifers that did not become pregnant had numerically the highest (382.7 $\mu m \cdot l^{-1}$ concentration of serum NEFA. Twenty

Table 6. Changes in concentration of non-esterified fatty acids in Angus heifers from 35 d postpartum to the beginning of breeding, $\mu m \cdot l^{-1}$

			PPI-1[a]			
Day[b]	Days pp[d]	Event[c]	Short	Long	Not pregnant	SE
Number of animals			8	17	5	
1	35	$PGF_{2\alpha}$ & GnRH	485.18	519.79	514.80	19.57
10	45	$PGF_{2\alpha}$	472.04	435.68	497.04	19.44
14	49	E_2	290.07	301.84	302.91	32.03
21	56	$PGF_{2\alpha}$ & GnRH	355.40	360.68	398.06	27.03
28	59	E_2	207.42	248.81	200.74	13.27
Overall Mean			362.02	374.84	382.71	13.11
28 d post breeding			330.74	398.95	397.86	15.84

[a]Postpartum interval-1 = days from exposure to the bull to conception.
Short PPI-1 = 0 to 16 d.
Long PPI-1 = 18 to 83 d.
[b]Day of the hypothalamic-pituitary-ovarian evaluation.
[c]Event, represents what was performed on the heifers
$PGF_{2\alpha}$ = prostanglandin-F-2-alpha, 5 mg i.m.
GnRH = gonadotrophin releasing hormone, 10 μg i.m.
[d]Days postpartum.
No significant difference detected ($P > .10$).
SE = standard error of the pooled mean.

eight days following the end of the breeding season heifers with a short PPI-1 still had numerically the lower amount of serum NEFA (330.74 vs 398.95 $\mu m \cdot l^{-1}$) than heifers with a long PPI-1. Although similar to heifers with a long PPI-1, concentration of NEFA of nonpregnant heifers was still the highest.

Nonpregnant heifers had gained the most body weight from the time of their first calving to the end of the second-parity breeding season. Heifers that did not become pregnant were heavier at the beginning of the breeding season, they gained the most BW and fat during the breeding season but had the highest concentration of serum NEFA.

Profile of Basal Reproductive hormones (PPI-1)

Gonadotropins. Table 7 shows basal hormonal concentrations of reproductive hormones for first-calf Angus heifers with either a short or a long PPI-1. During the first 13 d of the evaluation of the hypothalamic-pituitary-ovarian axis (approximately 35 d postpartum, range 13 to 63 d) basal serum LH concentration did not vary significantly between the three groups of heifers. However, serum LH concentration of the blood sample taken on d 14 at 14 h following E_2 administration was lower ($P < .05$) (.93 and .62 vs 2.07 $ng \cdot ml^{-1}$) in heifers with either a short or a long PPI-1, respectively when compared to heifers that failed to become pregnant. This was because one heifer from the nonpregnant group experienced the peak of the LH surge

Table 7. Means of basal serum gonadotropins of first-calf Angus heifers from 35 d postpartum to the beginning of breeding

Day[a]:	1	10		14	24	28	
Event[b]:	$PGF_{2\alpha}$ GnRH	$PGF_{2\alpha}$		Post E_2	$PGF_{2\alpha}$ GnRH	Post E_2	
Sampling time, h:	0	0	1.0	14	0	14	Overall Mean
Heifer group[c]							
				Luteinizing hormone, $ng \cdot ml^{-1}$			
Short PPI-1	.61	.65	.50	0.93[d]	.54	1.49[f]	.80[d,e]
Long PPI-1	.60	.61	.51	0.62[d]	.54	0.59[g]	.57[e]
Not pregnant	.58	.65	.45	2.07[e]	.50	1.06[f]	.90[d]
SEM	.03	.03	.03	0.11	.03	0.17	0.04
				Follicle stimulating hormone, $ng \cdot ml^{-1}$			
Short PPI-1	2.17	2.17	2.34	1.93	2.03[d]	2.07	2.10[d]
Long PPI-1	2.52	2.46	3.03	1.95	2.72[e]	2.29	2.47[e]
Not pregnant	2.39	2.31	2.39	2.04	2.75[e]	2.43	2.39[d,e]
SEM	0.13	0.15	0.21	0.12	0.14	0.17	0.06

[a]Day in the series of hormonal evaluations that began at approximately 35 d postpartum.
[b]Event, $PgF_{2\alpha}$ = prostanglandin-F-2-alpha, 5 mg lutalyse i.m.
GnRH = gonadotropin-releasing hormone, 10 μg i.m.
E_2 = 17 ß-estradiol-3-benzoate, 1 mg i.m.
[c]PPI-1 = days from exposure to the bull to conception.
Short PPI-1 = 0 - 16 d, 35 heifers.
Long PPI-1 = 18 - 83 d, 37 heifers.
Not pregnant = 11 heifers.
[d,e]Means within a column with different superscripts differ (P<.05).
[f,g]Means within a column with different superscripts differ (P<.10).
SEM = Standard error of the mean.

prior to collection of the 14 h blood sample. When the LH reading of this heifer was excluded the resulting concentration was not significantly different (.78 $ng \cdot ml^{-1}$) from that of the heifers with either a short or a long PPI-1. On d 28, heifers with a short PPI-1 and those that did not become pregnant had higher ($P < .10$) serum LH concentration than heifers with a long PPI-1 (1.49 and 1.06 vs .59 $ng \cdot ml^{-1}$). Overall, mean basal LH was higher ($P < .05$) (.80 vs .57 $ng \cdot ml^{-1}$) for heifers with a short PPI-1 when compared to heifers with a long PPI-1. The overall mean LH concentration of heifers with a long PPI-1 was lower ($P < .05$) than that of heifers that failed to become pregnant.

Basal concentration of FSH did not differ ($P > .10$) between groups during the first 23 d of the evaluation. However, heifers with a short PPI-1 had numerically lower (2.15 vs 2.49 $ng \cdot ml^{-1}$) FSH concentrations than those with a long PPI-1. FSH concentrations than those with a long PPI-1. Heifers that did not become pregnant were intermediate (2.28 $ng \cdot ml^{-1}$). Serum concentration of FSH taken on d 24 at 14 h was lower ($P < .05$) (2.03 vs 2.72 $ng \cdot ml^{-1}$) for heifers with a short PPI-1 when compared to that of heifers with a long PPI-1 and heifers that did not become pregnant. Although statistically nonsignificant serum FSH taken on d 28 at 14 h following E_2 administration was lower (2.07 vs 2.29 $ng \cdot ml^{-1}$) for heifers with a short PPI-1 than in

heifers with a long PPI-1. Overall, basal mean concentration of serum FSH was lower ($P < .05$) (2.10 vs 2.47 $ng \cdot m^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1. Mean FSH of heifers with a short PPI-1 was numerically lower (2.10 vs 2.39 $ng \cdot ml^{-1}$) than that of nonpregnant heifers.

Ovarian Steroids. Table 8 shows serum concentrations of basal ovarian steroids. During the first 13 d of the hypothalamic-pituitary-ovarian axis evaluation process mean basal serum P_4 was numerically lower (.84 vs 1.14 $ng \cdot ml^{-1}$) for heifers with a short PPI-1 when compared to those with a long PPI-1. However, mean basal serum P_4 concentration of heifers that did not become pregnant was intermediate (1.06 $pg \cdot ml^{-1}$). Serum P_4 concentration of the blood sample taken on d 14 at 14 h following E_2 injection was numerically higher (.72 vs .51 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1 and was higher ($P < .05$) (.72 vs .37 $ng \cdot ml^{-1}$) than in nonpregnant heifers. Day 14 serum P_4 of heifers with a long PPI-1 was similar to that of nonpregnant heifers. On d 24 serum concentration of P_4 of heifers with a short PPI-1 was still numerically higher (2.26 vs 1.86 $ng \cdot ml^{-1}$) when compared to that of heifers with a long PPI-1 and those that did not become pregnant. Overall mean P_4 was similar for all heifer groups (1.08 $ng \cdot ml^{-1}$).

Table 8. Means of basal serum ovarian steroids of first-calf Angus heifers from 35 d postpartum to the beginning of breeding

Day[a]:	1	10		14	24	28	
Event[b]:	$PGF_{2\alpha}$ GnRH	$PGF_{2\alpha}$		Post E_2	$PGF_{2\alpha}$ GnRH	Post E_2	
Sampling time, h:	0	0	1.0	14	0	14	Overall Mean
Heifer group[c]				Progesterone, $ng \cdot ml^{-1}$			
Short PPI-1	.40	1.01	1.11	.72[d]	2.26	.85	1.05
Long PPI-1	.34	1.44	1.63	.51[d,e]	1.89	.69	1.07
Not pregnant	.47	1.23	1.48	.37[e]	1.83	.90	1.03
SEM	.02	0.11	0.12	.05	0.21	.08	0.05
				Estrogen, $pg \cdot ml^{-1}$			
Short PPI-1	3.49	7.73	6.63	-	3.87	-	6.18
Long PPI-1	3.19	5.79	7.09	-	4.06	-	6.27
Not pregnant	3.10	6.71	8.45	-	3.56	-	7.12
SEM	0.16	0.95	1.20	-	0.21	-	0.54
				Androstenedione, $pg \cdot ml^{-1}$			
Short PPI-1	84.65	105.25[d]	129.04[f]	-	121.84	-	107.41[d]
Long PPI-1	96.35	134.86[e]	146.37[g]	-	130.80	-	125.70[e]
Not pregnant	93.82	138.43[e]	149.36[g]	-	120.75	-	124.46[e]
SEM	2.96	4.75	4.03	-	5.05	-	2.40

[a]Day in the series of hormonal evaluations that began at approximately 35 d postpartum.
[b]Event, $PgF_{2\alpha}$ = prostanglandin-F-2-alpha, 5 mg lutalyse i.m.
GnRH = gonadotropin-releasing hormone, 10 μg i.m.
E_2 = 17 ß-estradiol-3-benzoate, 1 mg i.m.
[c]PPI-1 = days from exposure to the bull to conception.
Short PPI-1 = 0 - 16 d, 35 heifers.
Long PPI-1 = 18 - 83 d, 37 heifers.
Not pregnant = 11 heifers.
[d,e]Means within a column with different superscripts differ (P<.05).
[f,g]Means within a column with different superscripts differ (P<.10).
SEM = Standard error of the mean.

Basal E_2 was not statistically different among groups during the entire evaluation period. However, heifers with a short PPI-1 overall had lower (6.18 vs 6.27 $ng \cdot ml^{-1}$) serum E_2 concentration than heifers with a long PPI-1. Nonpregnant heifers had the highest (7.12 $ng \cdot ml^{-1}$) concentration of E_2.

At the beginning of the evaluation mean serum concentration of basal androstenedione of heifers with a short PPI-1 was numerically lower (84.65 vs 96.35 $pg \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers that had a long PPI-1. Although serum androstenedione increased for all heifers by d 10, heifers with a short PPI-1 still had the lowest ($P < .05$) concentration in comparison to heifers that either had a long PPI-1 or those that failed become pregnant. Thus, overall mean androstenedione concentration of heifers with a short PPI-1 was lower ($P < .05$) (107.41 vs 125.08 $pg \cdot ml^{-1}$) than that of heifers with a long PPI-1 or heifers that did not become pregnant.

Effect of Exogenous GnRH on Reproductive hormones (PPI-1)

Gonadotropins. Table 9 (d 1 and d 24) shows serum concentrations of gonadotropins released in response to exogenous GnRH. The magnitude of the response is shown in appendix F. On d 1 at 1.5 h following injection of GnRH heifers with a short PPI-1 released numerically less LH (7.25 vs 11.99 $ng \cdot ml^{-1}$) than heifers with a long PPI-1 and less LH ($P < .05$) (7.25 vs 14.9 $ng \cdot ml^{-1}$) when compared to

Table 9. Gonadotropin secretion in response to gonadotropin-releasing hormone and estradiol in first-calf Angus heifers

Day[a]:	1			10		14			24			28			
Event[b]:	$PGF_{2\alpha}$ GnRH			$PGF_{2\alpha}$		Post E_2			$PGF_{2\alpha}$ GnRH			Post E_2			
Sampling time, h:	0	1.5	3.0	0	1.0	14	16	18	0	1.5	3.0	14	16	18	Overall Mean
Heifer group[c]															
						---------- Luteinizing hormone, $ng \cdot ml^{-1}$ ----------										
Short PPI-1	.61	7.25[d]	21.75	.65	.50	.93[d]	7.58	10.59[d]	.54	9.22	16.97	1.49[f]	3.23[f]	6.83	6.06
Long PPI-1	.58	11.99[d,e]	19.61	.61	.51	.62[d]	4.46	14.58[d]	.54	7.72	16.50	.59[g]	1.36[g]	3.82	5.92
Not pregnant	.60	14.09[e]	15.77	.65	.45	2.07[e]	3.65	1.58[e]	.50	11.59	17.78	1.06[f]	1.47[g]	7.35	5.99
SEM	.03	0.96	1.25	.03	.03	0.11	0.76	1.75	.03	0.77	0.91	0.17	0.91	0.77	0.28
						---------- Follicle stimulating hormone, $ng \cdot ml^{-1}$ ----------										
Short PPI-1	2.17	3.38[d]	9.96	2.17	2.34	1.93	2.23[f]	4.36	2.03[d]	4.96	8.45[f]	2.07	2.26[d]	3.24	3.74[d]
Long PPI-1	2.52	6.00[e]	11.17	2.46	3.03	1.95	3.50[g]	5.95	2.72[e]	6.25	12.44[g]	2.29	2.44[d]	3.47	4.75[e]
Not pregnant	2.39	4.51[d,e]	10.40	2.31	2.39	2.04	3.19[g]	3.69	2.75[e]	6.36	11.64[g]	2.43	3.34[e]	3.54	4.39[d,e]
SEM	0.13	0.42	0.68	0.15	0.21	0.12	0.28	0.68	0.14	0.38	0.76	0.17	0.16	0.23	0.14

[a]Day in the series of hormonal evaluations that began at approximately 35 d postpartum.
[b]Event, $PgF_{2\alpha}$ = prostanglandin-F-2-alpha, 5 mg lutalyse i.m.
GnRH = gonadotropin-releasing hormone, 10 μg i.m.
E_2 = 17 ß-estradiol-3-benzoate, 1 mg i.m.
[c]PPI-1 = days from exposure to the bull to conception.
Short PPI-1 = 0 - 16 d, 35 heifers.
Long PPI-1 = 18 - 83 d, 37 heifers.
Not pregnant = 11 heifers.
[d,e]Means within a column with different superscripts differ (P<.05).
[f,g]Means within a column with different superscripts differ (P<.10).
SEM = Standard error of the mean.

heifers that failed to become pregnant. In contrast, three hours following GnRH administration heifers with either a short PPI-1 released numerically more LH (21.75 vs 19.61 $ng \cdot ml^{-1}$) than heifers with a long PPI-1 or heifers that did not become pregnant (15.77 $ng \cdot ml^{-1}$). This indicates that heifers with a short PPI-1 responded more slowly to GnRH than did heifers with a long PPI-1. For heifers with a short PPI-1 the degree of response of LH to GnRH at 1.5 h was 11.9 fold, whereas for heifers with a long PPI-1 it was 20.0 fold. Nonpregnant heifers had a 24.3 fold increase. The degree of LH response from 1.5 h to 3 h post-GnRH was 3.0 fold in heifers with a short PPI-1 and 1.4 fold in heifers with either a long PPI-1 or no pregnancy. Overall the magnitude of the LH response to GnRH on d 1 was lower (23.8 vs 26.3 fold increase) for heifers with a short PPI-1 than for heifers with either a long PPI-1 or no pregnancy. However, on d 24 10 μg GnRH resulted in a numerically higher release of LH (9.22 vs 7.22 $ng \cdot ml^{-1}$) at 1.5 h by heifers with a short PPI-1 than heifers with a long PPI-1. During the same period heifers that did not become pregnant released the most LH (11.49 $ng \cdot ml^{-1}$). Three hours following GnRH, LH concentration was slightly larger (16.74 vs 16.50 $ng \cdot ml^{-1}$) for heifers with a short than a long PPI-1, but heifers that did not become pregnant released the most LH (17.78 $ng \cdot ml^{-1}$). On d 24 heifers with a short PPI responded earlier than heifers with a long PPI-1. The d 1, 1.5 h and

3 h release of LH was numerically lower (13.82 vs 15.58 $ng \cdot ml^{-1}$) in heifers that had a short PPI-1 than those that had a long PPI-1. Nonpregnant heifers had numerically intermediate (14.89 $ng \cdot ml^{-1}$) release of LH. On d 24, 1.5 h and 3 h release of LH was numerically higher (13.09 vs 12.11 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1 and nonpregnant heifers released the largest (14.64 $ng \cdot ml^{-1}$) amount of LH. Thus, overall release of LH in response to GnRH was numerically lower (13.44 vs 13.80 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1. Nonpregnant heifers had released the highest (14.76 $ng \cdot ml^{-1}$) LH.

The 1.5 h release of FSH on d 1 was lower ($P < .05$) (3.38 vs 6.00 $ng \cdot ml^{-1}$) in heifers that had a short PPI-1 than in heifers that had a long PPI-1, whereas for heifers that failed to become pregnant FSH release was intermediate (4.51 $ng \cdot ml^{-1}$). The magnitude of response was also lower (1.56 vs 2.38 fold increase) in heifers that had a short PPI-1 than those with a long PPI-1 and the nonpregnant heifers had intermediate (1.89 fold) response. At 3 h post-GnRH heifers with a short PPI-1 still released numerically the least amount of FSH (9.96 vs 11.17 $ng \cdot ml^{-1}$) when compared to heifers with a long PPI-1 and heifers that did not become pregnant were still intermediate (10.40 $ng \cdot ml^{-1}$). However, the degree of response of FSH release from 1.5 h to 3 h was highest (2.95 vs 1.86 fold increase) for

heifers with a short PPI-1), indicating a slow response to GnRH by the gonadotrophs. On d 24 heifers with a short PPI-1 had numerically the lowest (4.96 vs 6.32 $ng \cdot ml^{-1}$) amount of FSH released in response to GnRH at 1.5 h when compared to heifers with either a long PPI or heifers that failed to become pregnant. At 3 h heifers with a short PPI still had an FSH release lower ($P < .10$) (8.45 vs 12.04 $ng \cdot ml^{-1}$) than that of heifers with either a long PPI-1 or no pregnancy. However, the degree of response of the gonadotrophs to release FSH at 1.5 h was similar (2.3 fold increase) for all heifer groups. The degree of response of FSH between 1.5 h and 3 h was smaller (1.7 vs 1.99 fold increase) for heifers with a short PPI-1 than heifers with a long PPI-1. This indicates that on d 24 heifers with a short PPI-1, relative to heifers of the other two groups responded early. The overall d 1 release of FSH was numerically lower (6.61 vs 8.58 $ng \cdot ml^{-1}$) in heifers that had a short PPI-1 than those that had a long PPI-1. Nonpregnant heifers had numerically intermediate (7.30 $ng \cdot ml^{-1}$) release of FSH. On d 24 overall release of FSH was still lower ($P < .05$) (6.85 vs 9.15 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with either a long PPI-1 or in those not pregnant. Total release of FSH on d 1 and d 24 was lower ($P < .01$) (6.74 vs 8.94 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1. Nonpregnant heifers released intermediate amounts of FSH (8.21 $ng \cdot ml^{-1}$).

Ovarian Steroids. Table 10 (d 1 and d 24) shows serum concentrations of ovarian steroids released in response to exogenous GnRH. The degree of the response is shown in appendix G. The amount of P_4 released in response to GnRH on d 1 at 1.5 h was similar (.60 $ng \cdot ml^{-1}$) for all heifers groups. However, the degree of response for heifers with a short PPI-1 was lower (1.50 vs 1.76 fold increase) than in heifers with a long PPI-1 and least in nonpregnant heifers (1.30 fold increase). Exogenous GnRH on d 24 did not affect P_4 release for heifers with either a short or a long PPI-1. Although statistically insignificant nonpregnant heifers responded to GnRH by releasing the highest amount of P_4. Serum P_4 released on d 24 was numerically higher (2.07 vs 1.76 $ng \cdot ml^{-1}$) for heifers with a short PPI-1 when compared to heifers that either had a long PPI-1 or did not produce a calf. Overall, P_4 was higher (1.17 vs 1.12 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1. Nonpregnant heifers had the least (1.09 $pg \cdot ml^{-1}$) amount of P_4.

Estradiol release in response to GnRH was not significantly different among all heifer groups during the evaluation process. Estradiol released in response to exogenous GnRH (appendix G) on d 1 and d 24 at 1.5 h was low (one fold increase) in all heifer groups. Although not high (< 3 fold increase) the release of E_2 in response to GnRH was apparent at 3 h. On d 1 at 1.5 h heifers with a

Table 10. Ovarian steroid secretion in response to gonadotropin-releasing hormone and estradiol in first-calf Angus heifers

Day[a]:	1			10		14			24			28			
Event[b]:	$PGF_{2\alpha}$ GnRH			$PGF_{2\alpha}$		Post E_2			$PGF_{2\alpha}$ GnRH			Post E_2			
Sampling time, h:	0	1.5	3.0	0	1.0	14	16	18	0	1.5	3.0	14	16	18	Overall Mean
Heifer group[c]															
	---------- Progesterone, $ng \cdot ml^{-1}$ ----------														
Short PPI-1	.40	.60	.54	1.01	1.11	.72[d]	-	-	2.26	2.11	2.02	.85	-	-	1.17
Long PPI-1	.34	.60	.66	1.44	1.63	.51[d,e]	-	-	1.89	1.62	1.89	.69	-	-	1.12
Not pregnant	.47	.61	.58	1.23	1.48	.37[e]	-	-	1.83	1.43	2.12	.90	-	-	1.09
SEM	0.02	0.04	0.06	0.11	0.12	0.05	-	-	0.21	0.16	0.19	0.08	-	-	0.04
	---------- Estrogen, $pg \cdot ml^{-1}$ ----------														
Short PPI-1	3.49	3.95	6.31	7.73	6.63	-	-	-	3.87	4.12	5.08	-	-	-	5.47
Long PPI-1	3.19	3.52	9.16	5.79	7.09	-	-	-	4.06	4.01	4.87	-	-	-	5.82
Not pregnant	3.10	3.83	7.87	6.71	8.45	-	-	-	3.56	3.59	5.58	-	-	-	6.15
SEM	0.16	0.19	0.83	0.95	1.20	-	-	-	0.21	0.17	0.30	-	-	-	0.29
	---------- Androstenedione, $pg \cdot ml^{-1}$ ----------														
Short PPI-1	84.65	104.57[d]	125.62	105.25[d]	129.04	-	-	-	121.84	135.89	155.05	-	-	-	119.40[d]
Long PPI-1	96.35	121.46[e]	107.88	134.86[e]	146.37	-	-	-	130.80	135.96	147.19	-	-	-	126.95[d,e]
Not pregnant	93.82	124.44[e]	135.50	138.43[e]	149.36	-	-	-	120.75	140.22	152.73	-	-	-	131.50[e]
SEM	2.96	3.56	6.29	4.75	4.03	-	-	-	5.05	3.95	5.13	-	-	-	1.78

[a]Day in the series of hormonal evaluations that began at approximately 35 d postpartum.
[b]Event, $PgF_{2\alpha}$ = prostanglandin-F-2-alpha, 5 mg lutalyse i.m.
GnRH = gonadotropin-releasing hormone, 10 μg i.m.
E_2 = 17 ß-estradiol-3-benzoate, 1 mg i.m.
[c]PPI-1 = days from exposure to the bull to conception.
Short PPI-1 = 0 - 16 d, 35 heifers.
Long PPI-1 = 18 - 83 d, 37 heifers.
Not pregnant = 11 heifers.
[d,e]Means within a column with different superscripts differ (P<.05).
[f,g]Means within a column with different superscripts differ (P<.10).
SEM = Standard error of the mean.

short PPI-1 released the higher amount of E_2 (3.95 vs 3.52 pg·ml^{-1}) than heifers with a long PPI-1 and nonpregnant heifers were intermediate (3.83 pg·ml^{-1}). On d 1 at 3 h heifers with a short PPI-1 released the least amount of E_2 (6.31 vs 9.16 pg·ml^{-1}) in response to GnRH (a 1.60 vs 2.60 fold increase) when compared to heifers with a long PPI-1. Heifers that did not become pregnant had intermediate release of E_2 (7.87 pg·ml^{-1}, a 2.05 fold increase). On d 24 at 1.5 h heifers with a short PPI-1 still had numerically the highest amount of E_2 (4.12 vs 4.01 pg·ml^{-1}) released than heifers with a long PPI-1, and nonpregnant heifers had the least amount (3.59 pg·ml^{-1}) of E_2 release. On d 24 at 3 h heifers with a short PPI-1 released the highest amount of E_2 when compared to heifers with a long PPI-1 (5.08 vs 4.87 pg·ml^{-1}). Heifers that did not become pregnant had the highest amount of E_2 (5.58 pg·ml^{-1}). Overall E_2 released in response to GnRH was numerically lower (4.87 vs 5.39 pg·ml^{-1}) in heifers with a short PPI-1 than heifers with a long PPI-1 and nonpregnant heifers were intermediate (5.22 pg·ml^{-1}).

Androstenedione released in response to GnRH at 1.5 h on d 1 was least ($P < .05$) (104.57 vs 121.46 pg·ml^{-1}) in heifers with a short PPI-1 than in heifers with a long PPI-1. However, the magnitude of response was similar (1.25 fold increase) for both groups of heifers. Androstenedione release of nonpregnant heifers was higher ($P < .05$) (124.44

vs 104.57 $pg \cdot ml^{-1}$) than that of heifers with a short PPI-1, but statistically similar to that of heifers with a long PPI-1. At 3 h, heifers with a short PPI-1 released numerically more androstenedione (125.62 vs 107.88 $pg \cdot ml^{-1}$) than heifers with a long PPI-1. Nonpregnant heifers released the highest amount of androstenedione (135.50 $pg \cdot ml^{-1}$). On d 24 concentration of androstenedione released at 1.5 h in response to GnRH and the magnitude of response to GnRH was similar (135.93 $pg \cdot ml^{-1}$ a 1.08 fold increase) for heifers that either had a short or a long PPI-1, respectively. At 3 h, release of androstenedione was numerically greater (155.05 vs 147.19 $pg \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1. However, the degree of response in both groups was still similar (1.11 fold increase). Overall, androstenedione released was numerically higher (130.28 vs 128.12 $pg \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1 and numerically highest (138.22 $pg \cdot ml^{-1}$) in nonpregnant heifers.

Effect of Exogenous Estradiol on Gonadotropins (PPI-1)

Table 9 (d 14 and 28) also shows data on gonadotropin release in response to exogenous E_2. The degree of the gonadotropin response to E_2 is also shown in Appendix G. Luteinizing hormone released on d 14 at approximately 16 h following E_2 administration was numerically higher (7.58 vs 4.46 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers

with a long PPI-1. The degree of response to E_2 was also higher (8.15 vs 7.2 fold increase) for heifers with a short PPI than for heifers with a long PPI-1. There was only a 1.8 fold increase in LH for nonpregnant heifers. At 18 h following E_2, serum concentration of LH was numerically lower (10.59 vs 14.58 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 when compared to heifers with a long PPI-1. There was also a smaller degree of response to E_2 from 16 h to 18 h (1.4 vs 3.3 fold increase) for heifers with a short PPI-1 than heifers with a long PPI-1. These results indicate that heifers with a short PPI-1 responded earlier to E_2 than heifers with a long PPI-1. One heifer from the short PPI-1 group appeared to have had peak LH concentration prior to the 14 h sampling time compared to five heifers from the long PPI-1 group. Twenty-three heifers with a short PPI had LH peak concentration between 16 and 18 h following E_2 administration when compared to 18 heifers from the group that had a long PPI-1. Twelve heifers from the short PPI-1 group did not respond to E_2, whereas, 13 from the long PPI-1 group did not respond to E_2. Luteinizing hormone release in response to E_2 was higher ($P < .10$) (3.23 vs 1.36 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1 and nonpregnant heifers had an intermediate release (1.47 $ng \cdot ml^{-1}$). However the degree of response was highest in heifers that had a long PPI-1 (11.6 vs 4.6 fold increase). This may suggest that heifers with a short PPI-1

responded early to E_2. Release of LH at 18 h was higher (6.83 vs 3.82 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1. However, the magnitude of response was similar (2.5 fold increase) for both groups. Overall LH released in response E_2 on d 14 was numerically lower (7.11 vs 9.65 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in those with a long PPI-1 and nonpregnant heifers released the least ($P < .05$) (2.61 $ng \cdot ml^{-1}$) amount of LH. However, on d 28, 16 h and 18 h release of LH was higher ($P < .05$) (4.81 vs 2.59 $ng \cdot ml^{-1}$) in heifers with either a short PPI-1 or not pregnant. Thus, d 14 and d 28 LH released was numerically higher (6.06 vs 5.43 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1 and nonpregnant heifers released the least (3.66 $ng \cdot ml^{-1}$) amount of LH.

On d 28 five heifers with a short PPI-1 had LH peak prior to collection of the 14 h post-E_2 sample compared to three from the heifers with a long PPI-1. Twenty-two of the heifers with a short PPI-1 had LH peak concentration between 16 and 18 h following E_2 administration when compared to 20 heifers from the group that had long PPI-1. Nine heifers from the short PPI-1 group did not respond to E_2 and 13 from the long PPI-1 group also did not respond to E_2.

On d 1 and at 16 h after the injection of E_2 the FSH response to E_2 was lower ($P < .10$) (2.23 vs 3.50 $ng \cdot ml^{-1}$)

in heifers with a short PPI-1 than in heifers with either a long PPI-1 or in those that did not become pregnant (3.19 $ng \cdot ml^{-1}$). The magnitude of response was also smaller (1.2 vs 1.8 fold increase) for heifers with a short PPI-1 than for heifers with a long PPI-1. At 18 h following E_2 heifers with a short PPI-1 still released numerically less FSH (4.3 vs 5.95 $ng \cdot ml^{-1}$) than heifers with a long PPI-1. Nonpregnant heifers released the least (3.69 $ng \cdot ml^{-1}$) amount of FSH and the degree of the response was similar for all groups (1.5 fold increase). Estradiol did not appear to have as much of an effect on FSH on d 28 at 16 h following it's injection as it did on d 14 in heifers with a short PPI-1. Heifers with a short PPI-1 released less FSH (2.26 vs 2.44 $ng \cdot ml^{-1}$, a 1.09 vs 1.07 fold, increase respectively) than heifers with a long PPI-1. Release of FSH was lower ($P < .05$) (2.35 vs 3.34 $ng \cdot ml^{-1}$) for heifers with either a short or a long PPI-1 when compared to heifers that did not become pregnant. Similarly at 18 h following E_2 administration FSH release had increased about 1.5 fold in all heifers but was still smallest in heifers with a short PPI-1 (3.24 vs 3.47 vs 3.54 $ng \cdot ml^{-1}$) when compared to heifers with either a long PPI-1 or not pregnant, respectively. Overall FSH released in response to E_2 was numerically lower (3.04 vs 3.80 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1 and

nonpregnant heifers had intermediate (3.43 $ng \cdot ml^{-1}$) FSH release.

Basal Prolactin (PPI-1)

Serum PRL concentration starting at approximately 35 d postpartum to the beginning of breeding is shown in Table 11. On d 1 heifers with a short PPI-1 had higher levels of basal PRL ($P = .11$) (100.47 vs 50.84 $ng \cdot ml^{-1}$) than heifers with a long PPI-1. Whereas nonpregnant heifers had PRL concentration similar ($P = .11$) (68.76 $ng \cdot ml^{-1}$) to that of heifers with either a short or a long PPI-1. Basal PRL was also numerically higher for d 10, 14 and 28 in heifers with a short PPI-1 than in heifers with a long PPI-1. For heifers that did not become pregnant basal PRL was highest on d 10, intermediate on d 14 and lowest on d 28 when compared to the other two groups. Day 24 PRL was still higher ($P = .06$) (79.42 vs 41.51 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1, but was lowest ($P = .06$) (36.20 $ng \cdot ml^{-1}$) in heifers that did not become pregnant when compared to heifers with a short PPI-1. Overall basal PRL was higher ($P < .05$) (77.40 vs 54.08 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1. Whereas nonpregnant heifers had intermediate (68.89 $ng \cdot ml^{-1}$) overall basal PRL.

Effect of Exogenous GnRH on Prolactin (PPI-1)

Release of PRL in response to GnRH is shown in Table 12 (d 1 and d 24). Concentration of PRL found at 3 h after

Table 11. Means of basal prolactin production starting at approximately 35 d postpartum to the beginning of the breeding season, $ng \cdot ml^{-1}$

Day[a]:	1	10		14	24	28	
Event[b]:	$PGF_{2\alpha}$ GnRH	$PGF_{2\alpha}$		Post E_2	$PGF_{2\alpha}$ GnRH	Post E_2	
Sampling time, h:	0	0	1.0	14	0	14	Overall Mean
Heifer group[c]							
Short PPI-1	100.47[d]	98.58	83.13	64.28	79.42[f]	38.54	77.40[h]
Long PPI-1	50.84[e]	105.25	60.36	43.45	41.51[g]	23.05	54.08[i]
Not pregnant	68.76[d]	151.52	76.26	59.50	36.20[g]	21.09	68.89[i]
SEM	10.97	16.27	10.76	6.48	7.99	4.00	

[a]Day of the 28 d hypothalamic-pituitary-ovarian challenge, starting at 35 d postpartum.
[b]Event, $PgF_{2\alpha}$ = prostanglandin-F-2-alpha, 5 mg lutalyse i.m.
GnRH = gonadotropin-releasing hormone, 10 μg i.m.
E_2 = 17 ß-estradiol-3-benzoate, 1 mg i.m.
[c]PPI-2 = days from birth of the first calf to birth of the second calf minus 281 d of gestation.
Short PPI-1 = 0 - 16 d, 35 heifers.
Long PPI-1 = 18 - 83 d, 37 heifers.
Not pregnant = 11 heifers.
[d,e]Means within a column with different superscripts differ (P = .11).
[f,g]Means within a column with different superscripts differ (P < .06).
[h,i]Means within a column with different superscripts differ (P < .05).

Table 12. Means of prolactin production starting at approximately 35 d postpartum to the beginning of the breeding season, $ng \cdot ml^{-1}$

Day[a]:	1			10		14			24			28			
Event[b]:	$PGF_{2\alpha}$ GnRH			$PGF_{2\alpha}$		Post E_2			$PGF_{2\alpha}$ GnRH			Post E_2			
Sampling time, h:	0	1.5	3.0	0	1.0	14	16	18	0	1.5	3.0	14	16	18	Overall Mean
Heifer group[c]															
Short PPI-1	100.47[d]	150.01	46.73[f]	98.58	83.13	64.28	70.27[h]	50.77	79.42[f]	85.64[d]	28.26	38.54	27.62	59.95[j]	70.73[l]
Long PPI-1	50.84[e]	118.70	27.80[f,g]	105.25	60.36	43.45	35.37[i]	37.55	41.51[g]	52.88[e]	21.07	23.05	19.18	33.80[k]	47.53[m]
Not pregnant	68.76[d]	85.22	18.31[g]	151.52	76.26	59.50	48.38[h,i]	63.80	36.20[g]	78.95[d,e]	27.82	21.09	16.85	21.68[k]	55.26[m]
SEM	10.97	16.12	4.60	16.27	10.76	6.48	5.00	6.30	7.99	7.21	2.49	4.00	2.76	5.45	2.47

[a]Day of the 28 d hypothalamic-pituitary-ovarian challenge, starting at 35 d postpartum.
[b]Event, $PgF_{2\alpha}$ = prostanglandin-F-2-alpha, 5 mg lutalyse i.m.
GnRH = gonadotropin-releasing hormone, 10 μg i.m.
E_2 = 17 ß-estradiol-3-benzoate, 1 mg i.m.
[c]PPI-1 = days from birth of the first calf to birth of the second calf minus 281 d of gestation.
Short PPI-1 = 0 - 16 d, 35 heifers.
Long PPI-1 = 18 - 83 d, 37 heifers.
Not pregnant = 11 heifers.
[d,e]Means within a column with different superscripts differ (P = .11).
[f,g]Means within a column with different superscripts differ (P < .10).
[h,i]Means within a column with different superscripts differ (P < .01).
[j,k]Means within a column with different superscripts differ (P < .05).
[l,m]Means within a column with different superscripts differ (P = .0001).

GnRH suggests that PRL is not secreted in response to GnRH. The increase that occurred between 0 and 1.5 h is probably a response to stress. At 1.5 h following GnRH on d 1 heifers with a short PPI-1 had numerically higher (150.01 vs 118.70 $ng \cdot ml^{-1}$) release of PRL than heifers with a long PPI-1. However, the magnitude of the response to handling was numerically lower (1.49 vs 2.35 fold increase) in heifers with a short PPI-1 than in heifers with a long PPI-1. At 3 h following GnRH heifers with a short PPI-1 still had higher PRL ($P = .07$) (46.73 vs 27.80 $ng \cdot ml^{-1}$) concentrations than heifers with a long PPI-1. However, release of PRL for both groups was lower than their respective baseline releases. At 1.5 and 3 h heifers that did not become pregnant released numerically less (85.22 and 18.31 $ng \cdot ml^{-1}$, respectively) PRL. On d 24 PRL levels at 1.5 h was higher ($P = .11$) (85.64 vs 52.88 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1. The magnitude of change from 0 h to 1.5 h was numerically less (1.08 vs 1.27 fold increase) for heifers with a short PPI-1 than heifers with a long PPI-1. Although nonpregnant heifers released intermediate (78.95 $ng \cdot ml^{-1}$) amount of PRL at 1.5 h, their magnitude of response was numerically greater (2.18 fold) than that of heifers with either a short or a long PPI-1. Prolactin release at 3 h was numerically higher (28.26 vs 21.07 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1.

Nonpregnant heifers had an intermediate release (27.82 $ng \cdot ml^{-1}$). As was the case on d 1 release of PRL at 3 h was below the basal level for all three groups of heifers.

Effect of Exogenous Estradiol on Prolactin (PPI-1)

Prolactin released in response to E_2 is also shown in Table 12 (d 14 and d 28) and as with GnRH it appears unlikely that E_2 caused the secretion of PRL. On d 14 approximately 16 h following E_2 injection heifers with a short PPI-1 secreted more ($P < .01$) (70.27 vs 35.37 $ng \cdot ml^{-1}$) PRL than heifers with a long PPI-1 and the magnitude of response was higher (1.09 vs -.81 fold increase) for heifers with a short PPI-1 than heifers with a long PPI-1. At 18 h following E_2 heifers with a short PPI-1 had a numerically greater (50.77 vs 37.55 $ng \cdot ml^{-1}$) amount of PRL, but secretion for both groups was lower than their respective basal levels. Prolactin levels in heifers that did not become pregnant did not change between 14 h or 18 h, but their PRL release was intermediate (48.38 $ng \cdot ml^{-1}$) to that of heifers with either a short or a long PPI-1. At 18 h following E_2 nonpregnant heifers secreted, numerically, the greatest (63.80 $ng \cdot ml^{-1}$, a 1.32 fold increase) amount of PRL. On d 28 in all heifers PRL levels did not change between 14 h and 16 h, but an increase occurred at 18 h. Heifers with a short PPI-1 secreted a numerically higher (27.62 vs 19.18 vs 16.85 $ng \cdot ml^{-1}$) amount of PRL at 16 h than heifers with either a long PPI-1 or

heifers that did not become pregnant, respectively. At 18 h heifers with a short PPI-1 secreted the highest ($P < .05$) (59.95 vs 33.80 $ng \cdot ml^{-1}$) amount of PRL. The magnitude of change was also numerically higher (2.17 vs 1.76 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1. Nonpregnant heifers had the least amount of PRL (21.68, a 1.29 fold increase. Overall, PRL concentrations were higher ($P = .0001$) (70.73 vs 47.53 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1 and nonpregnant heifers were intermediate (55.26 $ng \cdot ml^{-1}$).

Classification according to PPI-2

Nutritional status. Heifers were reclassified according to the length of time from birth of the first calf to conception (PPI-2). Under this classification 15 heifers that previously had a short PPI became switched to a long PPI and 16 that previously had a long PPI-1 became switched to a short PPI. Twenty heifers had a short PPI and 21 had a long PPI irrespective of classification. Although there was an equal number of heifers whose status changed from PPI-1 to PPI-2, the results were fairly similar between heifers with either a short or a long PPI-2. The results were also similar for when heifers were either classified under PPI-1 or PPI-2, therefore, to avoid duplication, the coverage of the results under PPI-2 classification are not as detailed as under PPI-1.

Table 13 shows performance of the first-calf Angus heifers with either a short or a long PPI-2. Birth and weaning weight of heifers with a short PPI-2 was greater than that of heifers with a long PPI-2. Performance of heifers under PPI-2 was similar to that of PPI-1 (Table 3) except for weaning weight and weaning BW:HH ratio which were greater in heifers with a short PPI-2 than in heifers with a long PPI-2, a reversal of PPI-1 results for these two variables.

Table 14 shows performance of heifers from 35 d postpartum to the beginning of the breeding season. Body weight and backfat results were similar to those of the PPI-1 classification in that heifers with a short PPI-2 had higher BW and more backfat from 35 d postpartum to the end of the 90 d breeding season. The only change from PPI-1 results is that 60 d following the end of the breeding season heifers with a short PPI-2 had more BW and backfat than heifers that had a long PPI-2. The pattern of BCS was also similar to that of PPI-1 except that at 35 d postpartum heifers with a short PPI-2 had a lower BCS than heifers with a long PPI-2.

Table 15 shows the performance of the first offspring of the heifers with either a short or a long PPI-2. Calves born to heifers with a short PPI-2 were lighter by .8 kg at birth. Also at the beginning of the heifers' nutritional and hormonal status evaluation (mean 35 d postpartum)

Table 13. Performance of first-calf Angus heifers with either a short or a long postpartum interval

	PPI-2[a]			
	Short	Long	Not pregnant	SE
Number of animals	36	36	11	
Body weights, kg[b]				
Birth	34.9	33.5	35.8	0.6
Weaning	268.2	261.5	264.9	2.6
Weaning BW:HH, [b] $kg \cdot cm^{-1}$	2.360	2.327	2.350	0.007
Weaning ADG, [c] $kg \cdot d^{-1}$	1.132	1.110	1.141	0.011
Age, d				
Weaning	217	219	213	2.000
First breeding	468[d]	443[e]	447[de]	4.000
First calving	749[d]	724[e]	728[de]	4.000
Second breeding	804	797	793	4.000

[a]Postpartum interval-2 = days from birth of the first calf to conception.
Short PPI-2 = 52 to 82 d.
Long PPI-2 = 83 to 125 d.
[b]Body weight to hip height ratio.
[c]Average daily gain.
[de]means with a different superscript differ ($P < .05$).
SE = standard error of the pooled mean.

Table 14. Performance of first-calf Angus heifers with either a short or a long postpartum interval from 35 d postpartum to the end of breeding

	PPI-2[a]			
	Short	Long	Not pregnant	SE
No. of animals	36	36	11	
Body weights, kg[b]				
35 d postpartum	455.5[c]	439.6[c,d]	432.2[d]	5.1
63 d postpartum	468.0	447.7	452.8	5.0
123 d postpartum	479.7	466.8	465.2	4.8
181 d postpartum	499.1(12)	477.5 (13)	515.7 (5)	9.5
213 d postpartum	493.6(24)[c]	488.6[c](22)	447.3[d](6)	4.8
35 d postpartum BW:HH, $kg \cdot cm^{-1}$	3.530[d]	3.452[e]	3.361[e]	0.040
Backfat estimates, mm[b]				
35 d postpartum	4.50	4.42	4.46	0.12
63 d postpartum	4.56	4.36	4.82	0.10
123 d postpartum	4.42[c]	4.50[c,d]	5.09[d]	0.13
181 d postpartum	4.75(12)	5.08(13)	5.60(5)	0.16
213 d postpartum	5.21(24)	5.09(22)	4.67(6)	0.16
Body condition score[b]				
35 d postpartum	5.32	5.38	5.13	0.07
63 d postpartum	5.53[c,d]	5.48[d]	5.85[c]	0.06
125 d postpartum	5.22	5.25	5.24	0.07
181 d postpartum	5.15(12)	5.40(13)	5.40(5)	0.09
213 d postpartum	5.83(24)	5.71(22)	5.40(6)	0.07
Mean PPI-2, d	70.22[c]	58.53[d]		1.17
Estrous cycles per conception	2[c]	4[d]	5+[e]	0.1

[a]Postpartum interval-2 = days from birth of the first calf to conception.
Short PPI-2 = 52 to 82 d.
Long PPI-2 = 83 to 125 d.

[b]63 d postpartum = beginning of breeding.
181 d postpartum = 28 d post-breeding (yr 2).
213 d postpartum = 60 d post-breeding (yr 1).
Numbers in brackets represent different sample size.

[cd]Means within a row with different superscript differ ($P < .05$).
SE = standard error of the pooled mean.

Table 15. Performance of first-born calves of Angus heifers with varying postpartum interval

	PPI-2[a]			
	Short	Long	Not pregnant	SE
Number of calves[b]	18F 18M	5F 21M	7F 4M	
Body weights, kg				
Birth	29.2	29.7	29.8	0.4
35 d postpartum	58.6	62.0	60.8	1.6
63 d postpartum	71.5	75.6	74.2	1.8
123 d postpartum	154.5	154.8	158.6	2.8
181 d postpartum	175.1[e](12)	189.79[ef](12)	198.13[f](5)	4.1
Weaning	244.7	248.8	242.2	0.4
Weaning ADG,[c] $kg \cdot d^{-1}$	1.132	1.110	1.141	0.011
Weaning BW:HH[d], $kg \cdot cm^{-1}$	2.150	2.185	2.150	0.027
Weaning age, d	210[e]	234[f]	219[e]	1.000

[a]Postpartum interval-2 = days from birth of the first calf to conception.
Short PPI-2 = 52 to 82 d.
Long PPI-2 = 53 to 125 d.
[b]F = Female
M = Male.
[c]Average daily gain.
[d]Body weight to hip height ratio.
Numbers in brackets represent different sample size.
[ef]Means within a row with different superscripts differ ($P < .05$).
SE = standard error of the pooled mean.

calves belonging to heifers with a short PPI-2 were lighter ($P < .05$) (58.6 vs 70.2 kg) than those belonging to heifers with a long PPI-1. Their BW was still lower ($P < .05$) (71.5 vs 83.7 kg) when their dams were exposed to the bull (63 d postpartum) and at 20 d following the end of the breeding season ($P < .05$) (175.09 vs 189.79 kg) and at weaning (244.7 vs 248.8 kg)

Table 16 shows NEFA concentration of heifers with either a short or a long PPI-2. Overall heifers with a short PPI-2 had numerically lower (367.58 vs 373.55 $\mu m \cdot l^{-1}$) concentration of NEFA than heifers with a long PPI-2.

An extension of the PPI beyond 60 d appears to benefit the calves because calves belonging to heifers with a long PPI-2 had (numerically) better growth performance (Table 5).

Lower levels of NEFA seen in heifers with a short PPI-2 suggest that these heifers were not mobilizing their body stores. The results are also in agreement with the observation that heifers gaining body condition will have lower levels of NEFA.

Reproductive Hormonal Profiles. Table 17 shows means of basal gonadotropins. There was no significant difference in basal LH among heifer groups from d 1 to d 10 and on d 28 of the evaluation. On d 14 heifers with a short PPI-2 had LH concentration numerically higher (.80 vs .74 $ng \cdot ml^{-1}$) than that of heifers with a long PPI-2. Nonpregnant

Table 16. Changes in concentration of non-esterified fatty acids in Angus heifers from 35 d postpartum to the beginning of breeding, $\mu m \cdot l^{-1}$

Day[b]	Days PP[d]	Event[c]	PPI-2[a] Short	Long	Not pregnant	SE
Number of animals			12	13	5	
1	35	$PGF_{2\alpha}$ & GnRH	536.53	483.05	514.80	19.21
10	45	$PGF_{2\alpha}$	444.09	450.29	497.04	19.66
14	49	E_2	216.56	373.32	302.91	32.95
21	56	$PGF_{2\alpha}$ & GnRH	381.86	337.88	398.06	27.76
28	59	E_2	248.97	223.20	200.74	13.53
Overall Mean			367.58	373.55	382.71	13.12
28 d post breeding			379.48	374.95	397.86	16.80

[a]Postpartum interval-2 = days from birth of the first calf to conception.
Short PPI-2 = 52 to 82 d.
Long PPI-2 = 83 to 125 d.
[b]Day of the hypothalamic-pituitary-ovarian evaluation.
[c]Event, represents what was performed on the heifers
$PGF_{2\alpha}$ = prostanglandin-F-2-alpha, 5 mg i.m.
GnRH = gonadotrophin releasing hormone, 10 μg i.m.
[d]Days postpartum.
No significant difference detected (P>.10).
SE = standard error of the pooled mean.

Table 17. Means of basal serum gonadotropins of first-calf Angus heifers from 35 d postpartum to the beginning of breeding

Day[a]:	1	10		14	24	28	
Event[b]:	$PGF_{2\alpha}$ GnRH	$PGF_{2\alpha}$		Post E_2	$PGF_{2\alpha}$ GnRH	Post E_2	
Sampling time, h:	0	0	1.0	14	0	14	Overall Mean
Heifer group[c]							
				Luteinizing hormone, $ng \cdot ml^{-1}$			
Short PPI-2	.58	.63	.51	0.80[d]	.60[f]	1.00	.69
Long PPI-2	.61	.63	.51	0.74[d]	.47[g]	1.01	.67
Not pregnant	.60	.65	.45	2.07[e]	.50[g]	1.06	.90
SEM	.03	.03	.03	0.11	.03	0.17	0.05
				Follicle stimulating hormone, $ng \cdot ml^{-1}$			
Short PPI-2	2.35	2.38	2.44	1.91	2.39	2.07	2.23
Long PPI-2	2.35	2.26	3.27	1.96	2.38	2.29	2.37
Not pregnant	2.39	2.31	2.39	2.04	2.75	2.43	2.39
SEM	0.13	0.15	0.21	0.12	0.14	0.17	0.06

[a]Day in the series of hormonal evaluations that began at approximately 35 d postpartum.
[b]Event, $PgF_{2\alpha}$ = prostanglandin-F-2-alpha, 5 mg lutalyse i.m.
GnRH = gonadotropin-releasing hormone, 10 μg i.m.
E_2 = 17 ß-estradiol-3-benzoate, 1 mg i.m.
[c]PPI-2 = days from birth of the first calf to conception.
Short PPI-2 = 52 - 82 d, 35 heifers.
Long PPI-2 = 83 - 125 d, 37 heifers.
Not pregnant = 11 heifers.
[d,e]Means within a column with different superscripts differ (P<.05).
[f,g]Means within a column with different superscripts differ (P<.10).
SEM = Standard error of the mean.

heifers had significantly higher (2.07 $ng \cdot ml^{-1}$) LH. These results are similar to the PPI-1 results (Table 9). On d 24 heifers with a short PPI-2 had more ($P < .05$) basal LH than heifers with a long PPI-2. Follicle stimulating hormone did not vary significantly among heifer groups during the evaluation. Overall, heifers that had a short PPI-2 had numerically lower levels of FSH when compared to heifers that had a long PPI-2 or did not become pregnant. A similar pattern was observed with PPI-1 results. Basal P_4 (Table 18) was the same for heifers with either a long or a short PPI-2 at the beginning of the evaluation. From d 2 to the end of the evaluation P_4 was lower in heifer with a short PPI-2 when compared to heifers with a long PPI-2. On d 24 and d 28 the P_4 difference was significant ($P = .06$). Overall P_4 was lower ($P < .05$) (.91 vs 1.22 $ng \cdot ml^{-1}$) in heifers with a short PPI-2 than in heifers with a long PPI-2. Concentration of E_2 and androstenedione did not vary significantly between heifer groups for the duration of the evaluation process, but heifers with a short PPI-2 had lower levels of E_2 and androstenedione at all times. Day one and d 24 androstenedione results were similar to PPI-1 results in that under androstenedione did not vary significantly between groups.

Effect of GnRH (PPI-2)

Gonadotropins. Table 19 (d 1 and d 24) shows the amount of gonadotropin released in response to GnRH. (The

Table 18. Means of basal serum ovarian steroids of first-calf Angus heifers from 35 d postpartum to the beginning of breeding

Day[a]:	1	10		14	24	28	
Event[b]:	$PGF_{2\alpha}$ GnRH	$PGF_{2\alpha}$		Post E_2	$PGF_{2\alpha}$ GnRH	Post E_2	
Sampling time, h:	0	0	1.0	14	0	14	Overall Mean
Heifer group[c]							
				Progesterone, $ng \cdot ml^{-1}$			
Short PPI-2	.37	1.22	1.28	.53[de]	1.55[f]	.59[f]	0.91[d]
Long PPI-2	.37	1.24	1.66	.69[d]	2.58[g]	.94[g]	1.22[e]
Not pregnant	.47	1.23	1.48	.37[e]	1.83[f]	.90[g]	1.03[d,e]
SEM	.02	0.11	0.12	.05	0.21	.08	0.05
				Estrogen, $pg \cdot ml^{-1}$			
Short PPI-2	3.19	6.45	5.83	-	3.72	-	5.89
Long PPI-2	3.48	7.05	8.63	-	4.22	-	6.59
Not pregnant	3.10	6.71	8.45	-	3.56	-	7.12
SEM	0.16	0.95	1.20	-	0.21	-	0.54
				Androstenedione, $pg \cdot ml^{-1}$			
Short PPI-2	89.39	120.23	134.79	-	122.16	-	115.43
Long PPI-2	91.94	120.70	147.42	-	130.73	-	118.94
Not pregnant	93.82	138.43	149.36	-	120.75	-	124.46
SEM	2.96	4.75	4.03	-	5.05	-	2.45

[a]Day in the series of hormonal evaluations that began at approximately 35 d postpartum.
[b]Event, $PgF_{2\alpha}$ = prostanglandin-F-2-alpha, 5 mg lutalyse i.m.
GnRH = gonadotropin-releasing hormone, 10 μg i.m.
E_2 = 17 ß-estradiol-3-benzoate, 1 mg i.m.
[c]PPI-2 = days from birth of the first calf to conception.
Short PPI-2 = 52 - 82 d, 36 heifers.
Long PPI-2 = 83 - 125 d, 36 heifers.
Not pregnant = 11 heifers.
[d,e]Means within a column with different superscripts differ (P<.05).
[f,g]Means within a column with different superscripts differ (P = .06).
SEM = Standard error of the mean.

Table 19. Gonadotropin secretion in response to gonadotropin-releasing hormone and estradiol in first-calf Angus heifers

Day[a]:	1			10		14			24			28			
Event[b]:	$PGF_{2\alpha}$ GnRH			$PGF_{2\alpha}$		Post E_2			$PGF_{2\alpha}$ GnRH			Post E_2			
Sampling time, h:	0	1.5	3.0	0	1.0	14	16	18	0	1.5	3.0	14	16	18	Overall Mean
Heifer group[c]															
						Luteinizing hormone, $ng \cdot ml^{-1}$									
Short PPI-2	.58	7.79[d]	14.67[f]	.63	.51	0.80[d]	1.82	13.33[d]	.60[h]	7.29	15.02	1.00	3.00	6.32	5.13[d]
Long PPI-2	.61	11.58[d,e]	26.19[g]	.63	.51	0.74[d]	9.15	11.60[d,e]	.47[i]	9.61	18.43	1.01	1.64	4.50	6.93[e]
Not pregnant	.60	14.09[e]	15.77[f]	.65	.45	2.07[e]	3.65	1.58[e]	.49[i]	11.49	17.78	1.06	1.47	7.35	5.99[d,e]
SEM	.03	0.96	1.25	.03	.03	0.11	0.76	1.75	.03	0.77	0.91	0.17	0.91	0.77	0.28
						Follicle stimulating hormone, $ng \cdot ml^{-1}$									
Short PPI-2	2.35	5.17	12.13	2.38	2.44	1.91	2.45	5.58	2.39	5.89	11.09	1.97	2.22[d]	3.29	4.38[g]
Long PPI-2	2.35	4.36	9.14	2.26	3.27	1.96	3.17	4.72	2.38	5.36	10.14	2.46	2.50[d,e]	3.43	4.14
Not pregnant	2.39	4.51	10.40	2.31	2.39	2.04	3.19	3.69	2.75	6.36	11.64	2.43	3.34[e]	3.54	4.39
SEM	0.13	0.42	0.68	0.15	0.21	0.12	0.28	0.68	0.14	0.38	0.76	0.17	0.16	0.23	0.14

[a]Day in the series of hormonal evaluations that began at approximately 35 d postpartum.
[b]Event, $PgF_{2\alpha}$ = prostanglandin-F-2-alpha, 5 mg lutalyse i.m.
GnRH = gonadotropin-releasing hormone, 10 μg i.m.
E_2 = 17 ß-estradiol-3-benzoate, 1 mg i.m.
[c]PPI-2 = days from birth of the first calf to conception.
Short PPI-2 = 52 - 82 d, 36 heifers.
Long PPI-2 = 83 - 125 d, 36 heifers.
Not pregnant = 11 heifers.
[d,e]Means within a column with different superscripts differ (P<.05).
[f,g]Means within a column with different superscripts differ (P<.0001).
[h,i]Means within a column with different superscripts differ (P<.10).
SEM = Standard error of the mean.

magnitude of the response is shown in appendix H). At d 1 and 1.5 h after GnRH, LH was released in a pattern similar to that of PPI-1 (Table 9). Although not significantly different d 1 LH release at 1.5 h was lower (7.79 vs 11.58 $ng \cdot ml^{-1}$) in heifers with a short PPI-2 than in heifers with a long PPI-2 and nonpregnant heifers released the most ($P < .05$) (14.09 $ng \cdot ml^{-1}$) LH when compared to heifers with a short PPI-1. Thus, the overall d 1 LH release was lower ($P < .01$) (10.92 vs 18.45 $ng \cdot ml^{-1}$) in heifers with a short PPI-2 than in heifers with a long PPI-2 and nonpregnant heifers released had intermediate (14.89 $ng \cdot ml^{-1}$) LH. The rate of the gonadotrophs response to GnRH on d 1 was the same for both groups (i.e. both groups responded early). On d 24 LH released in response to GnRH was not significantly different between groups, however, LH released by heifers with a short PPI-2 was still lower (7.29 vs 9.61 $ng \cdot ml^{-1}$) at 1.5 h and at 3.0 h (15.02 vs 9.61 $ng \cdot ml^{-1}$) than that released by heifers with a long PPI-2. Overall d 24 LH release was lower ($P = .07$) (11.15 vs 14.36 $ng \cdot ml^{-1}$) in heifers with either a short PPI-2 or those not pregnant.

Follicle stimulating hormone released in response to GnRH did not vary significantly between groups on both d 1 and d 24. On d 1, FSH released at 1.5 and 3.0 h was numerically higher (5.17 and 12.13 vs 4.36 and 9.14 $ng \cdot ml^{-1}$, respectively) in heifers with a short PPI-2. The degree of response was also higher (2.2 and 5.2 vs 1.9 and 3.9,

fold increase, respectively) in heifers with a short PPI-2 than in heifers with a long PPI-2. Both groups responded late to GnRH. Similarly, on d 24, at 1.5 h and 3.0 h following GnRH heifers with a short PPI-2 had numerically larger amount of FSH released (5.89 and 11.09 vs 2.38 and 10.14 $ng \cdot ml^{-1}$, respectively).

Ovarian steroids. Table 20 show concentration of ovarian steroids released in response to GnRH. On d 1 and at 1.5 h and 3 h following GnRH heifers with a short PPI-2 released less ($P < .10$) (.50 and .44 vs .7 and .76 $ng \cdot ml^{-1}$, respectively) P_4 than heifer with a long PPI-2, whereas, nonpregnant heifers released intermediate (.61 and .58 $ng \cdot ml^{-1}$, respectively) amount of P_4. Similarly, on d 24 at 1.5 h heifers with a short PPI-2 released less ($P < .10$) (1.50 vs 2.22 $ng \cdot ml^{-1}$) and numerically less (1.71 vs 2.21 $ng \cdot ml^{-1}$) at 3 h, than heifers with a long PPI-2. Overall P_4 released by heifers with a short PPI-2 was lower ($P < .01$) than in heifers with a long PPI-2. Estrogen and androstenedione released in response to GnRH did not vary significantly between groups on both d 1 and d 24. Heifers with a short PPI-2 released numerically more E_2 on d 1 (5.97 vs 5.54 $pg \cdot ml^{-1}$) (mean of 1.5 and 3 h) and on d 24 (4.64 vs 4.39 $pg \cdot ml^{-1}$) than heifers with a long PPI-2. Nonpregnant heifers had intermediate (5.85 and 4.59 $pg \cdot ml^{-1}$) E_2. On d 1 androstenedione was numerically higher in heifers with a short PPI-2 (116.48 vs 113.28 $pg \cdot ml^{-1}$) than

Table 20. Ovarian steroid secretion in response to gonadotropin-releasing hormone and estradiol in first-calf Angus heifers

Day[a]:	1			10		14			24			28			
Event[b]:	$PGF_{2\alpha}$ GnRH			$PGF_{2\alpha}$		Post E_2			$PGF_{2\alpha}$ GnRH			Post E_2			
Sampling time, h:	0	1.5	3.0	0	1.0	14	16	18	0	1.5	3.0	14	16	18	Overall Mean
Heifer group[c]															
	---------- Progesterone, $ng \cdot ml^{-1}$ ----------														
Short PPI-2	.37	.50[d]	.44[d]	1.22	1.29	.53[f,g]	-	-	1.56[d]	1.50[d]	1.71	.59[d]	-	-	0.96[h]
Long PPI-2	.37	.70[e]	.76[e]	1.24	1.66	.69[f]	-	-	2.58[e]	2.22[e]	2.21	.94[e]	-	-	1.33[i]
Not pregnant	.47	.61[d,e]	.58[d,e]	1.23	1.48	.37[g]	-	-	1.83[d]	1.43[d]	2.12	.90[e]	-	-	1.09[h,i]
SEM	0.02	0.04	0.06	0.11	0.12	0.05	-	-	0.21	0.16	0.19	0.08	-	-	0.04
	---------- Estrogen, $pg \cdot ml^{-1}$ ----------														
Short PPI-2	3.19	3.65	8.28	6.46	5.83	-	-	-	3.72	3.92	5.36	-	-	-	5.59
Long PPI-2	3.48	3.80	7.27	7.05	8.63	-	-	-	4.22	4.21	4.57	-	-	-	5.72
Not pregnant	3.10	3.83	7.87	6.71	8.45	-	-	-	3.56	3.59	5.58	-	-	-	6.15
SEM	0.16	0.19	0.83	0.95	1.20	-	-	-	0.21	0.17	0.30	-	-	-	0.29
	---------- Androstenedione, $pg \cdot ml^{-1}$ ----------														
Short PPI-2	89.39	115.73	117.22	120.23	134.79	-	-	-	122.16	127.78	148.88	-	-	-	121.61
Long PPI-2	91.94	110.77	115.79	120.70	147.42	-	-	-	130.73	144.08	153.14	-	-	-	125.11
Not pregnant	93.82	124.44	135.50	138.43	149.36	-	-	-	120.75	140.22	152.73	-	-	-	131.50
SEM	2.96	3.56	6.29	4.75	4.03	-	-	-	5.05	3.95	5.13	-	-	-	1.78

[a]Day in the series of hormonal evaluations that began at approximately 35 d postpartum.
[b]Event, $PgF_{2\alpha}$ = prostanglandin-F-2-alpha, 5 mg lutalyse i.m.
GnRH = gonadotropin-releasing hormone, 10 μg i.m.
E_2 = 17 ß-estradiol-3-benzoate, 1 mg i.m.
[c]PPI-2 = days from birth of the first calf to conception.
Short PPI-2 = 52 - 82 d, 36 heifers.
Long PPI-2 = 83 - 125 d, 36 heifers.
Not pregnant = 11 heifers.
[d,e]Means within a column with different superscripts differ (P<.10).
[f,g]Means within a column with different superscripts differ (P<.05).
[h,i]Means within a column with different superscripts differ (P<.01).
SEM = Standard error of the mean.

in heifers with a long PPI-2. Nonpregnant heifers had the most (129.97 $pg \cdot ml^{-1}$) androstenedione. On d 24 heifers with a short PPI-2 released numerically less (135.93 vs 148.61 $pg \cdot ml^{-1}$) androstenedione than heifers with a long PPI-2. Nonpregnant heifers had intermediate (146.48 $pg \cdot ml^{-1}$) androstenedione level.

Effect of Estradiol (PPI-2)

Table 19 (d 14 and d 28) shows gonadotropins released in response to E_2. (The magnitudes of response is shown in appendix I). On d 14 at 16 h following E_2 injection heifers with a short PPI-2 released the less ($P < .05$) (1.82 vs 9.15 $ng \cdot ml^{-1}$) LH than heifers with a long PPI-2. But at 18 h post-E_2 heifers with a short PPI-2 released numerically the most LH (13.33 vs 11.60 $ng \cdot ml^{-1}$). The degree of the LH response to E_2 on d 14 was 2.3 and 12.4 (between 14 and 16 h for heifers with a short and a long PPI-2 , respectively. The degree of response between 16 h and 18 h was 7.3 for heifers with a short PPI-2 and 1.3 for heifers with a long PPI-2. This indicates that heifers with a short PPI-2 responded late to E_2. Two heifers with a short PPI-2 responded early, 21 responded later and 13 did not respond compared to four heifers from the long PPI-2 group that responded early, 20 responded late and 12 did not respond.

On d 28, at 16 h and 18 h heifers with a short PPI-2 released numerically more (3.0 and 6.32 $ng \cdot ml^{-1}$, respectively) LH in response to E_2. Heifers that had a long

PPI-2 released less (1.64 and 4.50 $ng \cdot ml^{-1}$) LH. The degree of response at 16 h was 1.3 vs 1.6 fold increase for heifers with a short PPI-2 when compared to heifers with a long PPI-2. At 18 h the degree of the response was a 2.3 and 1.5 fold increase for heifers with short and long PPI-2, respectively. On d 28 heifers with a short PPI-2 still responded late to E_2. Four of the heifers with a short PPI-2 responded early, 19 responded late and 13 did not respond compared to four heifers from the long PPI-2 group that responded early, 21 responded late and 11 did not respond.

Prolactin Secretion Results (PPI-2)

Table 21 and 22 shows PRL secretions. Prolactin followed a pattern similar to that of PPI-1, in that heifers with a short PPI-2 secreted the most ($P < .05$) PRL (overall basal PRL 77.40 vs 54.08 $ng \cdot ml^{-1}$) than heifers with a long PPI-2 and nonpregnant heifers secreted intermediate amount of PRL (68.89 $ng \cdot ml^{-1}$). As was the case when heifers were classified according to PPI-1, PRL secretion did not appear to be influenced by either GnRH or exogenous E_2, but by perhaps handling stress, because the greatest amount was secreted at 0 h except on d 1.

Regression Models Results

Tables 23 to 26 show the multiple regression equations generated by the stepwise procedure of SAS. The five variables that explained the most variation ($R^2 = .59$) in the interval from exposure to the bull to conception (PPI-

Table 21. Means of basal prolactin production starting at approximately 35 d postpartum to the beginning of the breeding season, $ng \cdot ml^{-1}$

Day[a]:	1	10		14	24	28	
Event[b]:	$PGF_{2\alpha}$ GnRH	$PGF_{2\alpha}$		Post E_2	$PGF_{2\alpha}$ GnRH	Post E_2	
Sampling time, h:	0	0	1.0	14	0	14	Overall Mean
Heifer group[c]							
Short PPI-2	84.18	130.66[d]	78.91	70.94[f]	60.20	33.49	77.40[f]
Long PPI-2	66.69	65.02[e]	53.68	36.22[g]	59.68	25.40	54.08[g]
Not pregnant	68.76	151.52[d]	76.26	59.50[f]	36.20	21.09	68.89[g]
SEM	11.24	15.43	10.74	6.32	8.23	4.06	

[a]Day of the 28 d hypothalamic-pituitary-ovarian challenge, starting at 35 d postpartum.
[b]Event, $PgF_{2\alpha}$ = prostanglandin-F-2-alpha, 5 mg lutalyse i.m.
GnRH = gonadotropin-releasing hormone, 10 μg i.m.
E_2 = 17 ß-estradiol-3-benzoate, 1 mg i.m.
[c]PPI-2 = days from birth of the first calf to birth of the second calf minus 281 d of gestation.
Short PPI-2 = 52 - 82 d, 35 heifers.
Long PPI-2 = 83 - 125 d, 37 heifers.
Not pregnant = 11 heifers.
[d,e]Means within a column with different superscripts differ ($P < .10$).
[f,g]Means within a column with different superscripts differ ($P < .05$).
[h,i]Means within a column with different superscripts differ ($P < .05$).

Table 22. Means of prolactin production starting at approximately 35 d postpartum to the beginning of the breeding season, $ng \cdot ml^{-1}$

Day[a]:	1			10		14			24			28			
Event[b]:	$PGF_{2\alpha}$ GnRH			$PGF_{2\alpha}$		Post E_2			$PGF_{2\alpha}$ GnRH			Post E_2			
Sampling time, h:	0	1.5	3.0	0	1.0	14	16	18	0	1.5	3.0	14	16	18	Overall Mean
Heifer group[c]															
Short PPI-2	84.18	118.07	32.97	130.66[d]	78.91	70.94[f]	63.77[d]	55.15	60.20	58.32	23.86	33.49	19.69	37.59[d,e]	62.01
Long PPI-2	66.69	123.43	41.04	65.02[e]	53.68	36.22[g]	39.38[e]	32.80	59.68	79.28	25.39	25.40	26.36	55.30[d]	52.66
Not pregnant	68.76	85.22	18.31	151.52[d]	76.26	59.50[f]	48.38[e]	63.80	36.20	78.95	27.82	21.09	16.85	21.68[e]	55.26
SEM	11.24	11.72	4.69	15.43	10.74	6.32	5.20	6.23	8.23	7.33	2.51	4.06	2.78	5.55	2.32

[a]Day of the 28 d hypothalamic-pituitary-ovarian challenge, starting at 35 d postpartum.
[b]Event, $PgF_{2\alpha}$ = prostanglandin-F-2-alpha, 5 mg lutalyse i.m.
GnRH = gonadotropin-releasing hormone, 10 μg i.m.
E_2 = 17 ß-estradiol-3-benzoate, 1 mg i.m.
[c]PPI-2 = days from birth of the first calf to birth of the second calf minus 281 d of gestation.
Short PPI-2 = 52 - 82 d, 35 heifers.
Long PPI-2 = 83 - 125 d, 37 heifers.
Not pregnant = 11 heifers.
[d,e]Means within a column with different superscripts differ ($P < .10$).
[f,g]Means within a column with different superscripts differ ($P < .05$).

1) (Table 23) were a combination (in descending order of partial R^2) of age of the calf when the heifer was bred for the second pregnancy (R^2 = .19), BCS (R^2 = .15) and backfat (R^2 = .12) of the heifer at the beginning of the evaluation, basal FSH (R^2 = .06) and BCS (R^2 = .06) at 60 d of the 90 d breeding season. Other variables being constant, the age of the calf at the beginning of the dam's breeding accounted for 19% of the variation in PPI-1. Of the five Variables influencing PPI-1, age of the calf when the dam was rebred, BCS and backfat contributed 47%.

Table 24 shows variables responsible for the variation in the interval from birth of the first calf to birth of the second calf minus 281 d of gestation (PPI-2). The three variables that explained the most variation (R^2 = .56) in PPI-2 was a combination (in descending order of partial R^2) backfat (R^2 = .20) at approximately 35 d postpartum, a change in BCS (R^2 = .19) from 35 to 63 d postpartum and BCS (R^2 = .17) at 63 d postpartum.

Table 25 shows a multiple regression equation of variables that accounted for the most variation in NEFA concentration (R^2 = .15). Change in BW of the calf from 35 d to 63 d postpartum accounted for all the variation in NEFA (R^2 = .14).

Table 23. Multiple regression equation variables for variables that explain (R^2 = .59) variation in the interval from exposure to the bull to conception (PPI-1)

Variable[a]	Partial R^2	Parameter estimate	Standard error	Prob > T
Intercept		-21.36	36.08	.56
CALFAGE	.20	-0.82	0.19	.0004
IBCS	.15	20.18	8.77	.003
IBFM	.12	-14.08	3.92	.002
BASALFSH	.06	-6.77	3.92	.10
MIDBRBCS	.06	11.31	5.51	.05

[a]CALFAGE = Age of the first calf when the heifer was bred, d.
IBCS = Heifer BCS at 35 d postpartum.
IBFM = Heifer backfat at 35 d postpartum, mm.
BASALFSH = Basal FSH, $ng \cdot ml^{-1}$.
MIDBRBCS = BCS at 60 d of the 90 d breeding season.

Table 24. Multiple regression equation for variables that explain the variation (R^2 = .56) in the interval from birth of the first calf to birth of the second calf minus 281 d gestation (PPI-2)

Variable[a]	Partial R^2	Parameter estimate	Standard error	Prob > T
Intercept		37.32	34.45	.29
IBFM	.20	-13.96	3.39	.01
CBCS	.19	-36.06	8.72	.001
FBCS	.17	21.97	7.82	.01

[a]IBFM = Heifer backfat at 35 d postpartum.
CBCS = Change in heifer BCS from 35 d to 63 d postpartum.
FBCS = Heifer BCS at 63 d postpartum (breeding).

Table 25. Multiple regression equation for variables that explain (R^2 = .15) variation in the concentration of non-esterified fatty acids

Variable[a]	Partial R^2	Parameter estimate	Standard error	Prob > T
Intercept		268.99	49.97	.0001
CCALFBW	.144	6.93	3.08	.03

[a]cCALFBW = Change in BW of the calf from 35 d to 63 d postpartum, kg.

Discussion

Nutritional Status

Heifers with a short PPI-1 had less BW (8.3 kg) and condition (Table 3) but were six days older at weaning than heifers with a long PPI-1 and eight days older than nonpregnant heifers. This may suggest that heifers with either a long PPI-1 or those not pregnant had grown at a faster rate. Heifers that did not become pregnant had a BW gain that was similar to that of heifers with a long PPI-1. A positive correlation ($r = .19$, $P = .11$) was also observed between ADG from birth to weaning and PPI-1, suggesting that rapid growth may have negatively affected fertility.

The results of the multiple regression demonstrate that, in general, heifers whose BCS were 4.7 at approximately 35 d postpartum became pregnant soon upon exposure to the bull, whereas those with a BCS of 6.6 took 39 d before pregnancy occurred. Heifers with a backfat measuring 5.4 mm at 35 d postpartum became pregnant on the day they were exposed to the bull and those with 6.6 mm backfat became pregnant on d 34 after exposure. When considering the interval from birth of the first calf to conception (PPI-2, Table 24) heifers whose backfat was 8 mm at 35 d postpartum conceived by 40 d following the birth of their first calf. On the other hand heifers whose backfat was 3 mm at 35 d postpartum conceived their second calf 109

d after parturition. Heifers that lose BCS (Table 24) by 1.20 points between 35 and 63 d postpartum (beginning of breeding) will become pregnant 140 d following the birth of their first calf and those that gain by 1.80 will become pregnant 32 d following birth of their first calf. Heifers whose BCS was 4.2 at the beginning of the breeding season became pregnant 59 d following birth of the first calf, whereas, heifers whose BCS was 6.6 at the beginning of breeding conceived 112 d following the birth of their first calves (Table 24).

From the beginning to the middle of the breeding season (Table 4) heifers with a short PPI-1 gained less BW ($P < .05$) than heifers with a long PPI-1 and again there was a slight positive correlation ($r = 19$, $P = .11$) between this change in BW and PPI-1. A positive correlation ($r = .22$, $P = .06$) between backfat and PPI-1 during the first 60 d of the breeding season suggests that heifers that get fat during breeding are less likely to become pregnant. At 60 d into the breeding season heifers with a long PPI-1 had an ADG of .32 (vs .20 $kg \cdot d^{-1}$) and backfat change of .2 (vs -.14 mm) (Table 4). Similarly, a heifer whose BCS is 4.0 at 60 d of the breeding season (Table 23) is more likely to have conceived right at exposure to the bull, whereas, a heifer with a BCS of 6.6 would have conceived at 30 d following exposure to the bull.

Concentration of NEFA have been observed to increase in fasted sheep (Trenkle and Kuhlemeier, 1966; Heitmann et al., 1986), in lactating goats experiencing a decrease in energy balance (EB) (Dunes et al., 1990) and in fasted cattle (Canfield and Butler, 1991; DiMarco, 1981). According to the results of the multiple regression equation (Table 26), NEFA concentration of heifers (irrespective of PPI) whose calves had an ADG of .47 $kg \cdot d^{-1}$ was 282.95 $\mu m \cdot l^{-1}$. The heifers whose calves had an ADG of .89 $kg \cdot d^{-1}$ had serum NEFA of 448.28 $\mu m \cdot l^{-1}$. Average daily gain of the calves reflects the heifers' milk production ability. Calves whose dams produce more milk will have a higher ADG than calves whose dams produce less milk. Thus, heifers that produce more milk are likely to have elevated levels of NEFA because they mobilize more body fat. In the present study, heifers that had a long PPI-1 also had higher concentration of NEFA than heifers with a short PPI-1. In this study heifers that did not become pregnant gained the most ($P < .05$) BW but also had numerically the highest concentration of NEFA which appears to be in contradiction. It may be possible that the high concentration of serum NEFA seen in heifers with either a long PPI-1 or in those that were not pregnant did not necessarily reflect lipolysis but a slow rate of reesterification of the free fatty acids to glycerides. Non-esterified fatty acid released during lipolysis can

either enter the body pool or be reesterified to triglycerides or phospholipids. Concentration of NEFA was lower in heifers with a short PPI-1 from 35 d postpartum to the middle of the breeding season except at 45 d postpartum (d 10). The increase in NEFA may have been induced by high levels of E_2. Basal E_2 for heifers with a short PPI-1 was low at all times except on d 10. Green et al. (1992) observed that high levels of E_2 increases tissue NEFA. Basal E_2 was positively correlated ($r = .31$, $P = .09$) to NEFA.

A positive relationship ($r = .39$, $P < .01$) between sex of the first calf and PPI-1 suggests that heifers nursing bull calves (as was the case with the majority of heifers with a long PPI-1, 70%), were more likely to have a longer PPI than heifers nursing female calves. Heifers with a long PPI-1 consistently had higher concentrations of NEFA (Table 6) than heifers with a short PPI-1, which may indicate that they were mobilizing body fat. Other researchers have also noted that heifers nursing bull calves tend to have a longer PPI (Bellows et al., 1982).

Age of the calf when the dam was exposed to the bull for the second parity was negatively correlated ($r = -.25$, $P < .05$) to PPI-1. This suggests that heifers that calved early in the calving season became pregnant shortly after exposure to the bull. Thus, artificially extending PPI appeared to have a positive effect on fertility. The

results of the multiple regression equation (Table 23) indicate that heifers who calved 85 d before exposure to the bull became pregnant right away (d 1), whereas, heifers that calved 30 d before exposure to the bull became pregnant 42 d after exposure.

Profile of Reproductive hormones

Basal hormones. Ten days following injection of $PGF_{2\alpha}$ basal serum concentration of LH (Table 7) was similar to that of d 1 levels in all groups. However, basal P_4 levels had risen to above 1 $ng \cdot ml^{-1}$ in all groups, (with heifers with a short PPI-1 having less P_4 than heifers with either a long PPI-1 or not pregnant) indicating the presence of a functional CL. It is this high P_4 that may have resulted in low levels of LH because P_4 inhibits LH release. Day 10 basal E_2 levels were twice that of d 1 for all groups but heifers with a short PPI-1 had higher levels of E_2 than heifers with a long PPI-1, suggesting follicular growth. It is possible that when $PGF_{2\alpha}$ was injected on d 1 some heifers did not have a functional CL hence $PGF_{2\alpha}$ had no effect. The rise in P_4 coupled to the rise in E_2 and androstenedione between d 1 and d 10 may have resulted in low levels of LH in all heifers. Progesterone and low levels of E_2 inhibit the activity of the hypothalamic-pituitary axis by inhibiting the GnRH pulse generator (Acosta et al., 1983; Nett, 1987; Short et al., 1990). Progesterone decreases the frequency of GnRH pulses, thus

decreasing the frequency of LH pulses, whereas E_2 decreases the amplitude of LH pulses (Nett, 1987).

At the beginning of breeding, heifers with a short PPI-1 had higher ($P < .05$) LH than heifers with a long PPI-1, indicating resumption of estrous activity. Furthermore, a positive relationship existed between body condition and BW and basal LH during the evaluation ($r = .22$, $P < .05$ and $r = .32$, $P < .01$, respectively) suggesting that BW and body condition of heifers with a short PPI might be used as an indicator for early conception.

Day 10 basal FSH levels were not affected by the high levels of P_4, E_2 and androstenedione, because d 10 levels of FSH were similar to d 1 levels. Between d 14 and d 28 there was a negative relationship between P_4 and FSH, but overall FSH did not vary greatly even when ovarian steroids increased. This suggests that synthesis or release of FSH may not be as responsive to physiological, environmental or hormonal changes as is LH. Follicle stimulating hormone has been observed to be unaffected by the residual effects of gestational P_4 and E_2 (Gauthier et al., 1982; Manns et al., 1983; Nett, 1988) or suckling (Walters et al., 1982b; Cross et al., 1987).

Mean basal P_4 concentration from d 14 to d 28 was higher ($P < .05$) (1.28 vs 1.03 $pg \cdot ml^{-1}$) for heifers with a short PPI-1 when compared to heifers with a long PPI-1 and mean basal LH at the same time was also higher ($P < .05$)

(.99 vs .58 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than heifers with a long PPI-1. Heifers with a short PPI-1 would be expected to have LH levels lower than those of heifers with a long PPI-1 because they had higher P_4 because P_4 inhibits LH release. An explanation of these results is that the higher levels of E_2 (4.06 vs 3.07 $pg \cdot ml^{-1}$) and androstenedione (130.80 vs 121.84 $pg \cdot ml^{-1}$) observed from d 14 to d 28 in heifers with a long PPI-1 compared to heifers with a short PPI-1 may have contributed to inhibiting LH release by the gonadotrophs.

Acosta et al. (1983) suggested that sensitivity of the hypothalamus to the negative feedback of E_2 increases in suckled beef females. Both basal P_4 and E_2 were negatively correlated ($r = -.25$, $P < .05$ and $r = -.27$, $P < .05$, respectively) to PPI-1. An increase in E_2 indicates follicular growth and development and a rise in P_4 could also reflect follicular growth or the presence of a functional CL. A positive relationship between P_4 and PPI-1 which is understandable because P_4 inhibits LH release and heifers with a long PPI-1 had numerically higher P_4 and lower LH. Overall, basal P_4 and E_2 were numerically lower in heifers with a short PPI-1 than in heifers with a long PPI-1. Nonpregnant heifers had numerically the least P_4 and the most E_2. Overall, basal androstenedione was lower ($P < .05$) in heifers with a short PPI-1 than in heifers with either a long PPI-1 or in those not pregnant. However,

prior to breeding basal P_4 was numerically higher and E_2 and androstenedione were numerically lower in heifers with either a short PPI-1 or not pregnant than in heifers with a long PPI-1.

Effect of GnRH. Heifers that had a short PPI-1 released the least amount of LH at 1.5 h following GnRH administration at approximately 35 d postpartum, but released more LH at 3 h post-GnRH. However, heifers with a long PPI-1 responded early to GnRH, that is, they released the highest amount of LH at 1.5 h and a smaller amount at 3 h post-GnRH. Total d 1 LH release was numerically lower (14.50 vs 15.80 $ng \cdot ml^{-1}$) in heifers with either a short PPI-1 or not pregnant than in heifers with a long PPI-1. But d 24 total LH release was numerically higher (13.10 vs 12.11 $ng \cdot ml^{-1}$) in heifers with short PPI-1 than in heifers with a long PPI-1, nonpregnant heifers had the highest total (14.69 $ng \cdot ml^{-1}$). These results suggest that LH release in heifers with a long PPI-1 was being inhibited during this period. Beal et al., (1978) observed that heifers restricted in energy intake released more LH in response to exogenous GnRH. Rutter and Randel (1984) and Killen et al., (1989) also observed that heifers loosing body condition postpartum released higher levels of LH in response to GnRH than heifers maintaining moderate body condition. Inhibition of release of LH in heifers with a long PPI-1 could have been due to suckling-induced opioids

(Cross et al., 1987) because a larger number of these heifers were nursing bull calves. An explanation is that LH release in nutritionally stressed or in suckled beef females is inhibited, thus, a single massive dose of GnRH empties the gonadotrophs of the LH present. In a situation where release is inhibited more will be released when the inhibitory factor is overridden.

Progesterone released in response to GnRH on d 1 at 1.5 h was generally low (.20, .26 and .14 $ng \cdot ml^{-1}$) for heifers with a short PPI-1, a long PPI-1 and in those not pregnant, respectively. However, on d 24 and 1.5 h GnRH had no effect on P_4 release. This is understandable because production of P_4 by the ovarian follicles is induced by gonadotropins. A slight increase in ovarian steroids was noticeable at 3 h, this indicates that the follicles are in the process of producing steroids. Overall, d 1 P_4 released in response to GnRH was numerically lower (.57 vs .62 $ng \cdot ml^{-1}$) for heifers with a short PPI-1 than in heifers with either a long PPI-1 or not pregnant.

Effect of Estradiol. High levels of E_2 induce the preovulatory LH surge in nonluteal phase heifers and cows and the surge causes ovulation. Serum LH released on d 14 and 16 h following the E_2 injection was higher in heifers with a short PPI-1 than in heifers with a long PPI-1 or in those that failed to produce a calf. Thus, heifers with a short PPI-1 responded early to E_2. Day 24 LH release in

response to E_2 was lower than d 14 LH release in response to E_2 in all heifer groups. This could have resulted from some heifers having already experienced the LH surge because they were injected with $PGF_{2\alpha}$ three days (d 10) prior to the E_2 treatment (d 14). The FSH response to E_2 was very small in all heifers, about a 1.5 fold increase on d 14 and a 1.2 fold increase on d 28, 16 h following the E_2 injection. This further supports the hypothesis that FSH is not as rigorously controlled by ovarian steroids as is LH (Cross et al., 1987; Gauthier et. al., 1982; Manns et al., 1982b; Nett, 1987). Overall, LH released in response to E_2 was numerically lower (9.09 vs 9.52 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1, but both released more ($P < .05$) LH than nonpregnant heifers (2.62 $ng \cdot ml^{-1}$). On d 28, overall, LH release was higher ($P < .05$) (5.03 vs 2.59 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1 and nonpregnant heifers still released the least ($P < .05$) (1.26 $ng \cdot ml^{-1}$) LH. Follicle stimulating hormone release was numerically lower (3.30 vs 2.73 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1 and nonpregnant heifers released the least (2.62 $ng \cdot ml^{-1}$) FSH. Day 28 FSH release was numerically lower (2.75 vs 2.96 $ng \cdot ml^{-1}$) in heifers with a short PPI-1 than in heifers with a long PPI-1 and nonpregnant heifers released numerically the most (3.44 $ng \cdot ml^{-1}$) FSH.

Basal Prolactin

Overall, basal PRL was higher ($P < .05$) in heifers with a short PPI-1 than in heifers with a long PPI-1. All heifers would be expected to have similar levels of PRL if suckling stimulus was the major determinant of PRL secretion in these heifers because all were nursing calves. Suckling stimulus increases release of endogenous opioids (Gregg et al. (1986). Opioids are believed to antagonize dopamine thus removing the inhibition on PRL (Johnson et al., 1991). Thus, endogenous opioids increase PRL release (Connor et al., 1990; Johnson et al., 1991). However, effect of opioids on PRL will only be seen during suckling. Therefore, PRL secretion in our study reflected response to handling stress. The high levels of PRL observed in heifers with a short PPI-1 suggest either that these heifers were more responsive to handling stress or had a greater capacity to secrete prolactin than heifers of the other groups.

Samples collected on d 10 were both basal samples. However, PRL release was higher at 0 h than at 1 h this could have been because the lactotrophs were almost drained of PRL as a result of the stress incurred during collection of the first blood sample, thus by 1 h the cells were secreting less PRL than they were at 0 h. High levels of PRL observed on d 14, 24 and 28 sampling may have coincided with the peak of PRL release induced by handling.

Basal PRL was higher on each day of the blood sample collection in heifers with a short PPI-1 than in heifers with a long PPI-1 and, except for d 10, in heifers that did not become pregnant (Table 11) and PRL was highly correlated ($r = .31$, $P < .01$) to basal LH. These results may suggest that PRL may play a role in influencing PPI. Studies in rats (Azad et al. 1990) and in human females (McNeilly, 1980) have indicated that PRL influences GnRH secretion or release, thus, it can be speculated that PRL may mediate some of the factors that affect the GnRH neuron.

Effect of GnRH on Prolactin

Prolactin determined in blood samples collected at 1.5 h on d 1 and 24 was high in all heifer groups but declined to levels lower than basal by 3 h. Similarly Nett et al., (1988) observed that PRL release declined with time in some cows following collection of the first blood sample, but in their study blood was collected in a less stressful environment. Therefore, the concentration of PRL found at 1.5 h and 3 h following GnRH indicate that PRL is not secreted in response to GnRH. The increase that occurred between 0 h and 1.5 h is a probable response to stress. Overall basal PRL secretion was higher ($P < .0001$) in heifers with a short PPI-1 than in heifers with either a long PPI-1 or in the non pregnant. A similar observation was made when heifers were classified according to PPI-2.

Summary

The objective of this study was to characterize nutritional status and reproductive performance and hormonal profiles of reproductively efficient or inefficient first-calf Angus heifers. Conception within one estrous cycle following exposure to the bull and delivery of a life calf represented reproductive efficiency. Nutritional evaluation of these heifers revealed that they were not nutritionally stressed and instead the less efficient heifers tended to have a fatter body condition at the beginning and during the breeding season, which may suggest that a fatter body condition may have impaired reproductive performance. Reproductive hormonal profiles of heifers that were efficient indicated a higher basal LH, lower basal FSH, lower basal androstenedione and lower release of FSH in response to GnRH. Reproductively efficient heifers also appeared to be more responsive to handling stress or they perhaps had a greater capacity to secrete PRL than other groups.

Implications

The results of this study suggest that two year-old Angus heifers that conceived within the first estrous cycle after exposure to the bull had a mean BW of 460 kg with

mean backfat thickness of 4.63 mm and a BW:HH ratio of 3.61 $kg \cdot cm^{-1}$ and a BCS of 5.6. A larger BW gain postpartum and during the first 60 d of the breeding season appears to lead to be associated with delayed or lack of conception within a 90 d breeding season. Based on the results of this study excess body condition during breeding (high fat) may have contributed to lack of conception. The results of this study also imply that a reproductively efficient two-year Angus heifer will have higher basal LH (.80 vs .57 $ng \cdot ml^{-1}$), lower FSH (2.10 vs 2.47 $ng \cdot ml^{-1}$), lower androstenedione (107.41 vs 125.08 $pg \cdot ml^{-1}$), lower FSH released in response to GnRH (6.74 vs 8.58 $ng \cdot ml^{-1}$) and higher PRL secretion (77.40 vs 54.08 $ng \cdot ml^{-1}$) and is more likely to become pregnant during the first estrous cycle after exposure to the bull than the reproductively inefficient heifer.

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APPENDIXES

Appendix A System of Body Condition Scoring (BCS) for beef Cattle (Richards et al., (1986)

Group	BCS	Description
Thin Condition	1	EMACIATED - Cow is extremely emaciated with no palpable fat detectable over spinous process transverse process, hip bones or ribs. Tail head project quite prominently.
	2	POOR - Cow still appears somewhat emaciated but tail-head and ribs are less prominent. Individual spinous processes are still rather sharp to the touch but some tissue cover exists along the spine.
	3	THIN - Ribs are still individually identifiable but not quite as sharp to the touch. There is obvious palpable fat along the spine and over tail-head with some tissue cover over dorsal portion of ribs.
Borderline	4	BORDERLINE - Individual ribs are longer visually Condition obvious. The spinous process can be identified individually on palpation but feel rounded rather than sharp. Some fat cover over ribs, transverse processes and hip bones.
Optimum Moderate Condition	5	MODERATE - Cow has generally good overall appearance. Upon palpation fat cover over ribs feels spongy and areas on either side of tail-head now have palpable fat cover.
	6	HIGH MODERATE - Firm pressure now needs to be applied to feel spinous process. A high degree of fat is palpable over ribs and around tail-head.
	7	GOOD - Cow appears fleshy and obviously carries considerable fat. Very spongy fat cover over ribs and around tail-head. In fact "rounds" or "pones" beginning to be obvious. Some fat around vulva and in crotch.
Fat	8	FAT - Cow very fleshy and over-conditioned. Spinous Condition process almost impossible to palpate. Cow has large fat deposits over ribs, around tail-head and below vulva. "Rounds" or "pones" are obvious.
	9	EXTREMELY FAT - Cow obviously extremely wasty and patchy and looks blocky. Tail-head and hips buried in fatty tissue and "rounds" or "pones" of fat are protruding. Bone structure no longer visible and barely palpable. Animal's motility may even be impaired by large fatty deposits.

Appendix B Body Condition Scoring (BCS) System for Beef Cattle (Houghton et al., 1990)

Group	BCS[a]	Description
Thin	1	EXTREMELY THIN with severe wasted condition muscle development; may appear humped in the back with feet close together; usually weak; extremely prominent backbone, hooks, pins and ribs. Similar to condition scores 1 and 2 in the 9-point system.
	2	THIN with little or no wasting of muscle structure; vigorous, little or no fat in rump, rib or brisket; prominent backbone, hooks, pins and ribs but normal appearing muscle structure. Similar to condition scores 3 and 4 in the 9-point system.
Moderate	3	IDEAL CONDITION. Thrifty with normal condition muscle structure; some evidence of fat deposited in the forerib, brisket and crop but limited around the tailhead; some smoothness over the shoulder, ribs, backbone, hooks and pins. Similar to condition score 5 in the 9-point system.
Fat condition	4	FAT but still firm; vigorous; considerable fat deposited over forerib; brisket protruding; tailhead full (bulging); very smooth over backbone with no skeleton visible except at hooks. Similar to condition scores 6 and 7 in the 9-point system.
	5	VERY FAT with considerable softness; very fat over the forerib and shoulder; large; prominent brisket; broad, flat topline; large patch fat deposits around the tailhead; body curvature become square in appearance. Similar to condition scores 8 and 9 in the 9-point system.

[a]This system was expanded for more accuracy using a minus (-), average (0) and plus (+) for each BCS to represents light deviations within the description of each condition score. For analysis purpose, $3^{-}=2.67$, $3^{0}=3.00$, $3^{+}=3.33$, for example.

Appendix C Schedule of Experimental Events

Day	Event
1	Start of experiment, start feeding experimental rations, start recording amounts of feed fed.
2	Weigh, backfat measures, $PGF_{2\alpha}$ injection, blood samples, feed and pasture samples collection.
10	$PGF_{2\alpha}$ injection.
11	7 a.m - 0 h - blood sample & GnRH injection. 9 a.m - 2 h - blood & Synchromate-B administration, feed and pasture sample collection.
20	Remove Synchromate-B or progestin pellet.
22	Artificial insemination, blood, feed and pasture samples collection.
33	Blood, feed and pasture samples collection.
44	End of corn grain supplementation, weigh, fat measures, bleeding, feed and pasture samples collection.
52	Beginning of natural breeding.
112	End of the breeding season.

Notes :
Blood samples were analyzed for :

(a) Progesterone to check whether ovulation had occurred (first sample), and for pregnancy diagnosis (the last two blood samples).
(b) Analysis was also for LH and FSH as indicators of pituitary response to GnRH challenge.
(c) Concentrations of NEFA was determined in order to indicate the degree of lipolysis.

$PGF_{2\alpha}$ = Prostanglandin-F2-alpha, a luteolytic molecule.

Synchromate-B is an ear implant containing norgestomet, which is a potent progestin that acts by inhibiting GnRH.

Appendix D Schedule of Experimental Events-35 d postpartum

		SAMPLE						
		WeigH		HF	Feed			Other
Day	Time	HF[1]	Calf	Fat[2]	Pas[3]	Fec[4]	Blood	EVENTS
1	8:00	X	X	X	X	X	X	Inject $PGF_{2\alpha}$[5]
	9.30						X	Inject GnRH[6]
	11:00					X	X	Hp-Hgt[7] Cond.[8] Score Admin.[9] marker
10	8:00					X	X	Inject $PGF_{2\alpha}$
	10:00					X	X	
13	18:00					X		Inject E_2[10]
14	8:00					X	X	
	10:00						X	
	12:00						X	
24	8:00					X	X	Inject $PGF_{2\alpha}$
	9:30						X	Inject GnRH
	11:00						X	
27	18:00					X		Inject E_2
28	8:00					X	X	
	10:00						X	
	12:00	X	X	X		X	X	Cond. Score

28 Initiation of natural breeding (90 d).

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[1]heifer.
[2]backfat measure.
[3]pasture sample.
[4]estimate of fecal sample collection dates.
[5]lutalyse, 5 μg i.m., prostanglandin-F-2-alpha.
[6]gonadotropin-releasing hormone, 10 μg i.m.
[7]hip height.
[8]body condition score.
[9]administer Cr_2O_3 bolus.
[10]17ß-estradiol-3-benzoate, 1 mg i.m.

Appendix E Schedule of Experimental Events- middle to the end of the breeding season

		SAMPLE						
		Weigh		HF	Feed			Other
Day	Time	HF[1]	Calf	Fat[2]	Pas[3]	Fec[4]	Blood	EVENTS
88	7:30	X	X	X	X	X	X	Cond.[5] Score Admin.[6]
96	8:00					X		
102	8:00					X		
112	8:00					X		
116	8:00					X		
118	End of the breeding season							
146 (year two)	8:00	X	X	X			X	Pregnancy Determination.
178 (year one)	8:00	X	X	X			X	Pregnancy Determination.

[1]heifer.
[2]backfat measure.
[3]pasture sample.
[4]estimated fecal sample collection dates.
[5]body condition score.
[6]administer Cr_2O_3 bolus.

Appendix F Degree of response of reproductive hormones to exogenous gonadotropin-releasing hormone of first-calf Angus heifers varying in the interval from exposure to the bull to conception

Day[a]:	1				24			
Event[b]:	GnRH				GnRH			
Magnitude of response, fold[c]:	T0 to T1	T0 to T2	T0 to $\frac{T1+T2}{2}$	T1 to T2	T0 to T1	T0 to T2	T0 to $\frac{T1+T2}{2}$	T1 to T2
Heifer group[c]								
	---------- Luteinizing hormone ----------							
Short PPI-1	11.9	35.7	23.8	3.0	17.1	31.4	24.3	1.8
Long PPI-1	20.0	32.7	26.3	1.6	14.3	30.6	22.4	2.1
Not pregnant	24.3	27.2	25.7	1.1	23.0	35.6	29.3	1.6
	------ Follicle stimulating hormone ------							
Short PPI-1	1.56	4.59	3.07	2.95	2.44	4.16	3.30	1.70
Long PPI-1	2.38	4.43	3.41	1.86	2.30	4.57	3.44	1.99
Not pregnant	1.89	4.35	3.12	2.31	2.31	4.23	3.27	1.83
	---------- Progesterone ----------							
Short PPI-1	1.50	1.35	1.43	0.90	.93	0.89	.91	0.96
Long PPI-1	1.76	1.94	1.85	1.10	.86	1.00	.93	1.17
Not pregnant	1.30	1.23	1.27	0.95	.78	1.16	.97	1.48

Appendix F Continued

Day[a]:	1				24			
Event[b]:	GnRH				GnRH			
Magnitude of response, fold[c]:	T0 to T1	T0 to T2	T0 to $\frac{T1+T2}{2}$	T1 to T2	T0 to T1	T0 to T2	T0 to $\frac{T1+T2}{2}$	T1 to T2
Heifer group[c]								
	--------- Estrogen ---------							
Short PPI-1	1.13	1.80	1.47	1.60	1.06	1.31	1.19	1.31
Long PPI-1	1.10	2.87	1.99	2.60	0.99	1.20	1.09	1.21
Not pregnant	1.24	2.54	1.89	2.05	1.00	1.57	1.29	1.55
	------ Androstenedione ------							
Short PPI-1	1.24	1.48	1.36	1.20	1.11	1.27	1.19	1.14
Long PPI-1	1.26	1.12	1.19	0.88	1.04	1.13	1.08	1.08
Not pregnant	1.33	1.44	1.39	1.09	1.16	1.27	1.21	1.09

[a]Gonadotropin-releasing hormone, 10 μg.
[b]Day of the 28 d hypothalamic-pituitary-ovarian challenge starting at 35 d postpartum
[c]PPI-1 = Days from exposure to the bull to conception.
Short PPI-1 = 0 - 16 d.
Long PPI-1 = 18 - 83 d.
[d]Magnitude of response to E_2:
T = 0.
T = 1, 1.5 h post GnRH.
T = 2, 3.0 h post GnRH.

Appendix G Degree of response of LH and FSH following exogenous estradiol[a] in heifers varying in the interval from exposure to the bull to conception

Hormone	Luteinizing hormone						Follicle Stimulating hormone					
Day[b]	14			24			14			24		
Postpartum Interval-1[a]	Short PPI-1	Long PPI-1	Not preg	Short PPI-1	Long PPI-1	Not preg	Short PPI-1	Long PPI-1	Not preg	Short PPI-1	Long PPI-1	Not preg
Number of heifers	35	37	11	35	37	11	35	37	11	35	37	11
Magnitude of response, fold[d]												
T=0 to T=1	8.2	7.2	1.8	2.2	2.3	1.4	1.1	1.8	1.6	1.1	1.1	1.4
T=0 to T=2	11.4	23.5	.8	4.6	11.6	6.9	2.3	3.1	1.8	1.6	1.5	1.5
T=1 to T=2	1.4	3.3	.4	2.1	2.8	5.0	2.0	1.7	1.2	1.4	1.4	1.1
T=0 to ((T=1 + T=2)/2	9.8	15.4	1.3	3.4	8.5	4.2	1.7	2.4	1.7	1.3	1.3	1.4

[a] 17ß-estradiol-3-benzoate, E_2, 1 mg i.m.
[b] Day of the 28 d hypothalamic-pituitary-ovarian challenge starting at 35 d postpartum
[c] PPI-1 = Days from exposure to the bull to conception.
[d] Magnitude of response to E_2:
T = 0, 16 h post E_2.
T = 1, 18 h post E_2.
T = 2, 20 h post E_2.

Appendix H Degree of response of reproductive hormones to exogenous gonadotropin-releasing hormone of first-calf Angus heifers varying in the interval from birth of the first calf to birth of the second calf minus 281 d.

Day[a] / Event[b]	1 GnRH				24 GnRH			
Magnitude of response, fold[c]	T0 to T1	T0 to T2	T0 to $\frac{T1+T2}{2}$	T1 to T2	T0 to T1	T0 to T2	T0 to $\frac{T1+T2}{2}$	T1 to T2
Heifer group[c]								
			---------- Luteinizing hormone ----------					
Short PPI-2	13.43	25.29	19.36	1.88	12.15	25.03	18.59	2.06
Long PPI-2	18.98	42.93	30.96	2.26	20.45	39.21	29.83	1.92
Not pregnant	23.48	26.28	24.88	1.12	23.45	36.28	29.87	1.55
			------ Follicle stimulating hormone ------					
Short PPI-2	2.20	5.16	3.68	2.35	2.46	4.64	3.55	1.88
Long PPI-2	1.86	3.89	2.87	2.10	2.25	4.26	3.26	1.89
Not pregnant	1.89	4.35	3.12	2.31	2.31	4.23	3.27	1.83
			---------- Progesterone ----------					
Short PPI-2	1.35	1.19	1.27	-0.88	-0.96	1.10	1.03	1.14
Long PPI-2	1.89	2.05	1.97	1.09	-0.86	-0.85	-0.86	1.00
Not pregnant	1.30	1.23	1.27	-0.95	-0.78	1.16	-0.97	1.48

Appendix H Continued

Day[a] / Event[b]	1 GnRH				24 GnRH			
Magnitude of response, fold[c]	T0 to T1	T0 to T2	T0 to $\frac{T1+T2}{2}$	T1 to T2	T0 to T1	T0 to T2	T0 to $\frac{T1+T2}{2}$	T1 to T2
Heifer group[c]								
	--- Estrogen ---							
Short PPI-2	1.14	2.60	1.87	2.27	1.05	1.44	1.11	1.37
Long PPI-2	1.09	2.09	1.59	1.91	1.00	1.08	1.04	1.09
Not pregnant	1.24	2.54	1.89	2.05	1.01	1.57	1.29	1.55
	--- Androstenedione ---							
Short PPI-2	1.30	1.31	1.30	1.01	1.05	1.22	1.13	1.17
Long PPI-2	1.21	1.26	1.23	1.05	1.10	1.17	1.14	1.06
Not pregnant	1.33	1.44	1.39	1.09	1.16	1.27	1.21	1.09

[a]Gonadotropin-releasing hormone, 10 μg.
[b]Day of the 28 d hypothalamic-pituitary-ovarian challenge starting at 35 d postpartum
[c]PPI-1 = Days from birth of the first calf to birth of the second calf minus 281 d.
Short PPI-2 = 52 - 82 d.
Long PPI-2 = 83 - 125 d.
[d]Magnitude of response to E_2:
T = 0.
T = 1, 1.5 h post GnRH.
T = 2, 3.0 h post GnRH.

Appendix I Degree of response of serum gonadotropins following exogenous estradiol[a] in heifers varying in the interval from birth of the first calf to birth of the second calf minus 281 d gestation

Hormone	Luteinizing hormone						Follicle Stimulating hormone					
Day[b]	14			28			14			28		
Postpartum Interval-2[a]	Short	long	Not preg	Short	Long	Not preg	Short	Long	Not preg	Sort	Long	Not preg
Number of heifers	36	36	11	36	36	11	36	36	11	36	36	11
Magnitude of response, fold[d]												
T=0 to T=1	2.3	12.4	1.8	1.3	1.6	1.6	3.0	1.6	1.4	1.1	1.0	1.4
T=0 to T=2	16.7	15.7	.8	2.9	2.4	1.8	6.3	4.5	6.9	1.7	1.4	1.5
T=1 to T=2	7.3	1.3	.4	2.3	1.5	1.2	2.1	2.7	5.0	1.5	1.4	1.1
T=0 to ((T=1 + T=2)/2	9.5	14.1	1.3	2.1	2.0	1.7	4.7	3.1	4.2	1.4	1.2	1.5

[a] 17ß-estradiol-3-benzoate, E_2, 1 mg i.m.
[b] Day of the 28 d hypothalamic-pituitary-ovarian challenge starting at 35 d postpartum
[c] PPI-2 = Days from birth of the first calf to birth of the second calf minus 281 d of gestation.
[d] Magnitude of response to E^2 :
Short PPI-2 = 52 - 82 d.
Long PPI-2 = 82 - 125 d.
T = 0, 16 h post E_2.
T = 1, 18 h post E_2.
T = 2, 20 h post E_2.

VITA

Lipalesa Motjope was born in Durban, South Africa and raised in Lesotho. She attended Mokhotlong Lesotho Evangelical Church Lower Primary School, Hlotse Controlled Higher Primary School, Hlotse Secondary School, and graduated from Lesotho High School in 1973. The following year she entered the University of Botswana, Lesotho and Swaziland in Swaziland and received her Diploma in Animal Husbandry under the National University of Lesotho in 1976. In 1977 she entered the University of Manitoba in Winnipeg, Canada and received her Bachelors degree Animal Science in 1981. She attended Washington State University from 1984 to 1986 where she received her Masters degree in Animal Science.

In August of 1988, she started a Doctor of Philosophy program with emphasis in Animal Nutrition and a minor focus in Reproductive Physiology at the University of Tennessee, Knoxville.

Between her academic training programs she was employed by the Ministry of Agriculture, Livestock Division and Research Division in Lesotho, where she will be returning to resume her duties.

The author is a member of The American Society of Animal Science, South African Society of Animal Production and Lesotho Science and Technology Association.