INFLUENCE OF BODY ENERGY RESERVES, EARLY WEANING AND TREATMENT WITH GONADOTROPIN RELEASING HORMONE ON LUTEINIZING HORMONE AND OVARIAN ACTIVITY IN BEEF COWS

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CHAPTER I

INTRODUCTION

Good management is essential for success of a cow-calf. Proper management during times of lower prices for beef requires incorporation of the most efficient techniques to decrease production costs. In times of higher prices, good management results in the sale of more pounds of weaned calf and increased income. Since cattle prices fluctuate frequently, the production of as many pounds of calf as economically as possible becomes the overall goal.

A common concern to cattlemen is the estimate that only about 75% of the females exposed to fertile bulls wean a calf the subsequent year (Bellows et al., 1979). Summaries of the net calf crops from disease free beef herds over a major portion of the U.S. indicate that the failure of cows to become pregnant was the primary cause of reduced efficiency (Dzuik & Bellows, 1983). Although not all cows exposed to fertile bulls during estrus become pregnant (Short et al., 1990), failure of beef cows to initiate estrous cycles during the breeding season (anestrus) is the main reason for reduced pregnancy rates at the end of the breeding season (Bellows et al., 1979).

Research since 1927, reviewed by Short et al. (1990), identified the hypothalamic-pituitary-ovarian axis as the site controlling resumption of estrous cycles in postpartum beef cows. If nutrient intake is inadequate and body energy reserves are depleted, the interval from calving to first estrus is extended (Wiltbank et al, 1962; Bellows and Short, 1978; Dunn and Kaltenbach, 1980; Selk et al.,1989). Severe nutritional restriction results in cessation of ovarian activity in beef (Imakawa et al., 1986a; Richards et al., 1989b) and dairy (Johnson et al., 1987) females.

The objective of this research was to study the effects of nutrition and body energy reserves on reproduction in beef cows. More specifically, the objective of experiment one was to evaluate the influence of body condition score at early weaning, on the onset of luteal activity and on concentrations of LH and IGF-I in serum of postpartum anestrous beef cows. Experiment two was conducted to determine if pulsatile administration of GnRH, to nutritional anestrous beef cows, will stimulate LH secretion and initiate ovarian function.

CHAPTER II

REVIEW OF LITERATURE

Domestic farm animal females experience periods during which they are receptive to the male and will stand for mating. Estrus occurs at a regular interval except during periods of anestrus. Absence of estrous cycles occurs before puberty, during pregnancy, early post partum and as a result of stresses such as insufficient nutrient availability. Hypothalamic-pituitary function, and in certain cases ovarian function, determine the length of anestrous intervals.

Endocrine Control of Reproduction

Gonadotropin Releasing Hormone

Gonadotropin synthesis and release from the anterior pituitary is stimulated by pulsatile secretion of gonadotropin releasing hormone (GnRH) from the hypothalamus (Clarke and Cummins, 1982). GnRH is a decapeptide (Matsuo et al., 1971; Momany, 1976) with the same structure for all domestic species that have been studied (pyro-Glu-His-Trp-Ser-Tyr-Gly-Leu-Arg-Pro-Gly-NH2). Transection of the pituitary stalk abolishes the control of the pituitary by GnRH and results in decreased concentration of luteinizing hormone (LH) in serum of ovariectomized monkeys (Plant et al., 1978), rats (Kanematsu et al., 1979), calves (Anderson et al., 1981) and ovariectomized ewes (Clarke and Cummins, 1982). Active immunization against GnRH results in reduced secretion of gonadotropins and cessation of estrous cycles in rats (Fraser, 1975) gilts (Esbenshade and Britt, 1985), mares (Garza et al., 1986), ewes (Clarke et al., 1978) and heifers (Johnson et al., 1988; Wettemann and Castree, 1988; O'Connell, 1990).

Factors responsible for GnRH synthesis and release are not fully understood. GnRH is synthesized by neurons in the hypothalamus and is present in hypophyseal portal blood of rhesus monkeys (Carmel et al., 1976) and sheep (Clark and Cummins, 1982). Concentrations of GnRH in hypophyseal portal blood, as well as in venous blood of castrated ewes (Nett et al., 1974), vary in a rhythmical pattern. Patterns of GnRH release were not highly correlated with pulses of LH in serum because a pulse of GnRH did not necessarily stimulate the release of sufficient LH to be identified as a pulse. Clark and Cummins (1982) determined that the pulsatile secretion of LH is a direct result of pulsatile release of GnRH from the hypothalamus via the hypothalamic-hypophyseal portal vessels.

Continuous infusion of GnRH results in reduced synthesis and secretion of gonadotropins due to down regulation of GnRH receptors in monkeys (Knobil, 1980), and sheep (Nett et al., 1981). Clark and Cummins (1985) were unable to document the down regulation hypothesis in sheep, but determined that the frequency of GnRH pulses determined the amount of the releasable LH pool and the amplitude of LH pulses. Continuous administration of GnRH caused short-lived increases in LH in anestrous ewes (McLeod et al., 1983) and suckled cows (Lamming and McLeod, 1988) and failed to consistently induce ovulation in postpartum cows (Jagger et al., 1987). Twice daily injections of GnRH resulted in release of LH from the pituitary of prepuberal bulls (Mongkonpunya et al., 1975). The amplitude of the pulses of LH, stimulated by successive injections of GnRH, decreased with days of injection. The decrease in LH release that they observed could be due to down regulation of GnRH receptors in the anterior pituitary or to a decreased releasable pool of LH. Nett et al. (1981) quantified GnRH receptors in the pituitary of ovariectomized ewes and determined that decreased LH response to continuous infusion of GnRH was associated with decreased numbers of receptors and was not due to a decrease in the releasable pool of LH. Control of the number of GnRH receptors by GnRH itself, or by steroids, is evident by the variation in LH release during the estrous cycle (Nett, 1990).

The gene encoding for GnRH receptors has not been isolated (Nett, 1990). Specific binding of GnRH with its receptors on the plasma membrane (Wise et al., 1984) results in synthesis and secretion of LH and FSH (Naor and Childs, 1986). The frequency of GnRH stimulation was associated with the regulation of GnRH receptors in the pituitary (Katt et al., 1985) and the pattern of GnRH release appears to have specific functions. Rhythmic secretions of GnRH into portal blood consists of large amplitude pulses which elicit the release of LH (Clark and Cummins, 1982) and pulses of smaller amplitude which maintain gonadotropin synthesis, without release (Clarke and Cummins, 1987a). The smaller pulses may also modify the pituitary responsiveness to large pulses of GnRH (Clark and Cummins, 1985).

Frequency of GnRH release influences the synthesis of specific ß mRNAs for LH or follicle stimulating hormone (FSH; Hamernick et al.,1986; Dalkin et al.,1989). Without the continual pulsatile stimulation by GnRH, secretion of LH and FSH decrease rapidly (Clark et al., 1983). There are specific mRNA for the α subunit and for LH ß and FSH ß subunits (John Marshal, personal communication).

The number of GnRH receptors, as well as the amount of GnRH in circulation, is important in regulation of gonadotrophs (Wise et al., 1984). Since the number of GnRH receptors in the pituitary of ewes increase prior to the ovulatory surge of LH during normal cycles (Crowder and Nett, 1984), but do not change in ewes (Crowder et al, 1982) or beef cows (Moss et al., 1985) with time post partum, it appears that the amount of GnRH released to stimulate gonadotrophs may be limited during postpartum anestrus.

Gonadotropins

The pituitary gonadotropins controlling reproduction in the bovine are LH and FSH. These glycoproteins are composed of α and β subunits. Within a species, the α subunits are identical for LH, FSH and thyroid stimulating hormone (TSH). LH and FSH are synthesized and secreted by the same gonadotroph (Childs et al., 1987) and both appear to be controlled by the same releasing hormone, GnRH (Akbar et al, 1974; Dalkin et al., 1989).

Luteinizing Hormone.

Pituitary concentrations of LH in the bovine increase from birth to a maximum at 3 months of age, vary considerably from 3 to 7 months and then decline through puberty (Desjardins and Hafs, 1968). Concentrations of LH in serum of heifers increase from birth to 3 months, decline from 3 to 6 months and then gradually increase until puberty (Schams et al., 1981). These observations support the concept that large concentrations of pituitary hormones often reflect minimal concentrations in blood, and vice versa.

LH is luteotropic in the bovine (Hansel, 1966). This coincides with minimal concentrations of LH in the pituitary during the first 15 days of the estrous cycle, which Desjardins and Hafs (1968) associated with luteal growth. Lamming and McCleod (1988) associated the increased number of LH pulses, that accompany increased LH secretion, with important physiological events including follicular growth and estrogen secretion prior to ovulation. Pulsatile secretion of LH signals the onset of puberty in heifers (Kinder et al., 1987) and is necessary for normal cycles in cows (Rahe et al., 1980) or the reinitiation of estrous cycles following parturition (Riley et al., 1981; Walters et al., 1982a; Humphrey et al., 1983).

Pituitary content of LH, but not FSH, increases linearly from day 6 (estrus = 0) to day 18 of a 20 day cycle, is reduced by 75% during the ovulatory surge, and is replenished to concentrations comparable to cyclic concentrations within 24 h after the surge (Nett et al., 1987). Receptors for GnRH in the anterior pituitary decrease as a result of increased frequency of GnRH stimulation prior to the ovulatory surge of LH, and the number of receptors remain minimal for approximately two days before increasing by day 6 of the following estrous cycle. The number of cytosolic receptors for estradiol were maximal one day before the ovulatory surge and were the first change signalling ovulation.

Concentrations of LH in anestrous, suckled beef cows generally increase before the onset of luteal activity (Schams et al., 1972; Echternkamp and Hansel, 1973; Arije et al., 1974; Humphrey et al., 1976). Increased mean concentrations of LH in serum represent increased frequency and magnitude of LH pulses (Carruthers and Hafs, 1980; Peters et al, 1981; Garcia-Winder et al., 1984). Indeed, re-establishment of LH secretion is a prerequisite for occurrence of the first postpartum estrus or ovulation (Walters et al., 1982b; Humphrey et al., 1983). A pulse frequency of one pulse every 1 to 2 hours usually precedes estrus in cattle (Carruthers and Hafs, 1980; Carruthers et al., 1980; Walters et al., 1982ab; Schallenberger, 1982).

Reinitiation of LH release in cattle and the initiation of estrous cycles after parturition may depend on repletion of LH reserves in the pituitary (Moss et al., 1985; Nett, 1990). Pituitary weight in cattle is not influenced by nutrient intake (Beal et al., 1978; Moss et al., 1982) or body energy reserves (Rasby et al., 1990). Pituitary content of LH is minimal from parturition to day 15 post calving (Moss et al., 1985; Nett et al., 1988). By the third week postpartum, the pituitary has maximized its ability to synthesize and release gonadotropins (Moss et al., 1985; Leung et al., 1986).

Follicle Stimulating Hormone.

FSH appears to have a permissive role in the onset of estrous cycles following parturition. Saiddudin et al., (1968) demonstrated that FSH is responsible for follicular growth and development. FSH stimulates progesterone synthesis (Hansel and Convey, 1983) and the production of estradiol by granulosa cells of the follicle (Fortune and Quirk, 1988). Heifers injected with FSH had increased numbers of medium and large follicles (Wise et al., 1984). The appearance of large, preovulatory follicles occurs relatively early in postpartum beef cows, compared to the onset of luteal activity (Spicer et al., 1986a).

The concentration of FSH in the pituitaries of beef cows is maximal at parturition and is minimal during the early postpartum period (Saiduddin et al.,1968: Moss et al., 1985). Minimal concentrations of FSH occur for only a few days post partum and linear increases in FSH concentrations were reported between 7 and 42 days postpartum (Leung et al., 1986). Concentrations of FSH in serum are similar in cyclic and acyclic cows (Carruthers et al., 1980; Williams et al., 1983; Acosta et al., 1983; Leung et al.,1986) so concentrations of FSH are not temporally related to the length of the postpartum anestrous interval.

Concentrations of FSH in the pituitaries of cyclic cows are maximal on day 18 of a 21 day cycle and are decreased by 73% at estrus (Hackett and Hafs, 1969). Concentrations of FSH in serum vary from 50 to 75 ng/ml during the bovine estrus cycle (Akbar et al., 1974). In daily samples prior to estrus, they observed a pulse (1.2 times basal concentration) of FSH associated with a concurrent pulse of LH. A pulsatile pattern of release of FSH from the anterior pituitary has been demonstrated in sheep (Goodman and Karsch, 1980) and beef cows (Walter et al.,1982bc; Parfet et al., 1989). The pulsatile release of FSH from the anterior pituitary did not change with days post partum or in response to $PGF_{2\alpha}$ (Parfet et al.,1989) but may increase following early weaning (Walters et al., 1982b). Pulsatile secretions of FSH were not detectable at 18 days postpartum in weaned or suckled cows (Cross et al., 1987). Factors that control the reinitiation of estrous cycles may influence the release of FSH in postpartum beef cows, however, results from most studies indicate that secretion of FSH is not a factor limiting the initiation of postpartum estrous cycles.

Ovarian hormones

Reproductive endocrine changes in cows from parturition to the first postpartum ovulation have been described (Wettemann, 1980; Schallenberger et al., 1982; Convey et al., 1983; Humphrey et al., 1983). The synchronization of events leading to the onset of estrous cycles following parturition is associated with changes in the concentrations of estrogens and progesterone in the blood of beef cows. Concentrations of these hormones, or the relationship between the concentrations, may be associated with anestrus.

Estrogens.

Gonadotropins are necessary for steroid production in most species (Leung and Armstrong, 1980). A two-cell theory for the production of estrogens in the bovine preovulatory follicle has been proposed (Hansel and Fortune, 1978; Fortune and Quirk, 1988). Theca interna cells, under the stimulation of LH, synthesize androgens from cholesterol. The androgens are aromatized to estrogens in the granulosa cells. The conversion in the granulosa cells probably does not require stimulation by FSH and LH (Fortune and Quirk, 1988). The three major estrogens produced by bovine follicles are estradiol, estrone and estriol.

Normal growth and development of follicles in the bovine may be continuous and independent of the stage of the cycle (Choudray et al., 1968; Donaldson and Hansel, 1968; Dufour et al., 1972; Spicer and Echternkamp, 1986) or may occur in either two (Rajakoski, 1960) or three (Ireland and Roche, 1983a) distinct periods during the estrous cycle. Through the use of ultrasound technology, follicular growth in cattle has been evaluated (Pierson and Ginther, 1984, 1987; Quirk et al., 1986; Fortune et al., 1988; Knopf et al., 1989). Follicular growth occurs in either two or three waves during the estrous cycle. The number of dominant follicles that occur during the cycle are related to the length of the estrous cycle of the cow. Genetic variation and environmental factors have been implicated as sources of variation in the number of waves of follicles that occurs within an individual heifer (Knopf et al., 1985).

Although variation in the growth rate of follicles may occur during the estrous cycle of cows, the largest follicle present on the ovary on day 18 has the greatest probability of ovulating (Dufour et al., 1972; Matton et al.,1981). Selection of the follicle destined to ovulate is manifested as selective growth of the preovulatory follicle and concurrent decreases in the diameter of the other follicles (Staigmiller and England, 1982). The time required for the normal growth of medium-sized (5 mm) follicles to ovulatory-sized (>10 mm) follicles is approximately 96 h (Staigmiller and England, 1982; Spicer and Echternkamp, 1986). Concentrations of estrogens in plasma are associated with the growth of the dominant follicle.

Variations in the length of normal estrous cycles (18-23 d) for beef cattle make the correlation between concentrations of estrogens and days of the cycle difficult. During the luteal phase, concentrations of estradiol-17ß in plasma of cattle are minimal (≈ 5 pg/ml) and a two to three fold increase occurs at the time of estrus (Wettemann et al., 1972; Echternkamp and Hansel, 1973; Dobson and Dean, 1974). Concentrations of estradiol must increase in blood of ovariectomized cattle to induce estrus (Allrich et al., 1984; Cook et al., 1986).

Concentrations of estrogens in the plasma of beef cows are maximal at parturition (Arije et al., 1974) because the placenta is a major source of estrogen production during late gestation (Gorski and Erb, 1959). Concentrations of estradiol decrease at parturition (Echternkamp and Hansel, 1973; Humphrey et al.,1983) to minimal concentrations that are maintained until the onset of follicular growth, which may occur as soon as 7 to 10 d post partum (Saiduddin et al., 1968). Estrone concentrations are ≈7 pg/ml of plasma after parturition and obtain maximal concentrations between 7 and 15 days post partum in association with follicular development (Humphrey et al.,1983).

Receptor specificity limits the effects of a hormone to a cell which contains the ability to bind that hormone. Estradiol receptors are present in cells of the anterior and medial basal hypothalamus of calves (Armstrong et al., 1977) and the anterior pituitary (Day et al., 1987) of prepuberal heifers. Likewise, receptors for estradiol are present in the anterior pituitary of cyclic (Nett et al.,1987) and postpartum (Nett et al.,1988) beef cows. The onset of ovarian activity at puberty was postulated (Day et al.,1987) to be associated with decreased numbers of estradiol receptors which decreased negative feedback of estradiol on LH secretion and would allow an increased LH secretion.

The number of estradiol receptors on the gonadotrophs may be related to stage of the estrous cycle. Nett et al. (1987) hypothesized that the increase in estradiol receptors, prior to the ovulatory surge of LH, was associated with increased responsiveness to GnRH. Increased estradiol receptors in the anterior pituitary within 15 days after parturition were associated with increased synthesis of LH (Nett et al., 1988). The location of the receptor, either the hypothalamus or pituitary, and the circulating concentrations of estradiol may determine the response to changes in receptor numbers.

Low concentrations of estradiol exert a negative feedback control on LH secretion. Ovarian inhibition of pulsatile LH release from the anterior pituitary is established by 6 wk of age in prepuberal heifers (Day et al., 1984; Anderson et al., 1985). Between 6 and 10 wk of age, the concentration of estradiol receptors in the anterior and posterior hypothalamus decreases in bull calves (Amann et al., 1986). Decreased estradiol receptors were associated with decreased concentrations of estradiol in plasma while the number of estrogen and GnRH receptors and the concentration of LH in the pituitary increased.

Pulsatile LH secretion was associated with the escape from the negative feedback of estradiol.

During the follicular phase of the estrous cycle, increased estradiol concentrations (Wettemann et al., 1972) may act as a positive stimulus on the hypothalamic-pituitary axis. Increasing the amount of estradiol in implants administered to ovariectomized cows stimulated an increase in the amplitude of LH pulses (Kinder et al., 1983; Stumpf et al., 1989). Linear increases in concentrations of LH were reported by Imakawa et al. (1986a) during the follicular phase of the estrous cycle. Estrogens increase the responsiveness of the adenohypophysis to GnRH (Kesner, et al.,1981; Nett, 1990). Increased amplitude of the LH pulses without increased frequency of GnRH release would indicate increased response to stimulation by GnRH.

Progesterone.

Adequate concentrations of progesterone are necessary to maintain pregnancy in beef cows. The major source of progesterone during pregnancy is the corpus luteum (Gorski and Erb, 1959). Concentrations of progesterone are maximal (≈ 10 ng/ml) within 30 d prepartum (Arije et al., 1974; Rasby et al., 1990) and decrease to near 1 ng/ml at parturition (Echternkamp and Hansel, 1973; Arije et al., 1974; Humphrey et al., 1976). Concentrations of progesterone are minimal early in the postpartum period and remain less than 1 ng/ml until the onset of events leading to normal estrous cycles (Donaldson et al., 1970; Echternkamp and Hansel, 1973; Arije et al., 1974; Corah et al., 1974; Humphrey et al 1976).

During the normal estrous cycle, concentrations of progesterone in plasma are correlated (r=.76) with weight of the corpus luteum (CL; Spicer et al., 1981). Concentrations of progesterone occur in a cyclic pattern and are minimal (< 1 ng/ml) at estrus, maximal during the mid-luteal phase, and decrease during the last 1-2 d prior to the subsequent estrus (Stabenfeldt et al., 1969; Wettemann et al., 1972; Echternkamp and Hansel, 1973; Humphey et al., 1976). Concentrations of progesterone greater than 1 ng/ml of plasma for at least 15 d indicate the presence of a normal CL (Stabenfeldt et al., 1969; Wettemann et al., 1972).

Concentrations of progesterone typical of a normal estrous cycle, may not occur following periods of ovarian inactivity. Transient increases in the concentration of progesterone in the blood of heifers have been reported prior to the first ovulation associated with puberty (Gonzalez-Padillo et al., 1975; Berradinelli et al., 1979; Schams et al., 1981). Short-term (2-5d) increases in the concentration of progesterone in blood of postpartum cows may (Donaldson et al., 1970; Corah et al., 1974; Humphrey et al., 1976; Rawlings et al., 1980; Williams and Ray, 1980; Spicer et al.,1986a) or may not (Echternkamp and Hansel, 1973; Arije et al., 1974) occur prior to the onset of normal ovarian activity. Subnormal luteal development, as estimated by progesterone concentrations, may occur in beef cows that have calves removed early in the postpartum period (Odde et al., 1980; Walters et al., 1982ab; Ramirez-Godinez et al.,1982; Smith et al., 1983). The length of the first estrous cycle after re-alimentation of diets fed to energy restricted cows was normal (Richards et al., 1989a). The presence of short cycles following nutritional restriction has not been documented.

Sources other than the CL may be associated with small increases in progesterone concentrations. The bovine adrenal gland produces progesterone (Wagner et al.,1979). The source of progesterone in heifers prior to ovulation was found to be nonpalpable luteal tissue within the ovary (Berradinelli et al., 1979). Treatment of postpartum anestrous cows with GnRH results in increased concentration of progesterone in plasma for 3 to 6 days (Wettemann et al., 1982). Luteinized-atretic follicles were recovered from cows that were injected with GnRH between 20 and 30 d postpartum (Spicer et al., 1987). Luteinization was thought to have resulted from increased LH and FSH pulses that resulted from GnRH stimulation (Spicer et al.,1986b).

The ovulatory surge of gonadotropins increased the number of estrogen-inactive (concentration of progesterone > estrogen) follicles in heifers when ovaries were removed between the ovulatory surge and ovulation (Ireland and Roche, 1983b). The concentrations of progesterone or estrogen in follicular fluid were not different between early weaned and suckled beef cows prior to initiation of cycles (Walters et al., 1982a). The follicle is avascular in cows. The ability of follicular fluid concentrations of progesterone to increase plasma concentrations during periods not associated with CL function have not been documented.

The occurrence of an increase in concentrations of progesterone in the plasma of beef cattle for 2 to 5 d before estrus and normal ovulation is thought to be necessary to synchronize endocrine function prior to the first ovulation at puberty or post partum (Ramirez-Godinez, 1982; Williams et al., 1983; Smith et al., 1987). The inhibition of gonadotropins by progesterone is documented in sheep (Goodman and Karsh, 1980). Exogenous progesterone administered to ovariectomized ewes decreased the frequency of GnRH pulses released from the hypothalamus. Similarly, the occurrence of GnRH pulses in hypophyseal portal blood were less frequent during the luteal phase in ewes compared to the number during the follicular phase of the cycle (Clarke et al., 1987). Since progesterone will synchronize ovulation in beef cattle, it probably alters the secretion of GnRH, however, this has not been documented.

The frequency of LH pulses in heifers increases as progesterone concentrations decrease at luteolysis (Ireland

and Roche, 1982; Imakawa et al., 1986b). Alternatively, concentrations of LH increase prior to ovulation and during the early luteal phase of the bovine estrous cycle (Convey et al., 1977). Synchro-Mate B (6 mg Norgestomet implant and 6 mg estradiol + 3mg Norgestomet injection) decreased the basal concentrations of LH in anestrous beef cows (Walters et al., 1982d) while removal of the progestrogen implant increased concentrations of LH released in response to GnRH compared to nonimplanted cows (Smith et al., 1983). Decreased LH release during gestation (Little et al., 1982) and during the mid-luteal phase of the estrous cycle (Rahe et al.,1980; Clarke, 1989) suggest inhibitory control of progesterone on LH secretion. Maximal concentrations of progesterone may allow for increased synthesis and storage of LH in the pituitary by decreasing the frequency of GnRH release in beef cows.

Relationship Among Metabolic and Endocrine Control of Reproduction

Anestrus in beef cattle has been reviewed extensively (Wiltbank, 1970; Dunn and Kaltenbach,1980; Wettemann, 1980; Lamming et al., 1981; Dziuk and Bellows,1983; Peters, 1984; Short and Adams, 1988; Short et al., 1990; Williams, 1990). Factors including the availability of nutrients to the cow and the effects of suckling have been suggested as the principal reasons for prolonged postpartum anestrus.

Nutrient Availability

Dietary restriction in humans (Frisch and Revelle, 1970; Frisch and McAuthur, 1974; Vigerski et al., 1977; Frisch, 1982; Carlburg et al., 1983) and non-human primates (Lee, 1987) delays the onset of menstrual cycles and is associated with prolonged amenorrhea due to mobilization of fat to provide energy to the body. Energy restriction in laboratory animals (Schneider and Wade, 1989) and pigs (Flowers et al., 1989) is associated with an absence of reproductive cycles. Horses with additional body fat responded more readily to attempts to shorten the transitional period from winter anestrus to normal reproductive cycles (Kubiak et al., 1987) and had increased fertilization rates (Henneke et al., 1983) than horses with lesser amounts of body fat. Puberty occurred earlier in beef heifers that had access to adequate nutrient intake diets compared to those fed restricted diets (Arije and Wiltbank, 1971; Day et al., 1986). Initiation and maintenance of reproductive cycles appears to be related to adequacy of nutrition in many species.

Restriction of nutrient intake compromises hypothalamic-pituitary function in cattle (Echternkamp et al., 1982; McCann and Hansel, 1986; Imakawa et al., 1986c; Killen et al., 1989; Richards et al., 1989a). However, the effect of nutrient restriction may depend on the body condition or energy reserves of the animal prior to the restriction period (Richards et al., 1986; Wettemann, et al., 1986; Selk et al., 1988). Nutrient availability should be considered as a summation of body reserves available for mobilization and those nutrients available in feed.

Body Energy Reserves.

Nutrients not used by mammals for maintenance or growth of tissues are stored in the body in the form of lipids, glycogen or labile proteins (Bauman and Currie, 1980). The major source of energy from body stores are lipids mobilized from fat stores (Bauman and Currie, 1980). Deposition of fat is a major energy requirement for the animal (Trenkle and Marple, 1983). Bos indicus and Bos taurus cows subjected to various nutritional regimes, varied greatly in the distribution and amount of fat (Holloway et al., 1990). The deposition of fat is related to the quality and quantity of nutrients in feed and the metabolic requirements of the animal.

To evaluate the relationships between various live animal estimates and actual carcass composition, mature Hereford cows were slaughtered (Wagner et al. 1988). Body condition scores (BCS) were estimated for mature Hereford cows both visually and by palpation, by two observers. Live weight (LW), weight to height ratio (WTHT) and BCS (1= severely emaciated; 9= obese) were related to carcass composition. BCS were more closely related to the energy available in the carcass and the percentage of fat in the carcass than any of the other estimates. The greatest correlation ($r=.92$) was between total carcass energy and BCS. The equation developed to estimate the energy available from the total carcass [TMCaL = -487.2 + 78.38 (BCS) + 1.3 (LW)] explained 90% of the variation in carcass energy among cows.

Dunn et al. (1983) using a similar 1-9 scale for BCS, found that the correlation between BCS and available energy as a percentage of live weight was .93 and the correlation with the calculated energy in the hot carcass was .95. Large correlations between BCS (0-5 scale) and total energy were also found in dairy (.93) and beef (.95) cows (Wright and Russel, 1984).

Wright et al. (1986) found that a portion (3200 MJ) of the prepartum energy required for maintenance could be obtained from the mobilization of 1 unit of BCS (0-5 scale). A gain of 1 unit of BCS during this period required 6600 MJ of metabolizable energy in feed. The maintenance requirements for nonpregnant Hereford cows in BCS of 3, 5 or 7 (1-9 scale) were 11.7, 13.6 and 14.9 Mcal ME/d, respectively (Wagner et al., 1988). Maintaining cows with excessive fat stores would be costly in terms of energy required and would only be feasible if the source of energy was available at low cost.

Nutrients Available in the Diet.

A basal amount of energy reserves is necessary for the initiation of estrus following parturition in cattle (Short and Adams, 1988). The interval between parturition and the first estrus of spring-calving Hereford cows with BCS between 3 and 7 ranged between 35 and 109 d (Wettemann et al., 1982). Restriction of prepartum energy that resulted in a 20% (1 BCS unit on a 1-9 scale) loss of body energy stores was associated with an additional 15 d delay in the onset of luteal activity after parturition. A one unit increase in BCS (0-6 scale) reduced the interval to estrus by 43 days in Hereford x Friesian and Blue-Gray cattle (Wright et al., 1987).

Dietary Energy. The postpartum interval to estrus is extended in beef cows by decreased energy intake in late pregnancy (Wiltbank et al., 1962, 1964; Hight, 1966; Corah et al., 1975; Bellows and Short, 1978; Dunn and Kaltenbach, 1980; Wettemann et al., 1982; Richards et al., 1986; Selk et al., 1988). BCS at parturition influences the effects of postpartum nutrition on reproductive traits (Wiltbank et al., 1962; Richards et al., 1986; Wettemann et al., 1987). Warren et al. (1988) found that the cows that calve with a BCS ≥ 5 have equivalent reproductive performance on high or low energy diets during the early postpartum period. Whereas, Wettemann et al. (1987) found that supplementation with additional protein and energy increased pregnancy rates when cows calved with a BCS of 5. Fall calving cows need additional energy in diets along with adequate BCS to have optional rebreeding efficiency (Rakestraw et al., 1986). Good BCS at calving will not insure adequate pregnancy rates for fall calving beef cows. BCS at calving and changes in body weight and condition during the postpartum period influence pregnancy rates in beef cows.

Supplemental Protein. Homeorrhesis, the ability to maintain nutrient flow and to support a physiologic need, allows the mobilization of fat and protein in the body to maintain lactation in dairy cows when nutrients are not available from feed (Bauman and Currie, 1980). The pool of amino acids, available from protein in feed or body stores, can be utilized as precursors for gluconeogenesis or may enter the tricarboxylic acid (TCA) cycle as a fuel source (Black et al., 1990). Mobilization of fat free lean tissue results in about 1.2 Mcal of energy per kg of tissue (Trenkle and Marple, 1983).

When beef cows have BCS between 3 and 7, the prediction of carcass protein by a change in BCS accounted for only 29% of the variation (Wagner et al., 1988). Within this range BCS is a better estimate of the storage of energy as fat than changes in protein stores. Martin and Ehle (1984) estimated the protein content in dairy cows with deuterium dilutions. Protein concentrations decreased following parturition and were associated with stage of lactation and age of the cow. Mobilization of protein stores appears to indicate severe losses of body condition and may indicate severe nutrient deprivation.

Separation of the effects of protein supplementation from those of energy in cows are difficult because protein supplements increase intake and digestibility of low quality forages (Kartchner, 1980). Additional protein may decrease (Blauwiekel et al., 1986) or increase (Blauwiekel and Kincaid, 1986) intake of isocaloric diets depending on the solubility of the source of the protein. Restricting protein in the diet of beef cows has been associated with extended postpartum intervals, decreased pregnancy rates after the first estrus, and fewer pregnancies at the end of a limited breeding season (Sasser et al., 1988).

Exceeding the recommendations for protein in diets fed to dairy cows increased the concentrations of insulin in serum, rumen ammonia concentrations and blood urea nitrogen, but had no affect on body weight or milk production of cows (Blauwiekel and Kincaid, 1986). Increasing the protein content (15 to 25%) in diets fed to cycling dairy cows, increased the basal concentration of LH but had no effect on the frequency of LH pulses, the content of LH or the number of LHRH receptors in the pituitary, or the concentrations of progesterone during the cycle (Blauwiekel et al., 1986). Restricting the protein concentration in diets fed to beef cows on limited amount of isocaloric diets decreased the frequency of LH pulses and increased the concentration of LH and FSH in the pituitary compared to control cows (Nolan et al., 1984, 1988). The decreased release of LH was probably due to restriction at the hypothalamic level, because the number of GnRH receptors in the pituitary was not influenced and protein restricted cows released greater concentrations of LH in response to exogenous GnRH compared to controls. Reports of decreased reproductive performance due to protein restriction are similar to those reported as a result of energy restriction (Beal et al., 1978; Dunn and Kaltenbach, 1980; Whisnant et al., 1985; Rasby et al., 1991).

Blood Constituents That Affect Reproduction

Body energy reserves, as reflected by BCS (Richards et al., 1986; Selk et al., 1988), are related to the resumption of luteal function following parturition. Cows that experience anestrous due to severe nutrient restriction (Imakawa et al., 1986b; Louw et al., 1988; Richards et al., 1989a) reinitiate estrous cycles at a weight and BCS greater than those at the initiation of anestrous. Loss of body weight in cattle is associated with increased concentration of non-esterified fatty acids (NEFA) and decreased concentrations of glucose, insulin (Trenkle, 1978; McCann and Reimers, 1985; Richards et al., 1989b) and insulin-like growth factor-I (IGF-I; Richards et al., 1989c; Spicer et al., 1990). The establishment of stable concentrations of these or other metabolic factors which are characteristic of homeostasis (Bauman and Currie, 1980) may signal the onset of gonadotropin secretion and the initiation of postpartum luteal activity.

Glucose.

Concentrations of glucose in plasma may influence reproductive performance in cattle. Glucose is the primary source of energy for brain cells in monogastric animals (Lund-Anderson, 1979; Li and Anderson, 1987) and the central nervous system of ruminants (Bergman, 1973; Brockman and Laarveld, 1986). The principal source of glucose in ruminants is gluconeogenesis in the liver; a process which proceeds both in fasted and fed states (Bergman, 1973; Young, 1976). However, concentrations of glucose in plasma decrease with feed restriction (Oxenreider and Wagner, 1971; McCann and Hansel, 1986; Richards et al., 1989b) and lactation (McClure, 1968; Oxenreider and Wagner, 1971; Bauman and Currie, 1980; Selk et al., 1988).

Concentrations of glucose in plasma are regulated by glucagon, catecholamines and cortisol, which enhance gluconeogenesis and insulin which stimulates uptake of glucose by most cells. Concentrations of glucose in plasma have been increased by intravenous infusion of glucose into postpartum cows (Garmendia, 1986; McCaughey et al., 1988) or by the infusion of propionate into the abomasum of prepubertal heifers (Rutter et al., 1983). Increasing the amount of glucose available to tissues in 30 d postpartum cows (Garmendia, 1986) and Brangus heifers (Rutter et al., 1983) increased secretion of LH in response to exogenous GnRH. When cattle were in good condition (BCS=6.4), the addition of glucose via continuous or short-term infusions (McCaughey et al., 1988) did not influence the amount of LH released in response to GnRH. Mobilization of body energy results in elevated plasma free fatty acids and stable or reduced concentrations of glucose in plasma (Bauman and Currie, 1980; Rutter and Manns, 1987). When cows calved in thin body condition, cows that became pregnant had greater concentration of glucose in plasma compared with cows that did not become pregnant (Selk et al., 1988). The amount of metabolic demand on the animal during growth or lactation may influence glucose concentrations and the benefit from increased glucose availability.

Insulin.

Cows with good BCS do not release similar amounts of insulin as thinner cows in response to exogenous glucose (Richards et al.,1989b). Continuous infusion of glucose resulted in a significant and sustained increase in concentrations of insulin in the serum of the cows studied by Garmendia (1986) but not in the cows studied by McCaughey et al. (1988).

Addition of insulin to culture media increased the basal and GnRH stimulated release of LH and FSH from rat pituitary cells (Adashi et al., 1981). Treatment with insulin increased ovulation rates in energy restricted heifers (Harrison and Randel, 1986). Concentrations of glucose and insulin in the blood of dairy heifers decreased during fasting, and fasted dairy heifers had decreased concentrations of LH in serum compared to control heifers (McCann and Hansel, 1986). Concentrations of LH and insulin increased with refeeding. Nutritional restrictions which result in anestrous in beef cows are associated with reduced concentrations of insulin and glucose in blood and nutrient restrictions decrease the ability of insulin to regulate glucose concentrations after infusion of glucose into anestrous cows (Richards et al., 1989b). Insulin concentrations or the ability of insulin to regulate blood glucose may be associated with adequate energy availability and the resumption of cycles after pregnancy or nutritional restriction.

Volatile Fatty Acids.

Volatile fatty acids (VFAs) provide 50-85% of the metabolizable energy in ruminants maintained on forage diets (Owens and Goetsch, 1988). The primary VFAs produced are acetate, propionate and butyrate. Typical molar concentrations in the rumen of nonlactating beef cows on forage are 78, 13 and 8 %, respectively (Scott, 1988). Gluconeogenesis, synthesis of glucose from non-hexose carbons, is the principal source of glucose in ruminants (Bergman, 1973; Young, 1976). Therefore, treatments which change the concentrations of VFAs in the rumen or molar percentage of particular VFAs may control insulin or glucose concentrations in blood. Infusion of butyrate or propionate into hepatic portal blood of sheep stimulates insulin release without increasing glucose concentrations (Manns et al., 1967; Manns and Boda, 1967). Pancreatic secretions of insulin by ruminants may be regulated by the liver because the liver regulates concentrations of VFAs in pancreatic portal blood (Manns et al., 1967).

Propionate infusion into the abomasum of prepubertal heifers (Rutter et al., 1983) increased concentrations of glucose in blood and was associated with increased release of LH in response to GnRH injection. Similarly, prepubertal heifers fed monensin, an ionophore which increases propionic acid production in the rumen, had greater release of LH in response to exogenous GnRH (Randel and Rhodes, 1980) or estrogen (Randel et al., 1982) compared to heifers on the same diets without monensin. Whether the concentrations of VFAs have a direct effect on LH secretion or the effect is mediated by insulin and glucose is unknown.

Nonesterified Fatty Acids.

Loss of body weight in ruminants is associated with increased concentrations of nonesterified fatty acids in plasma (Trenkle, 1978; McCann and Hansel, 1986; Richards et al., 1989b; Rasby et al., 1990). Nonesterified fatty acids are increased by mobilization of fat stores and circulate in the blood bound to plasma albumin and are energy sources for tissues including the heart, skeletal muscle, liver and mammary tissue. The sympathetic nervous system and the concentration of beta adrenergic receptors on cow adipocytes may regulate the mobilization of body fat stores (McNamera and Hillers, 1986a). Mechanisms unique to lactation influence adipose tissue metabolism in the early postpartum period (Bauman and Currie, 1980b; Mills et al., 1989).

Lipids.

Dietary fatty acids and de novo fatty acid synthesis are the sources of stored triglycerides in ruminants. Lipogenic activity in beef cows is minimal early post partum and increases rapidly following weaning (Mills et al., 1989). Reduced dietary intake and increased milk production decrease lipogenesis and esterification in adipose tissue of dairy cows (McNamara and Hillers, 1986b) but do not regulate basal lipolysis (McNamara and Hillers, 1986a). Increasing serum lipids by feeding encapsulated fat does not stimulate ovarian activity in nutritionally restricted heifers but does increase the sensitivity of the pituitary to exogenous GnRH (Johnson et al., 1987). Increased concentrations of lipids in tissue or conversely, decreased free fatty acids in blood, may signal homeostasis in the animal (Bauman and Currie, 1980).

Insulin-like Growth Factors.

Metabolic status of postpartum, lactating cows (Rutter et al., 1989, Spicer et al., 1990), nonlactating cows (Richards et al., 1989c), steers (Breier et al., 1986) and heifers (Houseknecht et al., 1988) is associated with concentrations of insulin-like growth factor-I (IGF-I) in serum. The principal source of IGF-I in blood is the liver and secretion is stimulated by growth hormone (Gluckman et al., 1987). Associations between IGF-I and growth hormone have been reviewed (Clemmons et al., 1988; Davis, 1988). IGF-I concentrations vary with dietary energy intake (Breier et al., 1986, Clemmons et al., 1988; Houseknecht et a., 1988; Elsasser et al., 1989; Richards et al., 1989) and protein content of the diet (Anderson et al., 1988). Energy balance of dairy cows (Spicer et al., 1990) and physiologic state in beef cows (Rutter et al., 1989) are associated with concentrations of IGF-I in serum. IGF-I mediates the anabolic actions of growth hormone in skeletal tissues (Daughaday et al., 1972) and IGF-I in follicular fluid is associated with progesterone production (Spicer et al., 1988).

Concentrations of growth factors, metabolic hormones or metabolites in blood may have direct or indirect actions on the secretion of gonadotropins and the initiation of estrous cycles. In general, the components in blood that signal increased energy availability to the animal are associated with increased reproductive performance.

Factors That Directly Influence Gonadotropin Secretion

Suckling Inhibition

Attempts to shorten the postpartum anestrus interval in beef cattle have included varying the number of calves nursing, temporary calf separation and early weaning of calves (Lamming, 1978; Edgerton, 1980; Williams 1990). The normal suckling pattern for beef calves includes from 5 to 10 events per day for a total of 45 to 90 min/d depending on whether cows are on range pasture (Wettemann et al., 1978; Odde et al., 1985) or confined to smaller areas (Spicer et al., 1986a). The length of the postpartum anestrous period varies with suckling intensity (Wettemann et al., 1978) and frequency (Randel, 1981; Reeves and Gaskin, 1981; Bluntzer et al., 1989).

Early Weaning.

Postpartum anestrus in suckled beef cows is associated with an inhibitory effect of suckling on hypothalamic-pituitary function (Edgerton, 1980; Wettemann 1980; Spicer and Echternkamp 1986; Short et al., 1990). Suckling decreases the release of GnRH from the hypothalamus, specifically the median eminence (Zalesky et al., 1990) and weaning increases the concentrations of GnRH in the preoptic area and total hypothalamus but not the stalk median eminence (Malven et al., 1986). Weaning of calves at 30 to 40 d postpartum may influence synthesis, storage, or release of GnRH.

Mean concentrations of LH and FSH, pulse frequencies of LH and FSH and the synchrony of LH and FSH pulses are reduced in suckled compared to nonsuckled cows (Williams et al., 1983). Suckling decreases LH release in anestrus beef cows (Saiduddin et al., 1968: Short et al., 1972; Randel et al., 1976; Lamming, 1978; Carruthers et al., 1980; Walters et al., 1982ab; Garcia-Winder et al., 1984, 1986; Edwards, 1985; Whisnant et al., 1986abc; Williams, 1990). Suppression of LH concentrations in serum of cows by suckling is the result of a reduction in frequency and amplitude of LH pulses (Carruthers and Hafs, 1980;

Carruthers et al., 1980; Walters et al., 1982a; Garcia-Winder et al., 1984). Suppression of the frequency of LH pulses by suckling is sufficient to delay the first postpartum estrus (Williams et al., 1987).

Weaning calves at 48 days of age shortened the postpartum interval without changing LH release (Acosta et al., 1983). Weaning calves from cows at 23 to 30 d post partum resulted in estrus between 6 and 10 d after weaning (Copelin et al., 1987). The interval from parturition to first estrus was shortened by weaning of calves and mastectomy at parturition (Short et al., 1972) but this procedure did not shorten the interval to conception.

Calf removal at 35 d post partum did not influence concentrations of FSH or LH in the pituitary, the number of GnRH receptors in the pituitary, or in vitro release of LH or FSH in response to GnRH (Parfet et al., 1986). Maximal response of LH to calf separation indicated by increased frequency of LH pulses occurred within 2 days (Carter et al., 1980; Walters et al.,1982d; Edwards, 1985; Williams et al., 1987; Shively and Williams, 1989). If calves were returned to cows after 48 (Walters et al., 1982d; Edwards, 1985) or 72 h (Shively and Williams, 1989) of separation the frequency of LH release was decreased. Periods of separation greater than 72 h are associated with increased ovulation rates (Shively and Williams, 1989).

Basal LH secretion increases (Kesler et al., 1977; Leung et al., 1986) and the suckling inhibition decreases

(Garcia-Winder et al., 1984) with time post partum. The length of time that calves are separated from cows as well as the interval between parturition and calf separation may influence results of weaning practices.

Suckling increases the postpartum anestrous interval independent of nutrient intake (Short et al.,1972). Early weaning of calves from heifers in thin condition results in an increased percentage of heifers with luteal activity, increased conception rates and decreased interval from calving to conception compared to suckled heifers (Lusby et al., 1981). Cows that calve in good condition do not benefit from calf removal (Warren et al., 1988). Inadequate (80% NRC) energy in the diet of postpartum cows delays the LH response to calf removal (Whisnant et al., 1985). A portion of the inhibition of LH release associated with suckling in beef cows may be due to decreased nutrient availability of the cow (Randel, 1990). Dietary energy and or body energy reserves may influence the response to early weaning of beef cows.

Opioids.

Neural stimulation unique to the calf is associated with suckling inhibition (Williams et al., 1983, 1987). Suckling inhibits the neural elements responsible for the synthesis and release of GnRH (Malven et al., 1986) and the release of LH (Malven, 1986). Weaning of calves increases

LH concentrations in serum and the frequency of LH pulses (Dunlap et al., 1981; Edwards 1985; Whisnant et al., 1985). Infusion of morphine (55 mg/ml of serum for 7 hr) decreases the frequency of LH release in weaned cows (Peck et al., 1988). Similarly, morphine infusions decrease the post-castrations increase in LH release in male and female sheep (Shanbacher et al., 1985; Shillo et al., 1985). The modulation of LH due to suckling may be associated with endogenous opioids.

Three families of opioids are known: enkephalins, dynorphins and endorphins. Proopiomelanocortin fibers have been identified in the preoptic area of the bovine hypothalamus using immunocytochemical procedures (Leshin et al., 1988). Concentrations of met-enkephaphalins and ß-endorphine have been quantified in the preoptic area, hypothalamus, stalk-median eminence and the neurointermediate lobe of the pituitary (Malven et al., 1986). Opioids decrease the response of neurons to stimulation (Malven et al., 1986). Concentrations of opioids near GnRH secretory neurons suggest that opioids mediate GnRH release.

Further evidence for opioid suppression of GnRH secretion involves the use of naloxone, an opioid antagonist. Naloxone administration increases LH secretion within 15 min of injection of postpartum, suckled, anestrus cows (Gregg et al., 1986; Whisnant et al., 1986 abc). Intravenous infusion of naloxone prior to suckling increases the concentration of LH released during the suckling event (Myers et al., 1989). Similarly, naloxone administrations increases the concentrations of LH released from ovariectomized suckled or nonsuckled cows, as well as, intact cows at 14 and 28 d postpartum (Rund et al., 1989). The concentrations of binding sites for tritiated naloxone were quantified in suckled beef cows during postpartum anestrus (Trout and Malven, 1988). Cows that initiated cycles had decreased concentrations of naloxone binding sites in the basal forebrain and preoptic area compared to anestrus cows. Increased binding of naloxone may suggest increased opioid activity.

The precise neural inputs associated with suckling inhibition are yet to be determined. Variations in the length of suckling inhibition may be associated with nutrition or body stores of energy or may be due to environmental factors which may regulate GnRH secretion.

Exogenous Gonadotropin Releasing Hormone Therapy

Exogenous GnRH causes release of LH stored in the pituitary of anestrous cows (Carter et al., 1980; Wettemann et al., 1982) and from pituitaries collected from cows on restricted diets (Short et al., 1982). Cows fed restricted diets (Moss et al., 1985; Wettemann et al., 1989) and cows during the postpartum anestrous period (Carruthers et al., 1980) have adequate stores of GnRH. Lack of ovarian activity during anestrus is associated with decreased GnRH release from the hypothalamus (Lishman et al., 1979; Wettemann, 1980; Lamming et al., 1981; Imakawa et al., 1986a). Supplemental administration of GnRH may decrease the length of anestrus periods.

Injection of GnRH has resulted in variable results. A single injection either intravenously (Lishman et al., 1979; Smith et al., 1983, 1986; Rodger and Stormshak, 1986; Lucy and Stevensen, 1986) or intramuscularly (Cross et al., 1987) stimulated release of LH but not all cows ovulated in response to GnRH. A single injection of GnRH induced ovulation in dairy cows (Kittock et al., 1973; Lucy and Stevenson, 1986) and nutritionally restricted cows (Lishman et al., 1979) but cows receiving GnRH treatments did not exhibit estrus. The concentrations of unbound receptors for LH in the CL induced by GnRH injection are decreased in heifers compared to tissues from cyclic heifers (Rodger and Stormshack, 1986). GnRH injected on d 2 of the cycle stimulated LH release but resulted in decreased concentrations of progesterone in serum compared to concentrations during normal cycles (Martin et al., 1990). Response to a single injection of GnRH may depend on the reproductive status of the animal. The pituitaries of cows are not able to respond to GnRH stimulation prior to d 10 post partum (Fernandez et al,. 1978). GnRH is incapable of stimulating progesterone release unless ovarian tissues are present to respond to LH (Foster et al., 1980) and the response to GnRH injection increases with time post partum (Kesler et al., 1977; Jaeger et al., 1987)..

To establish continuous stimulation by GnRH, encapsulated GnRH and a GnRH analog have been inserted (Britt et al., 1974; Roberts et al., 1989). Administration of subcutaneous implants containing GnRH to postpartum anestrous Holstein cows caused increased LH release for 4 h followed by a decrease at 6 h post-implantation (Britt et al., 1974). Cows ovulated one day after treatment and continued to cycle for the remainder of the study (65 d). Concentrations of LH vary in a biphysic manner as a result of stimulation by a GnRH analogue contained in a gelatin implants (Roberts et al., 1989). Concentrations of LH in serum vary in association with release of the analogue from the capsule. Continuous stimulation of LH release by GnRH or an analogue may result in downregulation of pituitary receptors. Lamming and McCleod (1988) reported that continuous infusion of GnRH increased concentrations of LH initially but concentrations decreased by 2 to 3 days of treatment to values similar to controls. Rate of delivery of GnRH from implants may be difficult to control.

Webb et al. (1977) injected GnRH into postpartum anestrous cows and reported that GnRH stimulated CL development but the life span of the induced CL was shortened compared to a normal CL. A second injection given 10 d after the first one resulted in normal luteal activity. Shortlived CLs, as a result of GnRH stimulation, may be associated with decreased LH release from a single injection.

The quantity of LH released from the pituitary of cows is increased with previous exposure to GnRH (Carruthers et al., 1980). Exogenous GnRH administered at 2 h intervals, delayed puberty in Holstein bulls (Miller and Amann, 1986) Frequent (2 h intervals) injections of GnRH were successful in shortening the post partum interval of beef cows (Riley et al., 1981; Walters et al., 1982c), however an increased incidence of short cycles was observed prior to the return to normal luteal function. Timing of GnRH injections and the appropriate interval between injections may be related to the response achieved by treatments.

McVey et al. (1989) established pulsatile infusion of GnRH using mini-osmotic pumps inserted under the skin of anestrous beef cows. Infusion of 2.5 μg/h of GnRH resulted in pre-ovulatory surges of LH and decreased fertility in cows synchronized with Synchromate-B. Continuous release of GnRH from osmotic pumps stimulated gonadotropin release but reduced the ability of cows to respond to bolus injections of GnRH (Lamming and McCleod, 1988). The timing of GnRH release and the quantity of GnRH entering the blood may vary with osmotic pump delivery.

Intravenous infusion of GnRH has been used to restore gonadotropin secretions in monkeys with lesions in the basal hypothalamus (Knobil, 1980) and ovariectomized ewes that are anestrus due to nutrient restriction (Kile et al., 1990). Intravenous infusion of a GnRH analog (ethylamide GnRH) stimulated release of LH and FSH in gilts that had been immunized against GnRH (Traywick and Esbenshade, 1988). Similarly, pulsatile infusion of a GnRH analog increased the concentration of LH and the amplitude of LH pulses in beef heifers that had been immunized against GnRH (O'Connell, 1990). Pulsatile stimulation with analogues to GnRH did not reinitiate estrous cycles in gilts (Traywick and Esbenshade, 1988) or heifers (O'Connell, 1990) that were anestrus after immunizations against GnRH.

The ability to initiate gonadotropin secretion is necessary to decrease postpartum anestrous intervals. Concentrations of hormones at parturition may decrease the ability of cows to release GnRH and gonadotropin necessary for luteal function. GnRH replacement therapy in nutritional anestrus cows has not been reported. Effects of factors such as nutritional environment and other neural cues on gonadotropin secretion remain to be evaluated in attempts to decrease the time a cow is anestrus.

CHAPTER III

BODY ENERGY RESERVES INFLUENCE THE ONSET OF LUTEAL ACTIVITY AFTER EARLY WEANING OF BEEF COWS

Abstract

The influence of body energy reserves at early weaning on the onset of luteal activity and concentrations of LH and insulin-like growth factor I (IGF-I) in serum was evaluated in postpartum anestrous beef cows. Multiparous Hereford and Hereford x Angus cows were maintained in prairie grass pastures during gestation and supplemented with protein to establish body condition scores at parturition (BCS, 1=emaciated; 9=obese) between 3 and 6. Concentrations of progesterone in plasma were determined weekly and body weights and BCS were recorded biweekly for 5 wk post partum (PP). Anovulatory cows and their calves (n=19) were confined in stalls on day 40 ± 3 PP. Jugular cannulae were inserted on day 44 PP and calves were weaned (Day 0) the following day. Blood samples were collected from all cows for 4 h (every 10 min) prior to weaning and on days 1, 2, 4, 6, 8 and 10 after weaning. On Day 10, cows were returned to range pasture and concentrations of progesterone were determined for an additional 6 wk. Within 25 d after weaning, 100% of the cows with a BCS ≥ 5 (n=7) had initiated luteal activity, whereas only 43% ($P<.01$) of the cows with BCS < 5 (n=12) had luteal activity. Mean serum IGF-I concentrations were correlated with BCS ($r=.50$, $P<.05$). Frequency of LH pulses was influenced ($P<.01$) by body condition at weaning but was not influenced by day after weaning. Mean concentrations of LH in serum and pulse amplitude were not influenced by BCS or day after weaning. Secretion of LH, serum IGF-I and the interval to the onset of ovarian activity after early weaning of anestrous beef cows were influenced by BCS.

Introduction

A period of ovarian inactivity occurs following parturition in beef cows. Postpartum anestrus in beef cattle is associated with reduced LH secretion (Short et al.,1972; Walters et al., 1982; Williams et al.,1983; Edwards, 1985). Suckling decreases concentrations of LH in serum of acyclic cows (Edwards, 1985) by decreasing pulsatile LH release (Kinder et al., 1984). The number of days between parturition and the onset of luteal activity varies with suckling intensity (Wettemann et al., 1978) and frequency (Randel, 1981; Reeves and Gaskin, 1981). LH release in response to exogenous GnRH is greater in short-term weaned compared to suckled beef cows (Carter et al.,

1980) and replacing the suckling stimulus diminished the post-weaning LH increase (Williams et al., 1983).

Body energy reserves of beef cows influence reproductive performance (Wiltbank et al., 1964; Richards et al., 1986; Selk et al., 1988). Anestrus has been induced in beef cows by restricting energy intake (Imakawa et al., 1986; Johnson et al., 1987), and Richards et al. (1989) observed reduced concentrations of LH in serum of energy deprived cows as BCS decreased.

Concentrations of IGF-I in follicular fluid are related to progesterone biosynthesis (Spicer et al., 1988). During negative energy balance, serum concentrations of IGF-I are suppressed in beef steers (Breire et al., 1986) and beef heifers (Houseknecht et al., 1988). Concentrations of IGF-I in serum are related to nutrient availability and physiologic state of beef cows (Rutter et al., 1989).

The objectives of this study were to evaluate the influence of body condition score, at early weaning, on the onset of luteal activity and on concentrations of LH and IGF-I in serum of postpartum anestrous beef cows.

Materials and Methods

Spring calving, multiparous Hereford and Hereford x Angus cows were maintained under range conditions. Cows were fed during gestation to achieve body condition scores

(BCS: 1=emaciated, 9=obese; Wagner et al., 1988) between 3 and 6 at parturition. During the first 45 d post partum (PP), cows grazed native grass pastures and received 1.8 kg/d of a 40% crude protein supplement. BCS were determined independently every 14 d by two individuals. Body weights were measured and recorded biweekly after cows were without feed and water for 16 hr.

Blood samples were collected every 7 days between 20 and 45 d PP via venipuncture. Oxalic acid (1.25 mg) was added to each 10 ml sample and samples were placed on ice. Samples were centrifuged (3000 x g for 20 min) within 4 h and plasma was decanted and stored at -20 C until progesterone was quantified by radioimmunoassay (Lusby et al., 1981).

Cows that exhibited luteal activity before 40 d PP, determined by two consecutive weekly plasma samples with progesterone concentrations ≥ 1 ng/ml (Stabenfeldt et al., 1969; Wettemann et al., 1972), were excluded from treatment. Anovulatory cows (n = 19), on day 40 ± 3 PP, and their calves were transported (18 km) to individual pens in a barn. Temperature (21 ± 4 C), relative humidity (50 ± 15%), and light (14 h/d) were controlled. Cows were fed ad libitum a 12% crude protein diet consisting of alfalfa pellets and cottonseed hulls. Jugular cannulae[1] (polyvinyl, i.d. 1.57 mm, o.d. 2.08 mm) were inserted on

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[1] Bolab Inc., BB317-v10, i.d. 1.57 mm, o.d. 2.08 mm, Lake Havasu City, Az.

day 44 ± 3 PP to facilitate sampling of blood.

Blood samples were obtained on Day 0 (day 45 ± 3 PP) commencing between 1100 and 1400 h and consisted of a 30 ml sample for plasma and 10 ml samples at 10 min intervals for 4 h for serum. Weaning occurred following collection of the last blood sample on Day 0. Calves were returned to the range pasture and cows remained in the barn. Blood samples were obtained, according to this protocol, on Days 1, 2, 4, 6, 8 and 10 after weaning.

Samples for serum were allowed to clot at 21 ± 4 C for 4 h and then stored at 4 C. The following day, samples were centrifuged (3000 x g for 20 min) and serum was decanted and stored at -20 C until assayed for LH (Hallford et al., 1979) and IGF-I (Spicer et al., 1988) by radioimmunoassays.

After blood samples were obtained on Day 10, cows were transported to range pastures and remained isolated from calves. Weekly plasma samples were obtained for 6 additional weeks and concentrations of progesterone were evaluated to determine the days post partum until the onset of luteal activity. The first of two consecutive weekly samples with progesterone ≥ 1 ng/ml was determined as the onset of luteal activity. Analyses of variance were used to determine the effect of BCS at weaning (≥5 or <5) on the intervals between weaning and the onset of luteal activity.

Characteristics of LH secretion were defined using a modification of the criteria of Goodman and Karsch (1980).

Concentration of LH was the average of all samples for a cow on a day. A pulse was defined as a value more than 1 standard deviation greater than the mean for the cow on a day, followed by two consecutive concentrations of lesser value. Pulse amplitude was the difference between the greatest value during a pulse and the nadir within 30 min before the pulse.

IGF-I was quantified in the first sample obtained each day and in weekly samples after weaning. For Pearson's correlation coefficients analyses, the mean for all IGF-1 concentrations for a cow was calculated. Average LH, LH pulse frequency and the amplitude of LH pulses, and IGF-I concentrations were analyzed by a split-plot analyses of variance (SAS, 1982) with BCS as the main plot and day after weaning as the subplot. Pearson's correlation coefficients were determined within day between BCS at early weaning, the number of days until the initiation of luteal activity and characteristics of LH secretion.

Results and Discussion

Mean concentrations of LH before (Day 0) and after weaning were not influenced by BCS of cows at weaning or days after weaning (Figure 1). Restriction of diets fed to cows sufficient to cause reduced BCS resulted in decreased concentrations of LH in weekly samples (Richards et al., 1989a). Suckling decreases the concentration of LH in plasma of anestrous cows (Williams et al.,1987) and inadequate energy in the diet of postpartum cows delays the increase in LH secretion after calf removal (Whisnant et al., 1985). Weaning calves during the first 3 to 5 wk post partum (Edwards, 1985; Williams et al., 1987) resulted in increased LH concentrations within 48 h. The lack of increase in concentrations of LH in the cows in this study after weaning may be related to the BCS of the cows at weaning. Williams et al. (1987) used cows in excellent body condition, whereas, we used thin cows that were anestrus at 40 d PP.

The number of LH pulses per 4 h was influenced ($P<.01$, Figure 2) by BCS of the cows at weaning. Cows with BCS ≥ 5 had an average of 2.3 ± .1 pulses/4 h and the thinner (BCS < 5) cows averaged 2.0 ± .1 pulses/4 h. Day after weaning did not influence the number of LH pulses/4 h. LH pulse frequency tended ($P<.1$) to increase in cows with BCS < 5 from Day 0 to Day 2 post-weaning. The decrease in LH secretion in nonlactating, multiparous beef cows associated with a decrease in BCS is related to a decrease in pulse frequency (Richards et al., 1989a). Similarly, ovariectomized heifers fed diets deficient in energy have decreased frequencies of LH release (Imakawa et al.,1986b). The lack of a day after weaning effect on LH pulse frequency may be due to BCS of the cows at weaning. The fattest cows in this study had a BCS of 5.5. Pulse frequencies may increase sooner in response to weaning if cows have greater body energy reserves, as observed by Williams et al (1987).

Amplitude of LH pulses (Figure 3) for cows in moderate condition (BCS ≥ 5, 2.5 ±.2) did not differ (P >.1) from that for thin cows (BCS < 5, 3.0 ±.2) and was not influenced by day after weaning. Amplitude of LH pulses was not influenced by energy restriction (Johnson et al., 1987) or changes in BCS associated with nutritionally induced anestrus (Richards et al., 1989a). LH pulse amplitude did not change following removal of suckling inhibition (Garcia-Winder et al, 1986; Rund et al., 1989) or as a result of returning the calf following 72 h separation (Edwards, 1975).

The BCS of cows at early weaning was not correlated with mean LH concentrations in serum or LH pulse amplitude. Table 1 depicts correlations between the number of LH pulses and BCS at weaning, and the number of days PP until the initiation of luteal activity. BCS was correlated (r=.47, P<.05) with the number of LH pulses/4 h prior to weaning (Day 0). LH pulse frequency was negatively correlated on Day 4 (r=-.50, P<.05) with days to luteal activity. The relationships between LH pulse frequency and the return to luteal activity and BCS indicate that cows with greater BCS initiate cycles earlier PP. The postpartum interval to estrus is extended in beef cows by decreased energy intake during late pregnancy (Dunn and Kaltenbach, 1980) and BCS influences the effects of

The number of days until the onset of luteal activity after weaning was influenced ($P<.06$) by BCS. Cows in moderate condition (BCS ≥ 5) initiated luteal activity in 19.1 ± 1.7 d after weaning, whereas, onset of luteal activity in thin cows (BCS < 5) occurred at 26.6 ± 1.6 d. The percentages of cows with luteal activity at various days after weaning is depicted in Figure 4. Within 25 days after weaning, 100% of the cows with BCS ≥ 5 (n=7) had luteal activity, whereas only 43% ($P<.01$) of the thin cows (BCS < 5, n=12) had luteal activity. In addition, less ($P<.05$) of the thin cows, compared to the cows with BCS ≥ 5, had LA at 30 and 35 days after weaning.

The relationship between BCS and days post-weaning until luteal activity is summarized in Figure 5. The regression equation that describes the relationship between days to luteal activity (Y) and BCS (X) is $Y = 55.5 - 6.98X$ ($R^2 = .18$; n=19). When nutrient intake is inadequate and body energy reserves are depleted, the interval from calving to first estrus is extended (Wiltbank et al., 1962; Wettemann, 1980). Body condition scores are a good estimate of body energy reserves (Dunn, 1983; Wagner et al., 1988). BCS of cows at calving is the most important factor that determines if a cow will become pregnant during the breeding season (Selk et al., 1988). If a cow is in thin (BCS = 4) to moderate (BCS = 5) condition near the initiation of the breeding period, short term calf removal will not enhance reproductive performance (Wettemann et al., 1986). Cows that initiated luteal activity prior to 45 d post partum did not have their calves weaned and were eliminated from this experiment.

Mean daily concentrations of IGF-I are depicted in Figure 6. There was a tendency ($P<.11$) for concentrations of IGF-I in serum to be greater in cows with BCS ≥ 5 when compared to thinner cows (BCS < 5). IGF-I concentrations in serum collected daily were correlated with BCS ($r=.50$, $P<.05$). IGF-I concentrations in samples collected weekly after weaning were not influenced by time after weaning. Concentrations of IGF-I in follicular fluid (Spicer et al., 1988) or serum (Rutter et al., 1989) did not change with time post partum in ad libitum fed beef cows. However, in cows fed restricted diets, serum concentrations of IGF-I decreased with time post partum and were positively correlated with energy availability (Rutter et al., 1989). IGF-I concentrations may indicate if adequate energy is available to the cow to initiate and maintain ovarian function.

We conclude that the interval to the onset of ovarian activity after early weaning of beef cows is influenced by BCS. BCS is correlated with LH pulse frequency before weaning, days to LA, and concentrations of IGF-I in serum of beef cows. Increased body energy reserves stimulate increased pulsatile release of LH, which initiates ovarian function.

Implications

Responses to early weaning or temporary separation of calves to initiate luteal activity in beef cows are varied. BCS of the cows at weaning influences LH secretion and the interval from weaning to the onset of luteal activity. BCS of cows must be considered when evaluating the use of calf separation or early weaning to enhance rebreeding of beef cows.

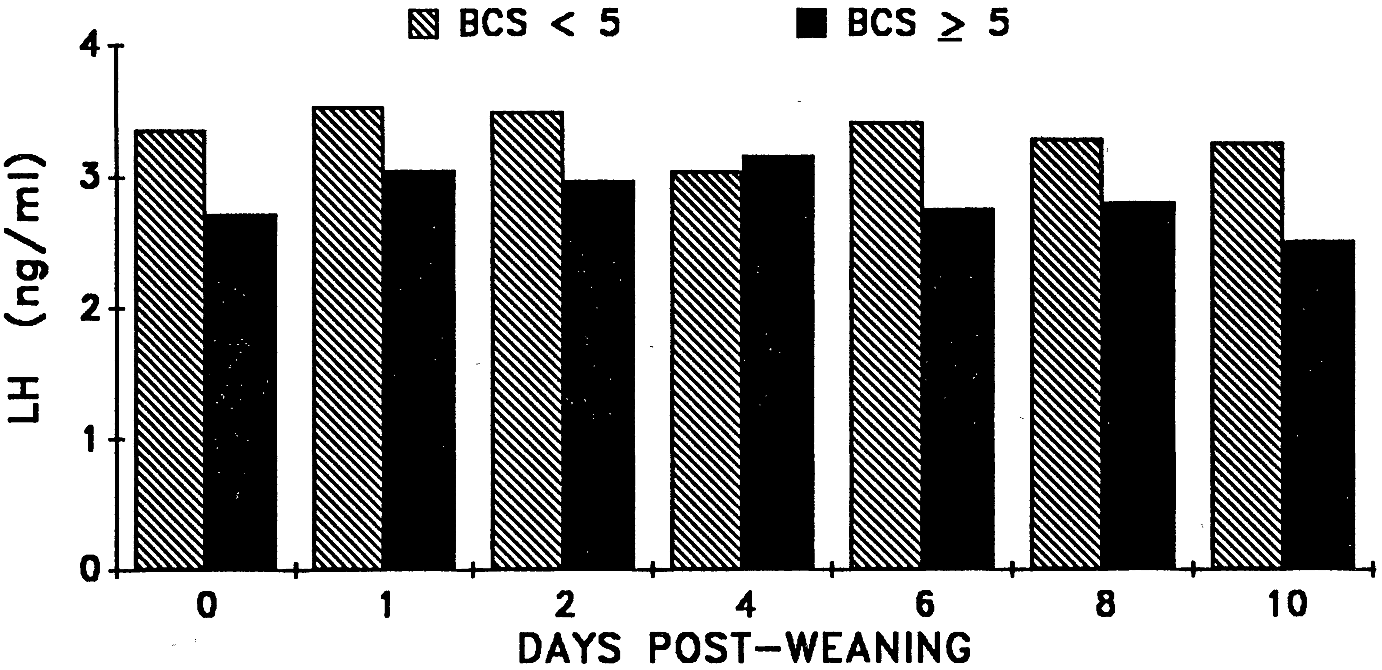

Figure 1. Influence of body condition score (BCS) at early weaning on concentrations of LH. Mean square error was .94.

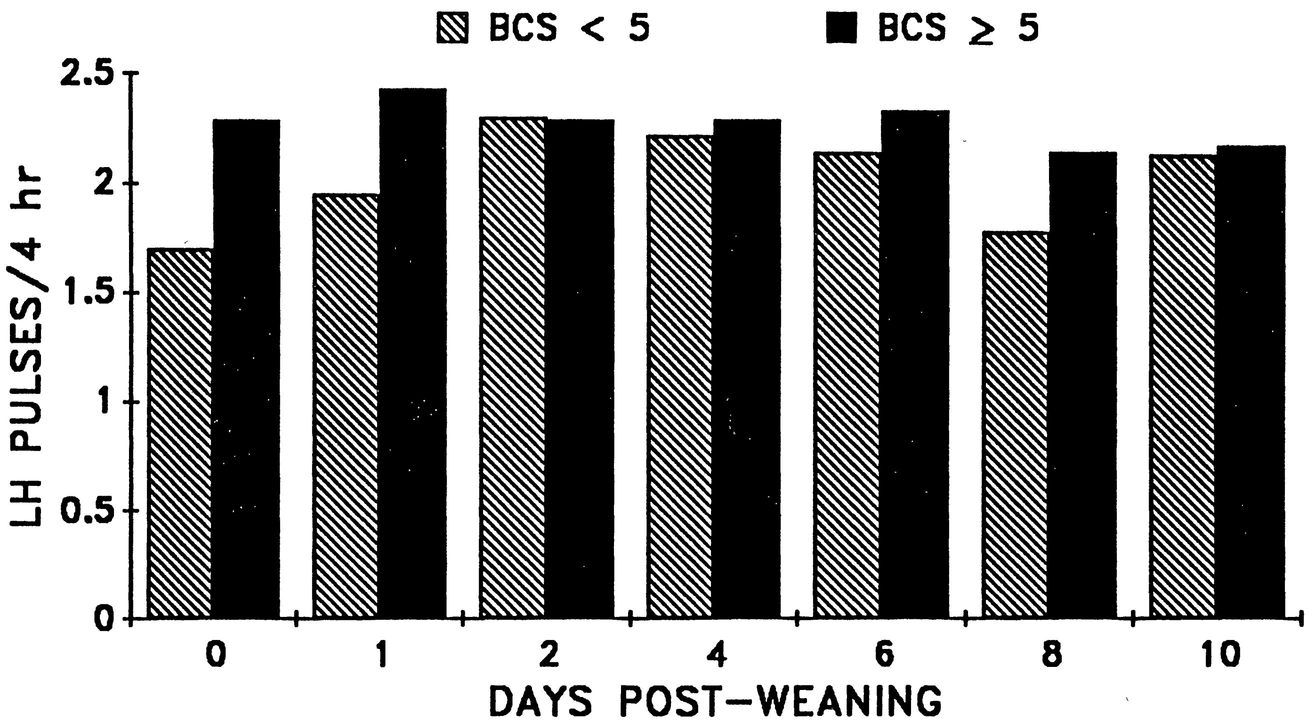

Figure 2. Influence of body condition score (BCS) at early weaning on LH pulse frequency. Mean square error was .71.

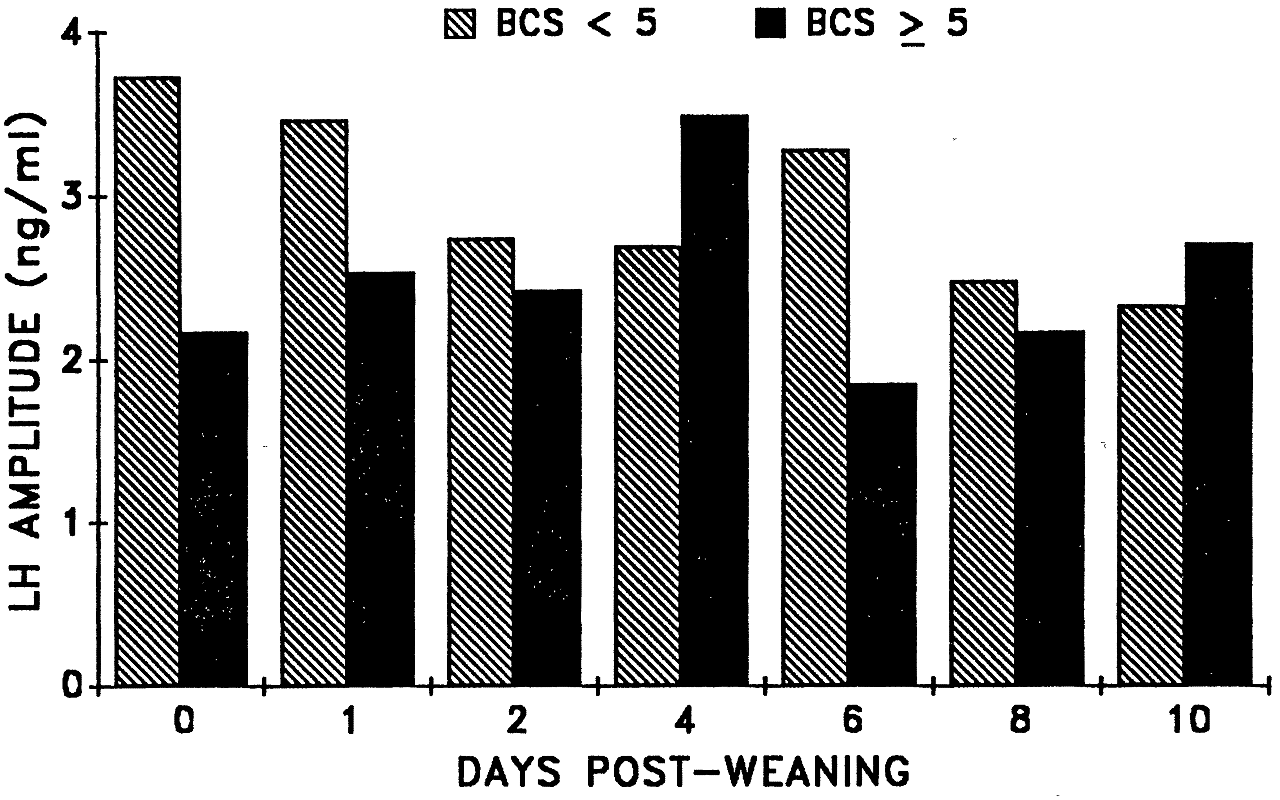

Figure 3. Influence of body condition score (BCS) at early weaning on the amplitude of LH pulses. Mean square error was 4.15.

Table 1. Correlations between LH pulse frequency[a] at various days after weaning and body condition score (BCS) and the number of days to luteal activity (LA) in beef cows

	Day after weaning						
	0	1	2	4	6	8	10
BCS	.47[b]	.12	-.20	.11	-.08	.26	-.05
LA	-.05	-.01	-.30	-.50[b]	-.18	-.29	.39

[a] Pulses of LH per 4 h.

[b] $P < .05$

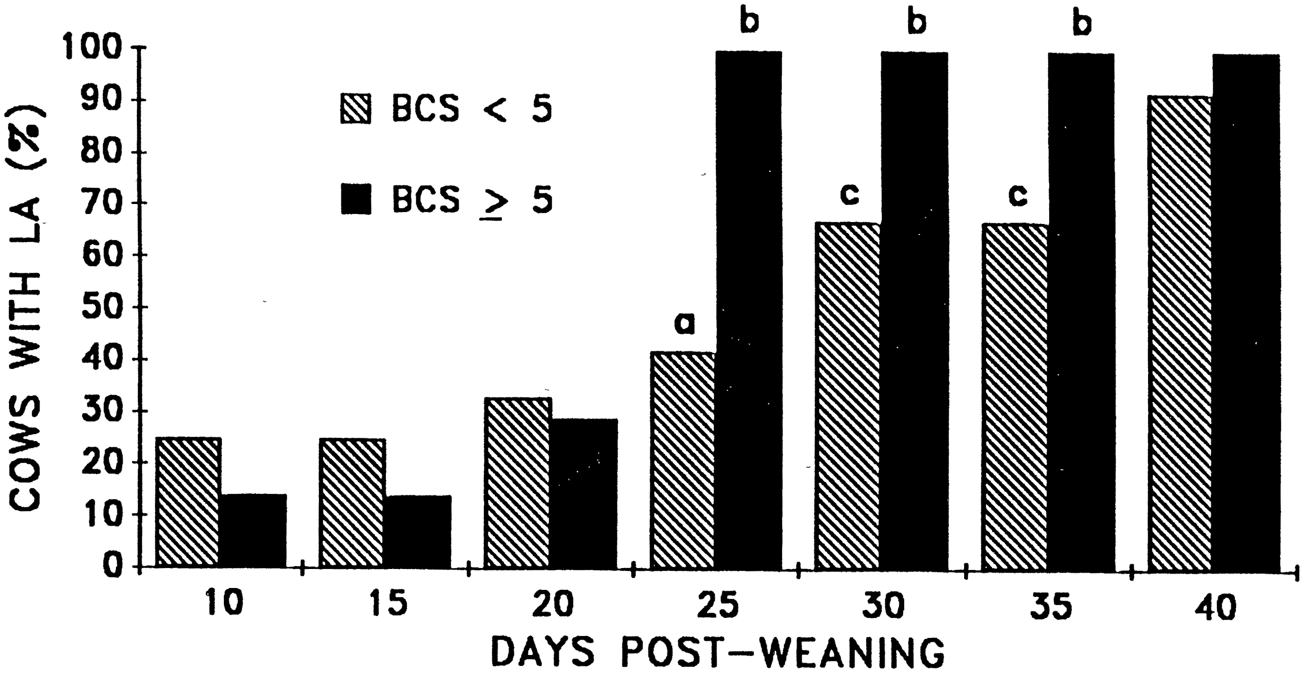

Figure 4. Influence of body condition score (BCS) at early weaning on the percentage of cows with luteal activity (LA) during the first 40 days after weaning. LA was determined by concentrations of progesterone ≥ 1 ng/ml for two consecutive weeks. (Columns with different letters on the same day differ: ab, $P<.01$; bc, $P<.1$)

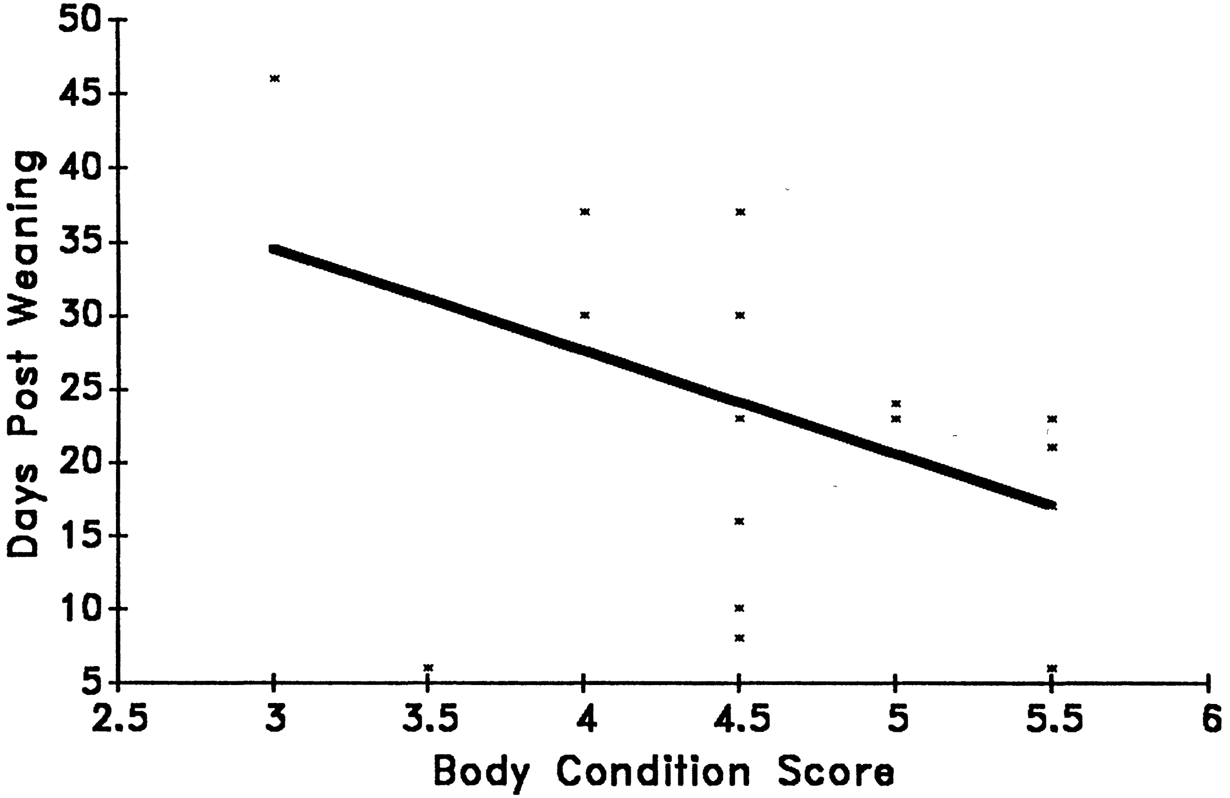

Figure 5. Relationship between body condition score (BCS) of beef cows at early weaning and days to luteal activity (LA). (Regression equation: $Y = 55.5 - 6.98X$; $n=19$, $R^2 = .18$)

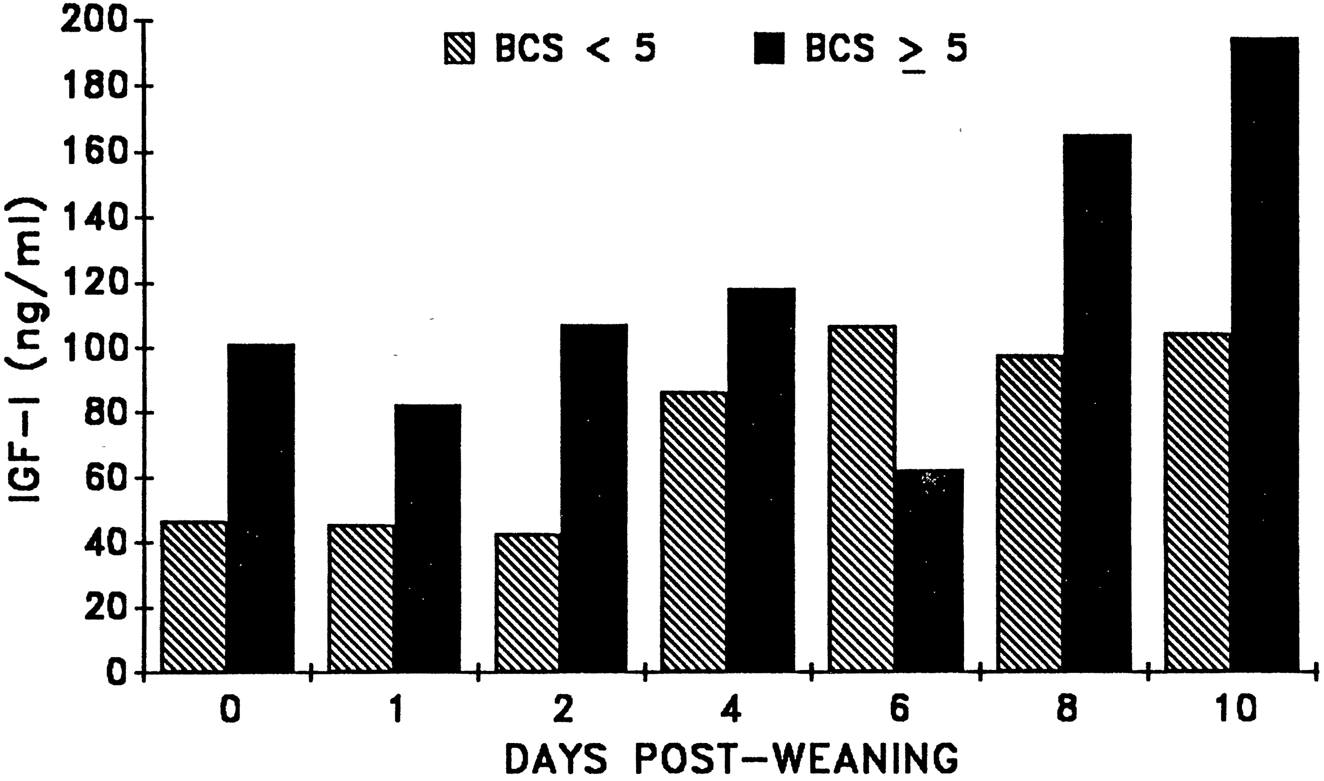

Figure 6. Influence of body condition score (BCS) at early weaning and days after weaning on concentrations of IGF-I in serum of beef cows. Mean square error was 3412.

CHAPTER IV

PULSATILE INFUSION OF GnRH INITIATES LUTEAL ACTIVITY IN NUTRITIONAL ANESTROUS BEEF COWS

Abstract

The ability of intravenous pulsatile infusion of GnRH to initiate ovarian function in nutritional anestrous beef cows was evaluated. Twenty-seven nonlactating Hereford and Hereford x Angus cows (469 ± 47 kg), with a body condition score (BCS) of 5.5 ± .6 that were exhibiting normal estrous cycles, were fed a diet to lose 1% of BW per week. BW and BCS were recorded every 2 wk and blood samples were collected every 7 d to monitor luteal activity. When concentrations of progesterone were < 1 ng/ml for three consecutive weeks, anestrous cows (BCS, 3.1 ± .7; BW loss, 24 ± 8%) were assigned to pulses (1.25 min) of saline (C, 2 ml every h), GnRH-4 (2 μg GnRH every 4 h) or GnRH-1 (2 μg GnRH every h). Cows were confined to stalls for 4 d before treatment and two jugular cannulae were inserted two d prior to infusion. Infusions began on D 0 and continued through D 14. Progesterone was quantified in daily blood samples and LH was quantified in samples collected every 10 min for 4 h on D -1, 0, 2, 4, 6, 8, 10, 12, 14, and 15. On D 16, cows were returned to pasture and blood samples were collected 3 times weekly through D 30. Pulsatile infusion of GnRH increased ($P<.05$) the amplitude of LH pulses, but had no effect on pulse frequency. Infusion of GnRH every 1 or 4 h, caused increased concentrations of LH in serum compared with C ($P<.001$) and cows given GnRH-1 had greater ($P<.005$) LH compared with cows given GnRH-4. Fewer C cows had luteal activity by D 10 ($P<.05$), D 15, D20, D25, and D30 ($P<.005$) compared with GnRH-4 and GnRH-1 cows. Fewer ($P<.01$) C cows, than GnRH treated cows, maintained LA after initiation during the infusion period. More GnRH-1 cows ($P<.1$) than GnRH-4 cows initiated LA by D 25. Once initiated, more GnRH-1 cows maintained LA during ($P<.1$) and after ($P<.005$) infusion compared to GnRH-4 cows. Pulsatile infusion of GnRH induced luteal activity in nutritional anestrous beef cows.

Introduction

Restriction of nutrient intake and body weight loss causes cessation of normal estrous cycles in cattle (Bond et al., 1958; Imakawa et al., 1986a; Johnson et al., 1987; Richards et al., 1989a). Cows fed restricted diets release more LH in response to exogenous GnRH (Whisnant et al., 1985; Rasby et al., 1991) and have decreased GnRH in the infundibular stalk-median eminence (Wettemann et al., 1989).

Repeated injections of GnRH increase secretion of LH in postpartum acyclic cows (Riley et al., 1981; Walters et al., 1982d). Pulsatile infusions of GnRH analogs stimulate release of LH and FSH in gilts (Traywick and Esbenshade, 1988) and LH in heifers (O'Connell, 1990) immunized against GnRH. The objective of this study was to determine if pulsatile treatment of nutritional anestrous cows with GnRH will stimulate secretion of LH and initiate ovarian function.

Material and Methods

Nonlactating, nonpregnant Hereford and Hereford x Angus cows with good to moderate body condition scores (BCS; 5.5 ± .6) were used in this study. BCS were independently determined by two people using the system where 1 = emaciated and 9 = obese (Wagner et al., 1988). Cows weighed 469 ± 8 kg and were 5.5 ± .8 years of age. All cows exhibited normal (21 ± 3 d) estrous cycles at the start of the study.

Cows were assigned by breed, BCS and age to maintain (M; n=9) or were fed a restricted (R; n=27) diet in a drylot. M cows were fed .45 kg/hd/d of cottonseed meal and had ad libitum access to prairie hay and a mineral mix. R cows had access to 2.72 kg/hd/d of prairie hay and access to the same amount of mineral mix as consumed by M cows. When ambient temperatures were < -10°C, R cows were fed an additional 1.4 kg of hay/hd/d to maintain intakes at approximately 50% of NRC (1984) requirements.

Cows were weighed and a BCS was assigned each 14 d after 16 h without feed and water. Blood samples (15 ml) were collected from R cows every 7 d via puncture of the tail vein. Oxalic acid (1.25 mg) was added to each sample and samples were placed on ice. Samples were centrifuged (3000 x g for 20 min) within 4 h and plasma was decanted and stored at -20°C.

Concentrations of progesterone in plasma were quantified by radioimmunoassay (Lusby et al., 1981). R cows were determined to be anestrous when concentrations of progesterone were ≤ 1 ng/ml of plasma for three consecutive weeks. Anestrous cows were confined in individual stalls in a barn and fed equal amounts (1.36 kg) of alfalfa pellets and cottonseed hulls at 0900 daily. Cows were acclimated to stalls for 4 d prior to treatment. A polyvinyl cannulae[1] was inserted into each external jugular of each cow 2 d prior to treatment to facilitate simultaneous infusion and blood collection.

Anestrous cows were randomly assigned to an infusion treatment consisting of 2 µg GnRH once every h (GnRH-1), 2

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[1] Bolab Inc., BB317-v10, i.d. 1.57 mm, o.d. 2.08 mm, Lake Havasu City, Az.

μg GnRH once every fourth h (GnRH-4) or saline (Saline; 2ml/h). Heparin (1 USP/ml) and penicillin (50 units/ml) were added to sterile saline to prevent clotting and bacterial contamination of cannulae during infusion. Infusions were conducted using a Harvard Infusion pump[2] that was controlled by an automatic timer[3]. This pump-timer unit was calibrated to deliver 2 ml of saline or GnRH (2 μg/2 ml saline) in 1.25 min at the desired intervals. Syringes were refilled every 12 ± 2 h. Treatments were initiated on D 0 at 1100 h and continued through 1500 h on D 14.

Cows on M diets were maintained in small grass lots and observed twice daily for estrus. When M cows were observed in estrus (ED=0), either spontaneous or as a result of prostaglandin $F_{2\alpha}$[4] injection, a jugular cannulae was inserted and the cow was confined in a stall adjacent to R cows. The diet for M cows (9 kg alfalfa pellets) was fed in equal amounts at 0800 and 1600 daily. M cows remained in the stalls through ED 19 of the cycle.

Blood samples (15 ml) were collected daily, from D -1 through D 15 for treated cows and during the cycle of M cows, Concentrations of of progesterone and estradiol (Hallford et al., 1979) were quantified in plasma. In addition, blood samples (10 ml) were collected from

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[2] Harvard Infusion/Withdrawal Pump, Model 931. South Natick, MA.
[3] Chron Trol, Model CD-4. Lindburg Ent. Inc. San Diego, CA.
[4] Lutalyse, The Upjohn Co., Kalamazoo, MI.

treated cows at 10 min intervals for 4 h on the day prior to infusions (D -1), and on days 0, 2, 4, 6, 8, 10, 12 and 14 of infusion and on the day after infusion (D 15). Frequent samples were also collected from M cows on days 2, 6, 12 and 19 of the estrous cycle. Blood samples for serum were allowed to clot at 21 ± 4 C for 4 h and then stored at 4 C for 16 h. Samples were centrifuged (3000 x g for 20 min) and serum was decanted and stored at -20 C until assayed for LH by RIA (Hallford et al., 1979). Following the last sampling period, all cows were returned to native grass pastures. Blood samples were collected from R cows on every second day from D 16 through D 30 relative to treatment.

Analyses of variance were used to determine the effect of treatment on concentrations of progesterone and estradiol and luteal activity. Orthogonal contrasts (saline vs GnRH-1, GnRH-4; GnRH-1 vs GnRH-4) were used to compare treatments. Concentrations of progesterone and estradiol in R cows after treatments were compared to concentrations at particular days of the estrous cycle of M cows using Bonferroni t-statistics (Gill, 1973).

Characteristics of LH secretion were defined using a modification of the criteria established by Goodman and Karsh (1980). A pulse of LH was defined as a value > 1 standard deviation greater than the mean for a cow on a day, followed by two consecutive concentrations of lesser value. Pulse amplitude was the difference between the greatest value during a pulse and the nadir within 30 min prior to the pulse. Criteria for LH secretion were analyzed by split plot analyses of variance (SAS, 1982) with treatment as the main plot and day of treatment as the sub plot. The effects of treatments on LH concentrations were compared using the same orthogonal contrasts described for steroid analysis. Bonferroni t-statistics were used to compare characteristics of LH secretion for anestrous cows after GnRH treatment, with concentrations at particular days of the estrous cycle of M cows.

Results and Discussion

Cows fed M and R diets weighed 476 ± 53 and 469 ± 47 kg and had BCS of 5.6 ± .5 and 5.5 ± .6, respectively when the diets were initiated. Restriction of nutrient intake and loss of BCS resulted in cessation of estrous cycles. R cows became anestrus when they had lost 24 ± 8% of their initial BW and had BCS of 3.1 ±.7 (Table 2). Imakawa et al. (1986) and Johnson et al. (1987) reported that heifers became anestrus when they had lost 20% of their initial BW. Multiparous cows (Richards et al. 1989a) fed restricted diets lost 24% of initial (429 ± 16 kg) BW and had a BCS of 3.5 when they became anestrus. Differences in percentage of BW and BCS lost could be due to variations of BW and BCS at the onset of feed restriction.

Concentrations of progesterone in R cows (Figure 7) were less than 1 ng/ml at the initiation of treatment. Intravenous pulsatile infusion of GnRH once per h or once every 4 h increased ($P<.01$) the concentrations of progesterone in plasma of nutritional anestrous beef cows. Lack of ovarian activity in cows is associated with decreased concentrations of LH in serum (Lishman et al., 1979; Imakawa et al., 1986). LH is luteotropic in the bovine (Hansel, 1966) and luteinization of follicles occurs when postpartum cows are injected with GnRH (Wettemann et al., 1982; Spicer et al., 1986). Increased concentrations of progesterone in R cows that were infused with GnRH may be associated with luteinization of follicles or formation of functional corpora lutea (CL) as a result of LH release.

During the infusion period (D 0 through 14), concentrations of LH (Figure 8) were greater in GnRH-1 and GnRH-4 cows compared with saline treated cows ($P<.001$). Concentrations of LH were greater ($P< .005$) in GnRH-1 compared with GnRH-4 cows. Concentrations of LH averaged 1.66, 2.22 and 3.49 for saline, GnRH-4 and GnRH-1 treated cows, respectively. Severe dietary restriction decreases hypothalamic-pituitary function (McCann and Hansel, 1986) and is associated with decreased concentrations of LH in serum of cows (Imakawa et al., 1986; Richards et al., 1989a). Intravenous infusion of GnRH restores gonadotropin secretion in ovariectomized ewes with lesions in the medio-basal hypothalamus (Clarke et al.,1984) and restores the mRNA for gonadotropins and secretion of gonadotropins in ovariectomized ewes after prolonged periods of nutrient restriction (Kile et al., 1990).

Cyclic cows had greater ($P<.05$) concentrations of LH in serum on the day 19 after estrus compared to d 2, 6 or 12 of the estrous cycle (Table 3). Concentrations of LH in serum from GnRH-1 cows on all days during infusion were similar to concentrations of LH in serum of M cows on D 19 and were greater ($P<.05$) than concentrations of LH in saline or GnRH-4 cows on D 2, 6, 10 or 14 of infusion. Increased concentrations of LH prior to estrus in cyclic cows has been associated with an increase in the amplitude of LH pulses (Rahe et al., 1980).

Infusion of GnRH (GnRH-1 and GnRH-4) increased ($P<.02$) the amplitude of LH pulses compared to cows infused with saline (Figure 9). The amplitude of LH pulses was similar for cows treated once per h with GnRH and once per 4 h. Clarke et al. (1984) reported greater amplitude of LH pulses when GnRH was infused into ovariectomized ewes at a frequency of once per 2 h compared to once per h. Infusion of a larger dose of GnRH resulted in greater release of LH from ewes infused with GnRH less frequently (Clarke et al., 1985). The amplitude of LH pulses in response to GnRH stimulation may reflect the quantity of LH available for release.

The number of pulses of LH was not influenced by infusion of GnRH or saline (Figure 10). Sampling intervals each day were established such that two blood samples (at 10 min intervals) were obtained prior to pulses of GnRH or saline. With this procedure a maximum of 3 pulses of LH could be detected in response to hourly treatment with GnRH. The average number of pulses detected per 4 h period were 1.84, 1.90 and 2.11 for saline ,GnRH-4 and GnRH-1 treatments, respectively. The frequency of LH pulses increases in cyclic cows in association with follicular growth (Rahe et al., 1980). The number of pulses of LH per 4 h was greater ($P<.05$) in cyclic cows compared to GnRH-4 cows on D 6, 10 or 14 of infusion. Nutrient restriction is associated with decreased frequencies of LH pulses (Imakawa et al., 1986; Richards et al., 1989a) and decreased response to exogenous GnRH as cows become anestrus (Johnson et al., 1987).

Concentrations of estradiol in plasma averaged 12.8 ± 4 pg/ml for R cow and were not influenced by treatments. Gonadotropin stimulation is necessary for estradiol production by the theca interna cells of the bovine ovary (Fortune, 1988). Concentrations of estradiol in plasma collected weekly from cows on restriced diets did not differ from cows on maintenance diets (Richards et al., 1989a). Decreased gonadotropin secretion associated with nutritional anestrus may not influence follicular growth.

Alternatively, and most probably, cows responding to GnRH stimulation may not have had detectable increases in estradiol concentrations due to variability among cows on a treatment.

The number of days that cows had progesterone concentrations ≥ 1 ng/ml is summarized by treatment in Table 4. Infusion of GnRH resulted in increased concentrations of progesterone for 12-18 d in 33 and 44% of the cows infused with GnRH-4 and GnRH-1, respectively. None of control cows had increased progesterone in plasma for more than one day. Concentrations of progesterone in M cows were ≥ 1 ng/ml of plasma for 16.7 ± .4 d during the estrous cycle. Concentrations of progesterone ≥ 1ng/ml indicate the presence of a CL (Stabenfeldt et al.,1969; Wettemann et al., 1972). Treatment of postpartum anestrous cows with a single dose of GnRH results in increased concentrations of progesterone for 3-6 d (Wettemann et al., 1982). Transient increases in progesterone occur prior to the first estrus associated with puberty (Gonzalez-Padillo et al.,1975; Schams et al.,1981) and the source of this progesterone is luteinized tissue within the ovary (Berradinelli et al., 1979). Response to exogenous GnRH may depend on the number and maturity of follicles in the ovary.

Concentrations of progesterone in plasma of cows that had luteal activity during the infusion period are depicted in Figure 11. Concentrations of progesterone in plasma of M cows during the mid-luteal phase of the estrous cycle (d 8-14) were greater ($P<.05$) than concentrations of progesterone in GnRH infused cows on D 11 (Table 5) but were similar to those on D 14 of infusion with GnRH.

The cumulative percentage of cows that had progesterone concentrations ≥ 1ng/ml (Figure 12) represents the number of cows with short-term (> 4 d) increases in progesterone concentrations as well as cows with luteal activity characteristic of normal estrous cycles. Fewer cows infused with saline had luteal activity during ($P<.05$) or after ($P<.005$) the infusion period compared to GnRH-4 and GnRH-1 cows. There was a trend ($P<.1$) for more GnRH-1 cows to have luteal activity compared to GnRH-4 by D 25 and once initiated more GnRH-1 cows maintained luteal activity during ($P<.1$) and after ($P<.005$) the infusion period. Pulsatile infusion was discontinued after D 14 of the study. Luteal activity on D 25 indicates spontaneous luteal activity in the absence of exogenous GnRH support.

In summary, intravenous pulsatile infusion of GnRH increased the concentration of LH in serum and the amplitude of LH pulses but did not influence the number of pulses per 4 h. Concentrations of progesterone in plasma were increased by the pulsatile infusion of GnRH to nutritional anestrous beef cows.

Implications

Restricted nutrient intake and loss of body condition decrease reproductive performance in beef cows. Pulsatile infusion of GnRH induced luteal activity in nutritional anestrous cows. This suggests that GnRH secretion is limiting in nutritional anestrous cows. Methods developed from research in nonlactating anestrous cows may be useful in attempts to decrease the interval from parturition to conception and to understand the influence of body energy reserves on reproductive performance.

Table 2. Body condition score (BCS) and body weight (BW) loss of beef cows at anestrous

Treatment	BCS at Anestrus	% of Initial BW	BCS Loss
Saline	2.94 ± .68[a]	23.6 ± 7.0	2.44 ± 1.18
GnRH-4	3.05 ± .76	24.6 ± 9.0	2.44 ± .88
GnRH-1	3.44 ± .76	22.9 ± 9.0	2.39 ± .92

[a] LS Mean ± SE

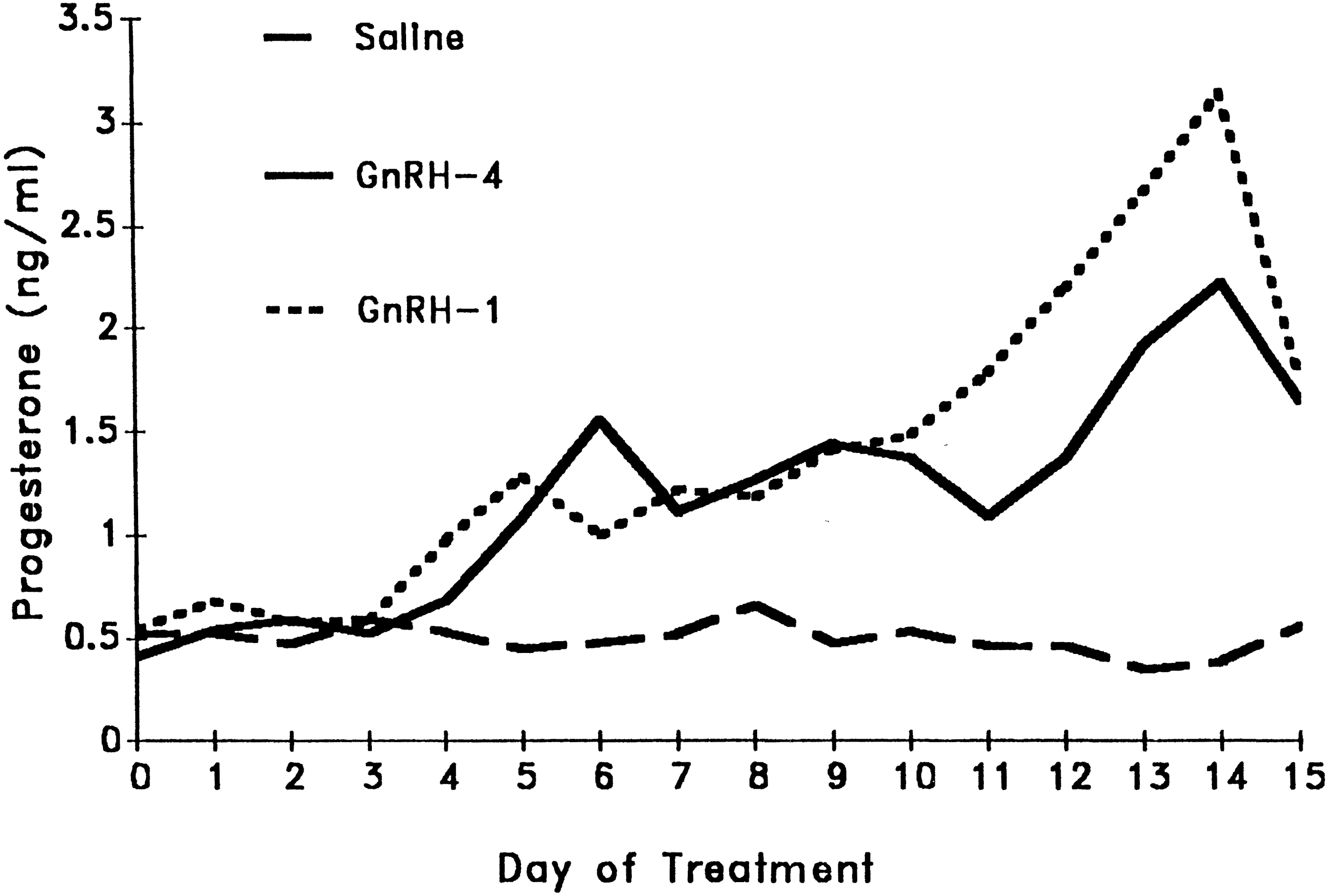

Figure 7. Mean concentrations of progesterone in plasma of nutritional anestrous cows infused with GnRH or saline.

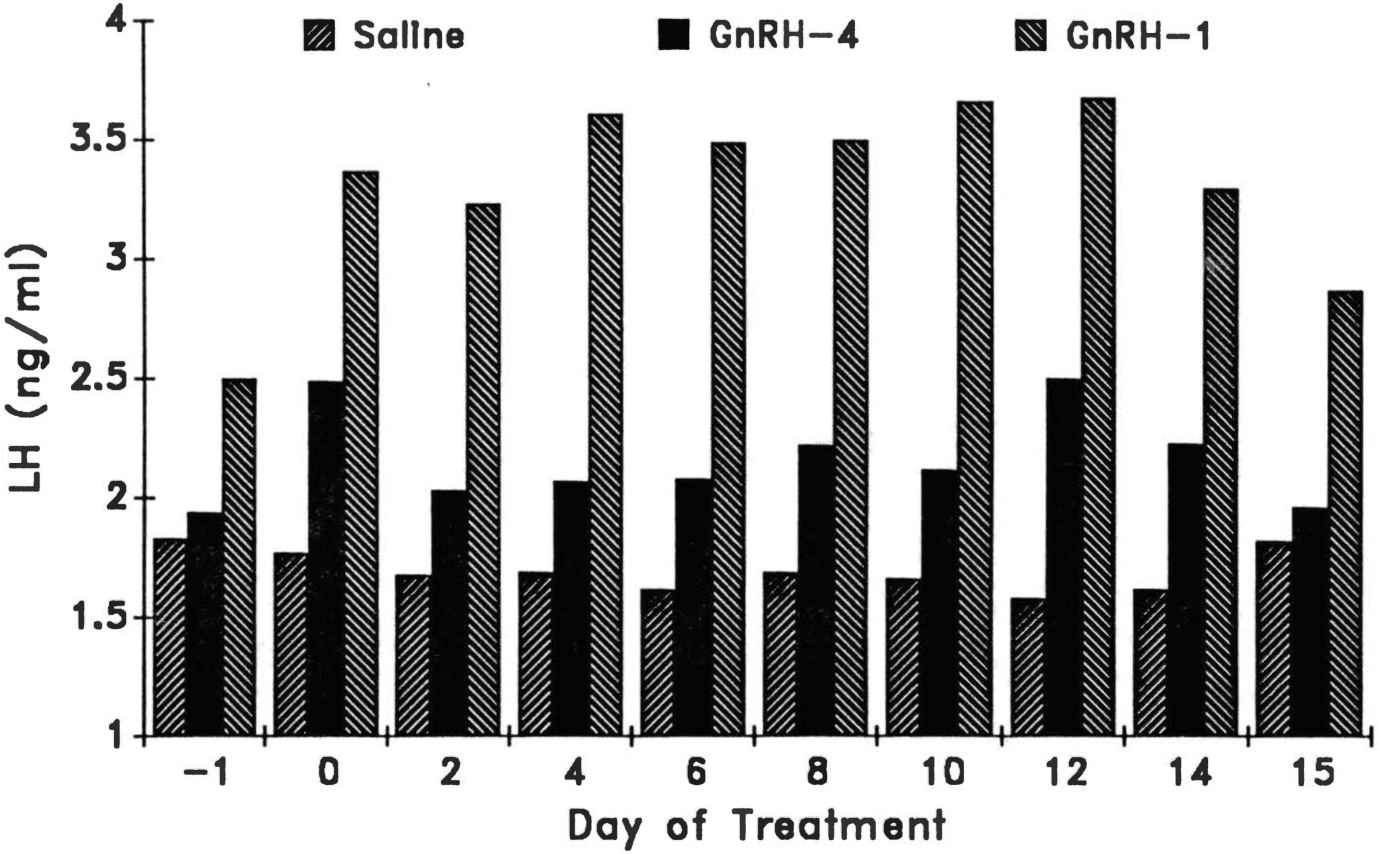

Figure 8. Least Squares Mean concentrations of LH in serum of nutritional anestrous cows infused with GnRH or saline. Mean square error was 0.305. During treatment, GnRH-4 and GnRH-1 vs Saline (P < .005) and GnRH-1 vs GnRH-4 (P < .005).

Table 3. Secretion of LH in beef cows during the estrous cycle

Day of cycle	Concentration	Frequency	Amplitude
2	2.72 ± 1.07[a]	2.88 ± .64[b]	1.79 ± 1.18[a]
6	2.52 ± 1.11	2.28 ± .48	2.07 ± 1.18
12	2.60 ± 1.40	2.80 ± .83	1.72 ± 1.39
19	5.53 ± 3.09	2.14 ± 1.07	8.13 ± 4.35

[a] Mean ± SE (ng/ml)
[b] Mean ± SE (pulses per 4 h)

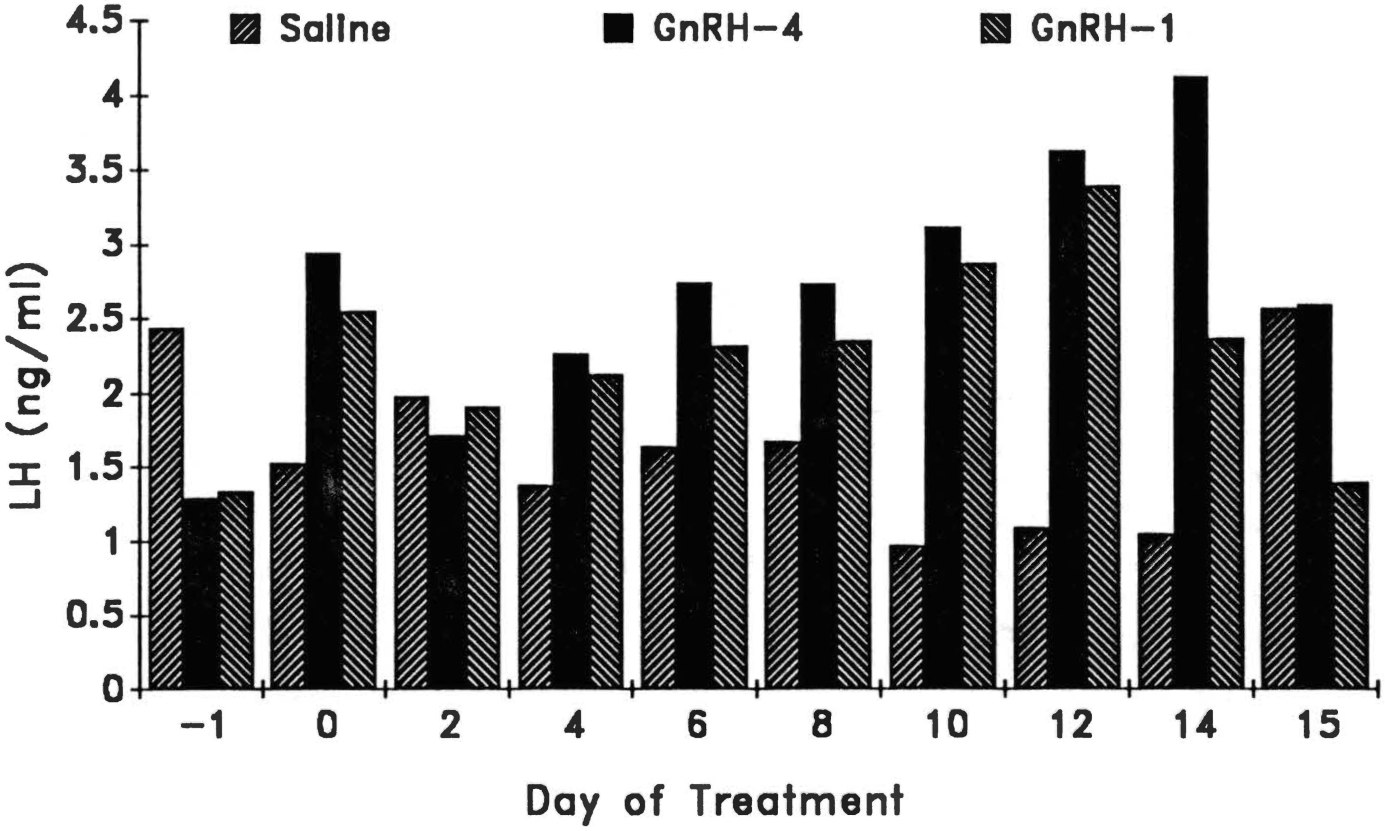

Figure 9. Least Squares Mean amplitudes of LH pulses in nutritional anestrous cows infused with GnRH or saline. Mean square error was 2.952. During treatment, GnRH-4 and GnRH-1 vs Saline (P < .02).

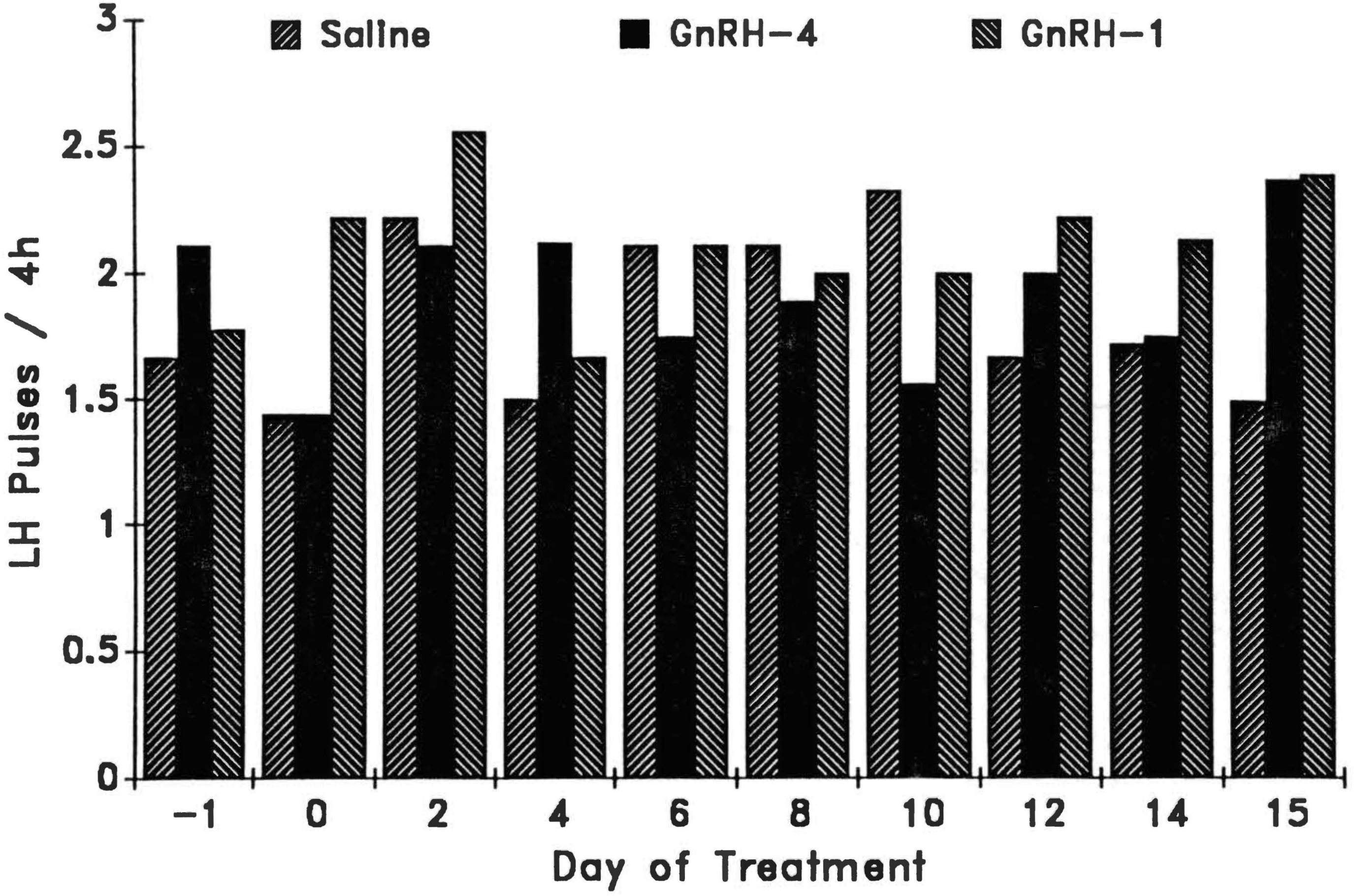

Figure 10. Least Squares Mean frequencies of LH pulses in nutritional anestrous cows infused with GnRH or saline. Mean square error was 0.612.

Table 4. Luteal response of nutritional anestrous cows treated with GnRH or saline

	Days with progesterone > 1ng/ml			
Treatment	≤ 1	2 - 4	5 - 11	12 -18
Saline	9[a]	-	-	-
GnRH-4	4	1	1	3
GnRH-1	-	1	4	4

[a] number of cows

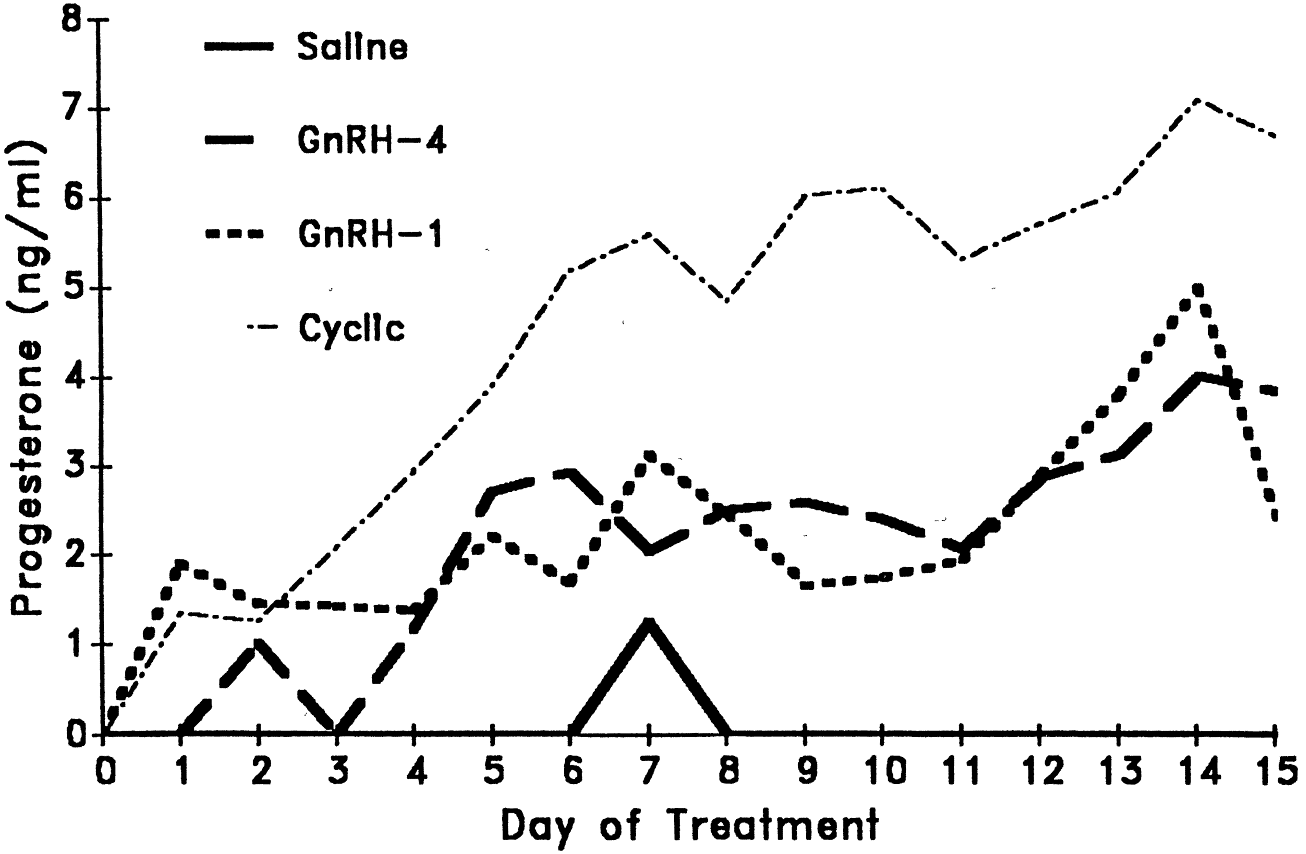

Figure 11. Concentrations of progesterone in plasma of nutritional anestrous cows, infused with GnRH or saline, that had luteal activity.

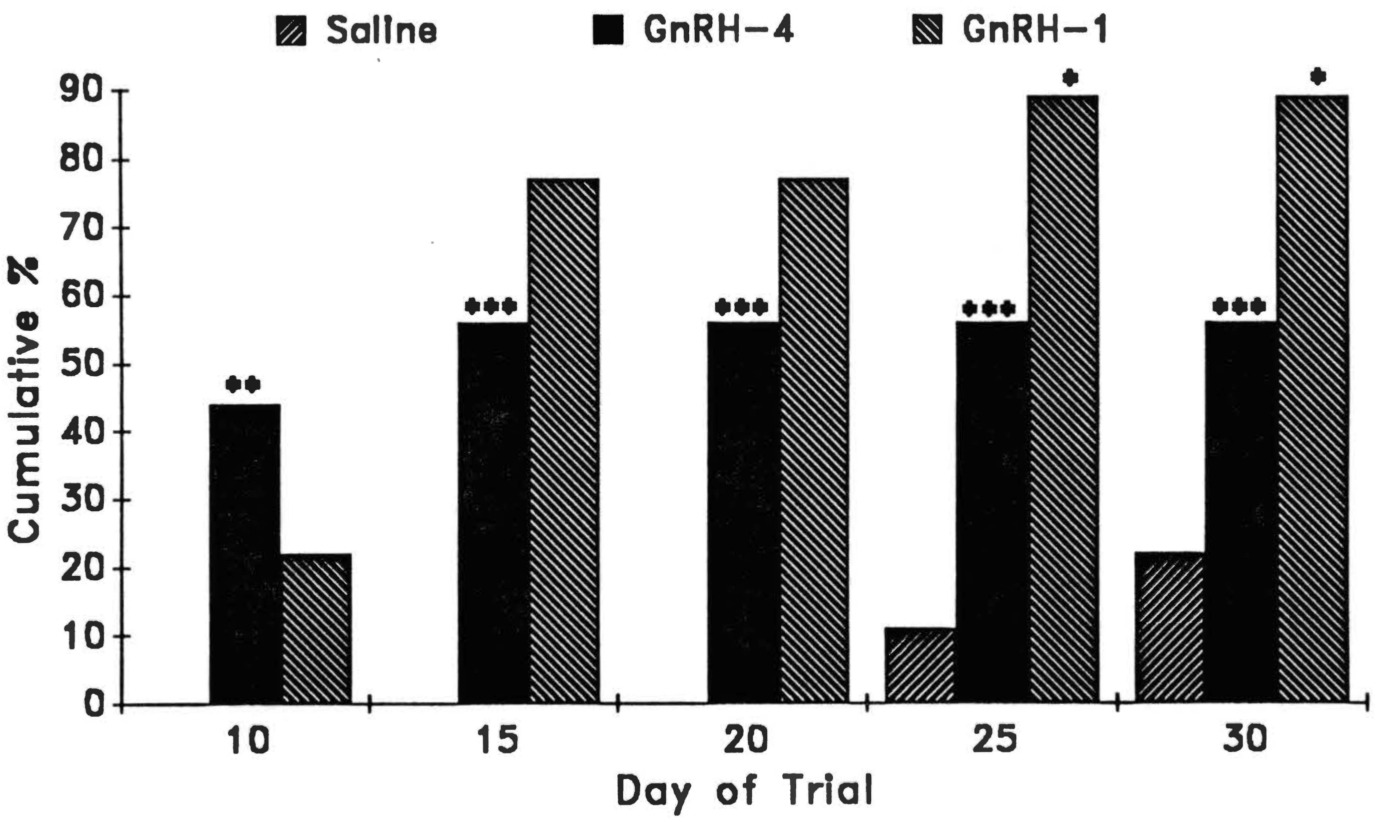

Figure 12. Cumulative percentage of nutritional anestrous cows infused with GnRH or Saline that had luteal activity. * GnRH-1 vs GnRH-4 ($P < .1$). ** GnRH-4 and GnRH-1 vs Saline ($P < .05$). *** GnRH-4 and GnRH-1 vs Saline ($P < .005$).

Table 5. Concentrations of progesterone in plasma of R cows during treatment and in M cows during the estrous cycle

	Day[a]			
	11		14	
Group	n[b]	concentration[c]	n	concentration
R cows				
GnRH-4	4	2.07 ± .74[d]	3	4.01 ± 1.04
GnRH-1	8	1.95 ± .59[d]	6	4.49 ± 2.65
M cows	9	5.31 ± 2.49[e]	9	6.81 ± 1.85

[a] Day of treatment for R cows; Day of cycle for M cows.
[b] Number of cows with luteal activity
[c] Progesterone (ng/ml); LS Mean ± SE
[de] Means with different letters on a Day differ ($P<.05$)

CHAPTER V

SUMMARY AND CONCLUSIONS

A pulse generator in the hypothalamus may cause pulsatile release of GnRH in the bovine, as in other species. The particular factor or factors that regulate pulsatile secretion of gonadotropins in cows and the onset of estrus cycles has not been determined. Nutrition and body energy reserves are two of the factors that influence gonadotropin secretion and the percentage of cows that become pregnant during the breeding season. Body condition scores (BCS) can be used to estimate body energy stores. Evaluation of gonadotropin secretion during different physiological conditions which influence synthesis and/or release of gonadotropins may provide insight to the mechanisms through which nutrition and body energy reserves regulate gonadotropin secretion.

Weaning calves from cows decreases nutrient demand for lactation and removes the suckling inhibition of gonadotropin secretion. Anestrous cows with BCS between 3 and 6 had calves weaned at 45 d post partum. Blood samples were collected frequently (every 10 min for 4 h) prior to weaning and on alternating days until D 10 after weaning.

Weekly blood samples were collected for an additional 6 wk post weaning to establish the onset of luteal activity.

Concentrations of progesterone were determined by radioimmunoassay to assess luteal activity. Within 25 d post weaning, 100% of the cows with BCS ≥ 5 (n=7) had initiated luteal activity, whereas only 43% ($P<.01$) of the cows with BCS < 5 (n=12) had luteal activity. The regression equation that described the relationship between BCS (X) and days to luteal activity (Y) was $Y = 55.5 - 6.98X$ ($R^2 = .18$, $P<.06$).

Concentrations of insulin-like growth factor 1 (IGF-I) in blood were determined after weaning in daily and weekly samples. Mean IGF-I tended ($P<.1$) to be greater in frequent samples from cows with BCS ≥ 5 compared to thin cows. Concentrations of IGF-I in samples collected during the first 10 d after weaning at 45 d post partum were correlated ($r=.50$, $P<.05$) with BCS. Concentrations of IGF-I in weekly samples were not influenced by BCS.

LH was quantified in frequent samples collected for serum by a double antibody radioimmunoassay. BCS of cows influenced ($P<.01$) the number of pulses of LH per 4 h but did not influence mean concentrations or the amplitude of LH pulses after weaning. The frequency of pulses of LH on the day prior to weaning was correlated ($r=.47$, $P<.05$) with the BCS of cows. LH pulse frequency on D 4 after weaning was negatively correlated ($r= -.50$, $P<.05$) with the onset of luteal activity after weaning. These correlations suggest that the frequency of LH pulses in lactating anestrous cows is influenced by BCS and cows with increased pulsatile release of LH after early weaning resume estrous cycles sooner than cows with less pulsatile release of LH.

Nutritional restriction resulted in loss of body weight (BW) and BCS. Nonlactating beef cows became anestrous when they had lost 24 ± 8% of their initial BW and had a BCS of 3.1 ± .7. Anestrous cows were randomly assigned to intravenous pulsatile infusion of saline or GnRH at 2μg per h (GNRH-1) or 2 μg per 4 h (GnRH-4). Blood samples were collected daily during the infusion period and concentrations of progesterone and estradiol were quantified via radioimmunoassay. Frequent samples were collected for quantification of LH on the day before infusions, on alternating days during the infusion period, and on the day after infusions. Plasma samples were obtained on Monday, Wednesday and Friday through D 30 post infusion.

Pulsatile infusion of GnRH (GnRH-1 and GnRH-4) increased the amplitude ($P<.05$) and mean concentration ($P<.001$) of LH compared with saline treated cows. Increased frequency of GnRH infusion (GnRH-1 vs GnRH-4) increased ($P<.005$) the amplitude of LH pulses. The number of pulses of LH per 4 h was greater ($P<.05$) in cyclic cows on d 2 of the estrous cycle compared with GnRH-4 treated cows during the infusion period. The amplitude of LH pulses was greater (P<.05) on d 19 of the estrous cycle compared with other days during the cycle. Infusion of GnRH increased the number of cows with luteal activity by D10 (P<.05), D15, D20, D25 and D30 (P<.005) compared with anestrous cows infused with saline. More GnRH-1 cows (P<.1) had luteal activity by D25 compared with GnRH-4 and once initiated, more GnRH-1 cows maintained luteal activity during (P<.1) and after (P<.005) the infusion period compared with GnRH-4 treated cows. Infusion of GnRH did not influence concentrations of estradiol in plasma.

The mechanisms by which nutrient restriction regulates gonadotropin secretion and the onset of estrous cycles remains to be illucidated. Absence of luteal activity is associated with changes in the amplitude or frequency of LH secretion and concentrations of LH in serum. Early weaning increased the frequency of LH release while infusion of GnRH increases the amplitude of pulses and mean concentrations of LH in serum of nutritional anestrous beef cows. Pulsatile release of gonadotropins is associated with the onset and maintenance of luteal activity in beef cows.

LH is released in a pulsatile manner from the pituitary in response to stimulation by GnRH from the hypothalamus. Mechanisms controlling GnRH release in the cow have not been determined. Pulsatile intravenous infusion and removal of suckling inhibition increase gonadotropin secretion suggesting that a pulse generator may be present in the hypothalamus of cows which regulates GnRH release. Nutritional regulation of gonadotropin secretion may be through inhibition of this pulse generator.

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