FACTORS INFLUENCING REPRODUCTION OF BEEF HEIFERS: AGE AT PUBERTY, NUTRITIONAL ANESTRUS, GLUCOSE IN PLASMA AND CONSUMPTION OF COBALT

By

JORGE A. VIZCARRA

Ingeniero Agronomo

Universidad de la Republica

Montevideo, Uruguay

1981

Submitted to the Faculty of the
Graduate college of the
Oklahoma State University
in partial fulfillment of
the requirements for
the degree of
MASTER OF SCIENCE
December, 1991

Dhaka,
17th
August

FACTORS INFLUENCING REPRODUCTION OF BEEF HEIFERS: AGE AT PUBERTY, NUTRITIONAL ANESTRUS, GLUCOSE IN PLASMA AND CONSUMPTION OF COBALT

Thesis Approved:

Robert P. Wettemann
Thesis Adviser

David M. Engle

D. G. Wagner

Thomas C. Collins
Dean of the Graduate College

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to Dr. Robert Wettemann for his guidance, and friendship during the course of my study and preparation of this thesis.

I wish to extend my gratitude to Dr. Donald Wagner for his help and advise in the first stages of my study.

Thanks also to Dr. David Engle and Dr. Archie Clutter for serving on my graduate committee.

Special acknowledgment is to the Instituto Nacional de Investigaciones Agropecuarias (formerly CIAAB), for providing financial assistance for my graduate studies.

I wish to extend special thanks to Dr. Arthur Klatt, for his friendship and administrative sponsorship.

My gratitude to Mrs. LaRuth Mackey and Mr. David Bishop for their friendship and help during the research.

Finally I wish to thank my mother Maria del Carmen Reyno, my wife Susana and our daughters Ana and Cecilia for their love and support.

This thesis is dedicated in loving memory of my father Jacinto Vizcarra.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure Page

CHAPTER I

INTRODUCTION

Increasing reproductive efficiency of beef cattle can improve efficiency of production. In heifers, age at puberty is a major factor influencing efficiency. If first parturition occurs at 2 yr of age instead of 3 yr of age, a heifer tends to produce more kilograms of calf during her lifetime (Lesmeister et al., 1973). Puberty in cattle has been defined as the age when first estrus accompanied by spontaneous ovulation occurs. Endocrine events at puberty are associated with morphological and functional changes in the gonads and interactions among the hypothalamus, pituitary, gonads and uterus, which result in developmental changes in the target organs (Short and Adams, 1988).

Nutritional management is a major factor controlling reproduction. Nutritional restriction can cause anestrus in cows or heifers that are having normal estrous cycles as well as delay the onset of puberty (Randel, 1990).

The mechanism by which nutrition causes anestrus in cattle remains unclear, but it has been demonstrated that body energy reserves control reproductive performance in cows (Selk et al., 1988; Spitzer et al., 1991).

Fertile estrous cycles can be reinitiated, after nutritionally induced anestrus, by increased nutrient intake. Resumption of luteal activity is associated with increased BW and BCS. There is also evidence that indicates that glucose may be an energy mediator for the resumption and maintenance of estrous cycles (Richards et al., 1989a, 1989b).

The objectives of this study were: to evaluate the relationship between the occurrence of puberty with the cessation of luteal activity after nutritional restriction and to determine if feeding Cobalt Dextrose Lactone (CDL) influences concentrations of glucose in plasma and alters ovarian activity in nutritional anestrous heifers during re-alimentation.

CHAPTER II

REVIEW OF LITERATURE

Puberty

Definition. Broadly defined, puberty is the condition of being or the period of becoming first capable of reproducing. It is marked by maturing of the genital organs and development of secondary sex characteristics (Webster's, 1988).

In heifers, puberty is the age when first estrus is accompanied by spontaneous ovulation. The age of first estrus in heifers varies considerably and one or more "quiet" ovulations may occur before heifers exhibit estrus or "standing heat" in conjunction with ovulation (Jainudeen and Hafez, 1987). Del Vecchio et al. (1990) observed that silent estrus and abnormally short or long estrous cycles occurred in 45% of the heifers during the first 2 estrous cycles, indicating that there are anomalies in the ovarian and uterine hormonal events necessary for normal estrous cyclicity during the pubertal transition period.

Endocrine changes. Endocrine changes at puberty are associated with morphological and functional changes in the gonads, and interactions among the hypothalamus, pituitary, gonads and uterus. These endocrine events result in developmental changes in target organs. The classical "gonadostat" theory, suggested by Ramirez and McCann (1963), states that a decrease in sensitivity of the hypothalamo-pituitary centers to negative feedback to estradiol results in gonadotropin secretion which is necessary for the onset of puberty. This theory may not be applicable to all species (Day et al., 1984; Dodson et al., 1988).

Conflicting results have been recorded for heifers. Some workers have found that LH secretion in prepubertal heifers is responsive to estradiol negative feedback and that decreased feedback occurs just prior to puberty (Scahms et al., 1981; Day et al., 1984; Jones et al., 1991). Kinder et al. (1987) observed pulsatile secretion of LH prior to the onset of puberty in heifers, while others have been unable to detect significant increase in mean concentration of LH, frequency of LH pulse or LH pulse amplitude before the onset of cyclic ovulatory activity (Gonzalez-Padilla et al., 1975; Page et al., 1987; Dodson et al., 1988).

Day et al. (1987) studied the concentration of receptors for estradiol in the hypothalamus and pituitary. They found a decline in the number of estradiol receptors in the hypothalamus and/or pituitary just prior to puberty. This indicates that a decrease in the number of estradiol receptors may be the mechanism responsible for the prepubertal decline in the negative feedback of estradiol on secretion of LH.

Factors affecting puberty in heifers

Nutrition. Reproductive rate has a major influence on production efficiency of beef cattle, and nutritional management limits or controls reproduction. Most of the work related to the effect of nutrition on reproductive processes has been focused on the effects of energy restriction. Other nutrient deficiencies such as protein, vitamins and minerals can also affect reproduction, but their effects are not well documented. The relative proportion of volatile fatty acids (VFA) in the rumen as well as glucose concentrations in blood can also have a profound effect on reproduction and production efficiency through effects on puberty in heifers (McCartor et al., 1979; Short and Adams, 1988).

Energy. Energy is the feed component required in the greatest quantity by beef cattle. The major energy-consuming processes in ruminants are related to biochemical processes such as ion transport across cell membranes in the gastrointestinal tract and liver, protein synthesis, protein degradation, substrate cycling and urea synthesis (McBride and Kelly, 1990).

Heifers fed diets with adequate energy reach puberty at an earlier age and are heavier than those fed diets with restricted energy (Bellows et al., 1967; Wiltbank et al., 1969; Arije and Wiltbank, 1971; Grass et al., 1982; Patterson et al., 1991). The effect of the source of energy has also been evaluated. Wilcox et al. (1990) fed heifers with diets composed mostly of concentrate or forage, insuring equal gains for heifers on both diets. The weight and age at puberty were similar for both diets, indicating that diets containing mostly grains, had no beneficial or detrimental effect on development of replacement heifers. The use of protein-protected lipids as an alternative form of feed energy was also evaluated (Rhodes III et al., 1978). Heifers that received 20% of their diet as a protein-protected lipid-feed, deposited more intramuscular and subcutaneous fat and had greater body condition than heifers fed an isocaloric diet without protected lipid. However, fewer heifers fed the protected lipid diet reached puberty during the experiment, compared with control heifers.

The effect of restricted energy intake on the endocrine system of prepubertal heifers has not been established. Beal et al. (1978) suggested that dietary energy restriction may influence LH release directly at the pituitary, as well as, indirectly through effects on ovarian steroid production. More recently, Day et al. (1986) proposed that a reduced nutrient intake during the prepubertal period delays puberty in heifers by retarding the prepubertal increase in secretion of LH. When a diet restricted in energy was fed to heifers, the prepubertal increase in secretion of LH did not occur and puberty was delayed. The release of LH from the pituitary, after treatment of heifers with GnRH, was also reduced in heifers fed diets containing less energy compared with the response of heifers fed a control diet.

Volatile fatty acids. VFA's are the main energy source for ruminants. Acetic, propionic and butyric acids are produced during fermentation of dietary plant materials and normally make up 95% of the total VFA's present in the rumen. Propionic acid accounts for between 25 and 44% of the total VFA's (Ward et al., 1961). Propionic acid serves as the primary precursor of glucose, which must be synthesized de novo because little glucose is absorbed into the hepatic portal vasculature (Huntington et al., 1981).

Rutter et al. (1983), studied the effect of abomasal infusion of propionate in prepubertal heifers. They concluded that treatment with propionate enhanced the capacity of the pituitary to respond to exogenous GnRH.

Monensin, a biological active compound produced by *Streptomyces cinnamonensis*, can change rumen fermentation patterns, increasing the ruminal production of propionate at the expense of acetate and butyrate (Dinius et al., 1976). The effect of feeding monensin to prepubertal heifers is well documented. Moseley et al. (1978) first demonstrated that heifers fed monensin reached puberty early than control animals. Later it was proposed that monensin increased the capability of the pituitary of prepubertal heifers to secrete LH upon multiple GnRH challenges (Randel and Rhodes III, 1980). The increased secretion of LH resulted in increased ovarian, luteal and follicular fluid weights, as well as, the number of follicles was increased (Bushmich et al., 1980).

Age. Age at puberty is an important factor that influences the efficiency of beef cattle production. Puberty normally occurs at about 11-15 months of age in beef breeds (Wiltbank et al., 1959, 1966, 1969; Stewart et al., 1980). Heifers that reach puberty during their first breeding season are able to calve as 2-years-old. In this situation, heifers have a greater lifetime calf production than those calving at 3 years of age or older (Donaldson, 1968). It is not only important that heifers reach puberty and conceive, but they should start estrous cycles early in the breeding season to increase production efficiency (Lesmeister et al., 1973).

Age at puberty was negatively correlated with weaning weight (Wiltbank et al., 1959), preweaning average daily gain (Arije and Wiltbank, 1971; Laster et al., 1972), postweaning average daily gain (Wiltbank et al., 1969) and with weight at first calving (Menge et al., 1960). Grass et al. (1982) reported that age at puberty was negatively correlated with weight, height, weight/height ratio and heart girth at 224 days, when heifers received limited nutrient intake, but these correlations were positive when the animals were given adequate diets.

Response to selection for age at puberty depends on the magnitude of its heritability. Heritability estimates for pubertal age range from .20 to .61 (Arije and Wiltbank, 1971; MacNeil et al., 1984; Morris et al., 1986). This lack of accuracy is probably a result of the use of different mathematic models (MacNeil et al., 1984) or the use of different populations, since heritability is a function of the group on which it is calculated (Preston and Willis, 1970).

Weight. Many experiments have demonstrated that after removing the effect of feed intake and breed, age at puberty is largely explained by differences in body weight, indicating that the onset of puberty is more closely related to body weight than to age (Wiltbank et al., 1966; Short and Bellows, 1971). Weight and age at puberty are positively correlated, indicating that heifers that reach puberty later tend to be heavier at puberty (Arije and Wiltbank, 1971; Laster et al., 1972; Little et al., 1981; Grass et al., 1982). Weight at puberty is positively correlated with pre and postweaning growth; heifers that grow more rapidly tend to be heavier at puberty (Wiltbank et al., 1969; Ferrell, 1982). However, the relationship between age and weight at puberty was negative when heifers were reared on different diets. Heifers with increased nutrient intake reached puberty at an earlier age and were heavier than those fed reduced amount of nutrients (Bellows et al., 1967; Wiltbank et al., 1969; Arije and Wiltbank, 1971; Grass et al., 1982).

The mechanism by which body weight influences the onset of puberty has not been established. Mechanisms related with a "critical" body weight in girls (Frisch and Revelle, 1970) and level of "fatness" in rats have been suggested (Frisch et al., 1977). Riumallo and Durnin (1988) characterized puberty in boys as a "fat-wave" during which children gain weight and the tissue is almost 40% fat. This is followed by the "growth spurt" during which they gain tissue that is almost 100% lean.

In heifers, it has been proposed that the onset of puberty does not depend on attaining a "critical" body weight (Kamwanja et al., 1980; Brooks et al., 1985). Some works support the idea that body composition is more important than body weight itself. Siebert and Field (1975) found that an adequate body weight is necessary for estrus to occur, but that the onset of puberty is more closely related to the body fat content of heifers (approximately 8.4% of the body weight) than body weight or total body water. More recently, Yelich et al. (1991), working with Angus x Hereford heifers, found that total body fat at puberty was greater in full fed animals compared to limited or maintenance fed heifers, concluding that the percentage body fat and body weight of heifers at puberty can be altered by diet.

Body Condition. Body condition scoring (BCS) allows the accurate estimation of body energy or fat reserves of cows (Wagner et al., 1988). Scoring systems have been developed in several countries (Earle, 1976; Grainger and McGowan, 1982; Richards et al., 1986), and in all cases the lowest value identifies the thinnest animal and the highest value the fattest animal.

Body energy reserves are probably major regulators of the age at puberty of heifers, however, little information is available on the effect of BCS on the onset of puberty. Ferrell (1982) reported that age at puberty was not related to heifers condition score, but BCS was associated with the mean weight at puberty. On the other hand, Rhodes III et al. (1978) established that heifers that received protein-protected lipid had a greater condition score than controls at puberty, but fewer heifers fed the protein-protected lipid attained puberty during the study. Recently, Yelich et al. (1991), reported that heifers receiving a diet composed mostly of grain, reached puberty earlier and with a greater BCS, when compared with heifers receiving a diet containing less energy.

Roberson et al. (1990) conducted an experiment with ovariectomized beef heifers to determine the influence of

BCS and restriction of dietary energy on secretion of gonadotropins. They found that the amplitude of LH pulses increased with decreasing daily gain in heifers with low BCS, but LH pulses were unrelated with decreasing daily gain in heifers with high BCS. Mean concentrations of LH and pulse frequency of LH were not related to changes in average daily gain in heifers with high and low BCS.

Breed. Age and weight at puberty is greatly influenced by the genotype of heifers (Gregory et al., 1966; Wiltbank et al., 1966; Laster et al., 1976; Ferrell, 1982; Warnick et al., 1990; Patterson et al., 1991). In general, breeds that have been selected for great milk production, reach puberty at a younger age and at a relative lighter weight than breeds that have been selected for beef production (Laster et al., 1979; Ferrell, 1982). Also, faster growing heifers, such as Continental and Zebu breeds, reach puberty later than British breeds (Laster et al., 1976; Stewart et al., 1980; Ferrell, 1982).

The effect of crossbreeding on puberty has been evaluated. Heterosis for age and weight at puberty have been observed when crossing British breeds (Kaltenbach and Wiltbank, 1962; Wiltbank et al., 1966) and with *Bos indicus* X *Bos taurus* crossbreds (Gregory et al., 1978; Laster et al., 1979 Sacco et al., 1987).

Differences in weight at puberty in different crossbreed heifers were similar to the differences in weaning weight, indicating that heterosis influences age at puberty through its effect on growth rate (Laster et al., 1972). Hawk et al. (1954) found that inbreeding delayed age at puberty in Holstein heifers and also significantly retarded growth rate.

Photoperiod. Cattle are not considered seasonal breeders, however photoperiod has an influence on reproduction (Hauser, 1984). Seasonal patterns of LH, FSH, prolactin and melatonin secretion in heifers and cows have been reported (Stanisiewski et al., 1988; Critser et al., 1987b, 1987c). Not only does the relative position of the sun to the earth influences reproduction, but the phase of the moon may be related to the reproductive performance of heifers (Roy et al., 1980).

It is possible that the pineal gland and melatonin may have a role in the measurement and transduction of photoperiod in heifers (Critser et al., 1987a; Webley and Luck 1986), but the relationship between the pineal, hypothalamus, pituitary and gonads has not been established.

Prepubertal heifers exposed to a long photoperiod achieve puberty at an earlier age than heifers exposed to a short photoperiod (Hauser, 1984; Hansen et al., 1983). However, Peters and Tucker (1978) found that long photoperiods (16-h light, 8-h dark) did not significantly affect onset of estrous cycles, compared to heifers exposed to natural photoperiod.

Critser et al. (1987c, 1988) tested the hypothesis that photoperiod influences gonadotropic hormones and melatonin secretion. They found that serum LH and prolactin concentrations were greater in heifers exposed to increasing photoperiod. Melatonin concentrations, measured at night, were greater in heifers exposed to decreasing photoperiod. In addition they found that melatonin is secreted episodically. There are diurnal changes in circulating concentrations of melatonin in the prepubertal bovine females, with concentrations higher during scotophase (dark period) than photophase.

The season of birth (spring or fall calving) influences the age at puberty of heifers (Little et al., 1981; Schillo et al., 1982). In late gestation and early postnatally, heifers born in the fall are exposed to decreasing day length, and between 3 and 9 months of age they are in an environment of increasing photoperiod. Several reports have demonstrated that heifers born in the spring reached puberty at younger ages than those born in the fall (Menge et al., 1960; Roy et al., 1980; Hauser, 1984). These effects of photoperiod are accompanied by changes in gonadotropin concentrations and in ovarian activity. Peters and Tucker (1978) reported that serum concentrations of prolactin increased when ambient temperature increased from 9 to 29 C and that the increase in prolactin due to the increase in temperature was greater in heifers exposed to long photoperiod. Hansen et al. (1983) concluded that photoperiod did not significantly influence PRL and LH concentrations, but Schillo et al. (1983) suggested that seasons may influence age at puberty by affecting serum concentrations of LH, prolactin, or growth rate. When heifers were exposed to different photoperiod but received the same diet (hay *ad libitum*), concentrations of LH and FSH were greater while concentrations of prolactin were reduced in heifers exposed to a shorter photoperiod than those exposed to a long photoperiod (Critser et al., 1987b). The present evidence indicates that age at puberty in the bovine female can be altered by photoperiod even though it is not a seasonal breeder, but the causes for this effect needs further investigation.

Ambient temperature. Environmental temperature is the most important climatic factor which may influence reproduction in beef cattle. Elevated ambient temperatures coupled with greater percentages of relative humidity, depress performance of dairy and beef cows by decreasing feed consumption (Morrison and Lofgreen, 1979; Collier et al., 1981; Minton, 1986; McGuire et al., 1988), milk production and estrous behavior (Johnson, 1965; Ludri, 1983; Collier et al., 1982). Cutaneous receptors and the CNS, which affect the neuroendocrine system via the hypothalamus and pituitary, are possible mechanism by which temperature influences reproduction (Ingram and Mount, 1975).

Continued exposure to elevated ambient temperature delayed puberty in gilts (Flowers et al., 1989) and heifers (Dale et al., 1959). Madan and Johnson (1973) demonstrated that hyperthermia decreases preovulatory and basal concentrations of LH in Guernsey heifers. Similarly, Miller and Alliston (1974), found that the LH surge was detected in only 38% of the heifers exposed to elevated ambient temperature, while 88% of the animals exposed to a thermoneutral environment had normal LH surges during the day of estrus. It has also been shown that increasing ambient temperature increased basal concentrations of prolactin but not growth hormone in prepubertal heifers (Wettemann and Tucker, 1974; Tucker and Wettemann, 1976).

It is generally accepted that the sweat glands are the main avenue of heat dissipation and body temperature regulation in cows (McDowell et al., 1961; McLean, 1963; Amakiri, 1974). Differences in sweating rates between breeds have been observed (Schleger and Turner, 1965; Amakiri and Onwuka, 1980; Finch et al., 1982). When exposed to the same environment, *Bos indicus* are subjected to less heat stress than *Bos taurus*, because external characteristics reduce the effect of the environmental heat load on the animal more effectively (Gatenby, 1986). Dale et al. (1959) observed that age at puberty in Santa Gertrudis heifers was not affected by increasing environmental temperature, but Shorthorn heifers exposed to 27 C required 137 more days to reach puberty than heifers adapted to 10 C.

Social interactions. In many species, the onset of puberty in females is influenced by the social environment (Levin and Johnston, 1986). For example, if female mice (*Mus musculus*) were exposed to an adult male, the onset of puberty was accelerated compared with females housed alone (Vandenbergh, 1967, 1976). In addition, suppression of sexual maturation of young females by their mothers or by other socially dominant adult females, has been suggested in the wolf (*Canis lupis*) and the rhesus monkey (*Macaca mulatta*) (Levin and Johnston, 1986). The presence of a male accelerated puberty in domestic female pigs (*Sus scrofa*). Gilts that were exposed to a boar reached puberty at an early age than gilts reared without being exposed to a boar (Brooks and Cole, 1970; Zimmerman et al., 1974; Thompson and Savage, 1978; Pearce and Hughes, 1987; Pearce et al., 1988).

The social organization of different species of hamsters can accelerate or delay puberty. This is an adaptative characteristic and may be correlated with the degree of gregariousness of a specie (Levin and Johnston, 1986).

Cattle have a gregarious social organization, but the effect of males on the onset of puberty in females is not well understood. Roberson et al. (1987) reported that the presence of mature bulls for 152 days did not alter the proportions of beef heifers reaching puberty. However, Pennel et al. (1986) found that using epididectomized mature bulls for 70 days, increased the percent of heifers with estrous cycles at the beginning of the breeding season. More recently, Roberson et al. (1991b) concluded that exposure of prepubertal heifers to bulls increases the proportions of heifers attaining puberty between 12 and 14 months of age. They also found a significant interaction between the growth rate of heifers and the bull effect, indicating that the stimulatory influence of bull exposure was greater within the high growth rate heifers than within the moderate growth group.

Results from studies designed to evaluate the social interaction between prepubertal heifers with a group of estrous heifers showed that the percentage of animals exhibiting estrus was the same for heifers reared with estrous females and for heifers that remain isolated (Roberson et al., 1983).

Izard and Vandenbergh (1982) studied the role of pheromones in the acceleration of the onset of ovarian activity. Prepubertal heifers treated with bull urine reached puberty early than those treated with water, supporting the hypothesis that there is a priming pheromone in bull urine that can hasten the onset of puberty in beef heifers.

The effect of bull exposure on accelerating the onset of ovarian activity may be beneficial to reproductive management, "but the role of pheromonal or other allelomimetic cues in the acceleration of the onset of cyclic ovarian function at puberty remains to be determined in the bovine" (Roberson et al., 1991b).

Nutritional regulation of cessation and initiation of estrous cycles in beef cows

The effect of nutrition on reproductive performance in beef cows has been recognized for many years. Several reviews have described the nutritional influences on reproduction (Lamond, 1970; Dunn and Kaltenbach, 1980; Wettemann, 1980; Short and Adams, 1988; Randel, 1990; Short et al., 1990). The most important finding in these reviews is that undernutrition affects postpartum rebreeding, modifies normal estrous cycles and extends the period from parturition to estrus. The mechanism by which undernutrition causes anestrus in cattle remains unclear.

Weight and Body Condition. Body weight (BW) and condition score (BCS) are indicators of energy status. First-calf beef cows calving with greater BCS returned to estrus and became pregnant earlier than cows with lesser BCS (Spitzer et al., 1991). Reduced energy or protein intake, before or after calving, reduced pregnancy rates and extends the postpartum interval in cows (Randel, 1990).

Reduced nutrient intake is associated with loss of BW which in turn is manifested in loss of BCS, decreased luteal activity and cessation of estrous cycles. Nonlactating Hereford cows fed to lose 1% of their initial weight each week, became anestrus after 182 days of a restricted diet (Richards et al., 1989a). At this time, cows had lost 100 kg (24% of their initial weight) and had a BCS of 3.5 (35% less of their initial BCS). Similarly, Bishop et al. (1990) using the same feeding schedule, found that Hereford and Hereford x Angus cows weighing 469 kg and with a BCS of 5.5, became anestrus at a BCS of 3.1 (44% less than their initial BCS) and had lost 113 kg (24% of their initial weight). Comparable results have been found for dairy heifers (Johnson et al., 1987), gilts (Armstrong and Britt, 1987) and ewes (Tatman et al., 1990).

Short et al. (1990) reviewed several works and estimated that estrous cycles could be maintained if BCS is 4 or greater, although this may differ depending on other factors such as breed and whether an animal is entering into or coming out of anestrus.

Fertile estrous cycles can be reinitiated, after nutritionally induced anestrus, by increased nutrient intake. Richards et al. (1989a) found that at the resumption of estrous cycles, cows weighed 88% of their initial BW and had a condition score that was 85% of their initial BCS. Imakawa et al. (1986a) found that postpubertal Angus x Hereford heifers reinitiated ovarian luteal activity at 452 kg (33% more than their initial weight). These findings and those of Louw et al. (1988) suggest that greater body fat reserves are required to reinitiate estrus cycles than to maintain cycles in cows that are losing weight (Richards et al., 1989a).

Endocrine changes. The effects of nutritional restriction during the estrous cycle on the ovarian, pituitary and hypothalamic function have been studied in cattle (Staigmiller et al., 1979; McCann and Hansel, 1986; Imakawa et al., 1986b; Richards et al., 1989a) gilts (Armstrong and Britt 1987) and ewes (Tatman et al., 1990). Results on the effects of underfeeding on serum concentrations of progesterone during the estrous cycle are not in agreement. Hill et al. (1970) found that heifers exhibiting normal estrous cycles and receiving 85% of the estimated daily maintenance requirement of energy and protein, had reduced concentrations of progesterone in plasma within 5 days. Similarly, heifers receiving 62% of their total TDN requirements had significantly reduced concentrations of progesterone in plasma during the second and third estrous cycles (Gombe and Hansel 1973). However, Apgar et al. (1975) described an experiment in which the dietary treatment was the same as that used by Gombe and Hansel (1973) but they found that progesterone concentrations in plasma were only slightly affected. In another experiment, concentrations of progesterone in plasma were consistently greater for cows fed restricted diets than for control cows

(Donaldson et al., 1970; Dunn et al., 1974). In all of these experiments, the body condition and age of cows, as well as the type of management and/or duration of restricted feeding were different, making it difficult to make comparisons or to formulate conclusions.

When heifers were fed submaintenance diets for seven consecutive estrous cycles (Imakawa et al., 1983), there was a decrease in both, concentrations of progesterone in serum and production of progesterone *in vitro* by CL tissue. However, concentrations of progesterone in serum during the last cycle before cessation of cyclic activity did not differ from previous cycles. These results indicate that cycle length and progesterone concentrations during the estrous cycle prior to cessation of cyclic activity are not different from previous cycles.

The "pseudohypophysectomy" theory developed by Mulinos and Pomerantz (1940), as a possible explanation for ovarian hypofunction under reduced energy intake, needs to be clarified. The effect of feed restriction on luteinizing hormone (LH) have discrepancies among experiments. Gombe and Hansel (1973), found that ovarian hypofunction under conditions of restricted energy intake is not due to reduced concentration LH in serum, since plasma LH in energy-restricted animals was significantly elevated, rather than depressed. On the other hand, dietary energy restriction did not affect (Hill et al., 1970; Spitzer et al., 1978 Staigmiller et al., 1982) or significantly decreased (Apgar et al., 1975; Imakawa et al., 1984) concentrations of LH in serum.

The alteration in the pattern of gonadotropin secretion in heifers fed diets with reduced energy content are dependent on direction of BW change (Roberson et al., 1991a). Beef heifers with either decreasing followed by increasing BW (D-I) or increasing followed by decreasing BW (I-D) had similar concentrations of LH in serum. Frequency of LH pulses increased as BW increased in heifers receiving D-I and I-D treatment. LH amplitude decline as BW increased, but this decline was greater in heifers receiving the D-I than heifers receiving the I-D treatment. Rasby et al. (1991) suggested that nutritional restriction in nonpregnant Hereford cows did not influence pituitary LH content after GnRH injection, but influenced the release of LH from the hypophysis, since thin cows had greater concentrations of LH in serum after GnRH than did moderate or fat cows.

Follicle-stimulating hormone (FSH), is probably not a limiting factor during postpartum anestrus, since the number of FSH receptors were not different in weaned or suckled anestrus postpartum cows (Walters et al., 1982) and FSH concentrations did not change at different days after parturition (Moss et al., 1985; Cermak et al., 1983). However Roberson et al. (1991a) observed that heifers that were losing BW had increased concentrations of FSH in serum compared with heifers that were gaining BW. These data do not support the hypothesis that restriction of dietary energy in female lambs suppresses the frequency of discharge of GnRH from the hypothalamus (Foster et al., 1989).

<u>Glucose.</u> The major portion of glucose available to the ruminant has to be supplied by gluconeogenesis, since little glucose is normally absorbed from the gastrointestinal tract (Bergman et al., 1974; Huntington et al., 1981). Concentrations of glucose in plasma are affected by body condition score (Adams et al., 1987) and may influence reproductive performance in cattle. High demands for glucose occur during late pregnancy and early lactation in cows (Bickerstaffe et al, 1974; Baird et al., 1983) and animals with greater fertility had grater concentrations of glucose in plasma compared with less fertile cows (Selk, 1986).

The relation between hypoglycemia and infertility in lactating cows is well documented (Oxenreider and Wagner, 1971; Patil and Deshpande, 1979; Selk et al., 1985; McCann and Hansel, 1986; Richards et al., 1989b). Reduced concentration of glucose in blood (less than 30 mg/100ml) are common in infertile cows and the inhibition of glycolysis is associated with the lack of estrous and failure of formation of functional corpora lutea (McClure, 1968; McClure et al., 1978).

Concentrations of glucose in plasma can be increased by infusion of glucose into cows (Garmendia, 1986; McCaughey et al., 1988; Sano et al., 1991). Anestrous cows infused with glucose had significantly more pulses of LH (Garmendia, 1986). Increasing glucose availability, via infusion of propionate into the abomasum in Brangus heifers, increased LH secretion in response to exogenous GnRH (Rutter et al., 1983). Controversially, McCaughey et al. (1988) working with Hereford-cross cows, reported that the infusion of glucose did not alter either LH concentration or LH pulse frequency and pulse duration. On the other hand, hypoglycemia alters gonadotropin secretion, resulting in inadequate concentrations of LH in serum to stimulate normal reproductive function (Rutter and Manns, 1987; Richards et al., 1989b). Glucose is the primary source of energy for the brain tissue, so it is probable that hypoglycemia may depress hypothalamic function (Howland et al., 1966). Inhibitors of both glycolysis and oxidative phosphorylation inhibited stimulation by GnRH of LH release in a time and dose dependent manner, indicating that GnRH stimulated LH release is dependent on an energy process (Sen et al., 1979).

Insulin. Insulin is a 5.8-kd protein hormone, secreted by the ß cells of the pancreas and is stimulated by glucose and the parasympathetic nervous system (Stryer, 1988). Insulin increases the rate of synthesis of glycogen and promotes the entry of glucose into muscle and fat cells. Hence, the level of glucose in the blood is reduced by insulin (Stryer, 1988).

The role of insulin in the regulation of GnRH, LH and FSH secretion has been demonstrated in rat pituitary preparations *in vitro* (Sen et al., 1979; Adashi et al., 1981), indicating that insulin may act either directly on the anterior pituitary or stimulates glucose metabolism in neural tissues, regulating the release of hypothalamic releasing factors (van Houten et al., 1979).

Energy restriction decreased insulin concentrations in heifers (Harrison and Randel, 1986; McCann and Hansel, 1986) and cows (Richards et al., 1989b), while hyperinsulinemia exists in obese heifers and sheep (McCann and Reimers, 1986; McCann et al., 1990).

The mechanism by which insulin influences reproduction has not been determined. Exogenous administration of insulin increased ovulation rate in energy restricted heifers (Harrison and Randel, 1986) but did not affect ovulation rate in ewes (Beam and Holcombe, 1990). Administration of insulin to gilts increased the number of small follicles and reduced the numbers of atretic follicles. However, systemic LH and FSH were not affected by insulin treatment (Matamoros et al., 1991). Similarly, Garmendia (1986) reported that concentrations of insulin were increased in cows treated with glucose, but the treatment did not affect LH secretion.

Conclusions

Age at puberty is an important trait in beef herds and may be influenced by level of nutrition, body weight, body condition, breed, photoperiod, temperature and social environment. Insufficient energy and protein intake delay puberty and cause anestrus in heifers, but the mechanism by which nutrition influences reproduction has not been established. Concentrations of glucose in the blood could be a factor that mediates the effect of nutrition on reproductive performance of beef heifers.

CHAPTER III

RELATIONSHIP BETWEEN THE OCCURRENCE OF PUBERTY IN HEIFERS AND THE CESSATION OF LUTEAL ACTIVITY AFTER NUTRITIONAL RESTRICTION

Abstract

The relationship between the occurrence of puberty with the cessation of luteal activity after nutritional restriction was evaluated in fifteen Angus x Hereford heifers. Heifers attained puberty at a body weight of 297 ± 6 kg and a BCS of 5.5 ± .1. After 154 ± 16 d of nutritional restriction, heifers became anestrus at a weight of 273 ± 8 kg and a BCS of 3.0 ± .2. The Spearman's rank correlation coefficient between date of puberty and date of cessation of luteal activity was ($r=-.49$; $P<.06$). This indicates that the heifers that attained puberty first were the last to cease luteal activity during nutritional restriction.

Introduction

Age at the onset of puberty is a major limitation for efficient beef production. Age and body weight at puberty in beef heifers is influenced by plane of nutrition (Arije and Wiltbank, 1971; Grass et al., 1982; Patterson et al., 1991), breed (Wiltbank et al., 1966; Warnick et al., 1990; Patterson et al., 1991), photoperiod (Little et al., 1981; Hansen et al., 1983; Hauser, 1984), temperature (Dale et al., 1959; Ludri, 1983; Collier et al., 1982) and social environment (Pennel et al., 1986; Roberson et al., 1987, 1991b).

Nutritional management is the major factor that limits or control reproduction. Heifers fed high energy diets reach puberty at an earlier age and are heavier than those fed low energy diets (Bellows et al., 1967; Wiltbank et al., 1969; Arije and Wiltbank, 1971; Grass et al., 1982; Patterson et al., 1991). The mechanism by which nutrition influences reproduction in cows has not been established, but it is documented that body weight and body condition influence reproductive performance (Wiltbank et al., 1966; Short and Bellows, 1971; Selk et al., 1988). Reduced nutrient intake is associated with loss of BW which in turn is manifested in changes in BCS, decreased luteal activity and cessation of estrous cycles (Richards et al., 1989a; Bishop et al., 1990).

The objective of this study was to evaluate the relationship between the occurrence of puberty with the cessation of luteal activity after nutritional restriction.

Materials and Methods

Fifteen Angus x Hereford heifers born in the spring of 1988 were fed a complete diet to supply NRC (1976) requirements from 8 months of age until puberty. Heifers were maintained in individual (5 x 10 m) outside pens and exposed to the natural photoperiod. About 3 months after all heifers exhibited normal luteal activity, nutritional anestrus was induced by feeding a limited diet of 3 kg of low quality hay per day. Body weights (BW) were determined every 14 d before and after the onset of puberty. Body condition scores (BCS: 1= emaciated, 9=obese; Wagner et al., 1988), were measured biweekly after the onset of puberty.

Blood samples were taken biweekly via venipuncture before puberty and weekly after puberty. 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).

Onset of puberty was considered to have occurred at the first blood sample when concentrations of progesterone were greater than 1 ng/ml. Cessation of ovarian luteal activity was indicated by concentrations of progesterone less than 1 ng/ml for more than one week.

Analyses of regression and correlation were performed between BW and BCS with the percentage of heifers with luteal activity. Angular transformation of the percentages was used (Steel and Torrie, 1980). Spearman's coefficients were used to calculate the rank correlation between dates at birth, puberty and cessation of luteal activity (SAS, 1985).

Results and Discussion

Heifers attained puberty at 423 ± 8 d of age. At this time, heifers weighed 297 ± 6 kg and had a body condition score of 5.5 ± .1. Heifers in this study were slightly heavier and older at puberty than the Angus x Hereford reported by Wiltbank et al., (1966); and Stewart et al., (1980) but BCS were less than for the heifers reported by Yelich et al., (1991).

At 3.5 months after the average date of puberty, at which time all heifers had exhibited at least one normal luteal cycle, diets were restricted to 3 kg of low quality hay per day to induce anestrus. Nutritional restriction was associated with loss of BW (1.1 ± .0% of their initial BW per week) and BCS (1.9 ± .0% of their initial BCS per week), and cessation of luteal activity (Figure 1). For each kg of BW that heifers lost, there was a decrease of .5% in the percentage of animals with luteal activity ($P < .001$), and for each unit loss of BCS, there was a decrease of 17% in the percentage of animals with luteal activity ($P < .001$).

At the initiation of nutritional restriction, heifers weighted 356 ± 3 kg and had a BCS of 5.4 ± .1. Luteal activity, ceased after diets of heifers were restricted for 154 ± 16 d. At the onset of anestrus, heifers weighed 273 ± 8 kg and had a BCS of 3.0 ± .2. Heifers had lost 23.1 ± .1% of their initial BW and 43.4 ± .1% of their initial BCS, relative to the initiation of nutritional restriction. Richards et al. (1989a) found that cows fed to lose 1% of their initial weight each week, became anestrus after 182 d. At that time, cows had lost 24% of their initial body weight and 43% of their initial BCS . Similarly, Imakawa et al. (1986a) found that heifers became anestrus 185 d after nutritional restriction (50% of energy requirement) and it was associated with a 20% loss of initial BW.

Although heifers were 316 ± 21 d older at the onset of anestrus than at puberty, they weighted 7.5 ± .1% less ($P < .02$) and had 44.4 ± .1% less BCS ($P < .01$) (Figure 2).

The number of days of restricted feeding to induce anestrus is summarized in Figure 3. Heifers were divided into three groups based on the number of days to puberty after the start of the evaluation of pubertal cycles. Heifers that initiated luteal activity during the first month that luteal activity was evaluated (early), required 185 d of nutritional restriction to become anestrus (n=8). Heifers that started ovarian cycles during 28 to 48 d of the study (moderate) required 136 d (n=3), and the animals that started cycling last (greater than day 48 of the evaluation period) needed 106 d (n=4) to stop cycling. Body weights and body condition scores did not differ between groups at the initiation of nutritional restriction or at the onset of anestrus (Table 1). However, the daily weight loss was greater in the "late" group compared with the "early" group.

Spearman's rank correlation coefficients were computed between dates of birth, puberty and anestrous (Table 2). The non significant correlation between date of birth and date of puberty indicates that heifers attained puberty independent of age. The significant negative correlation between date at puberty and date at cessation of estrous cycles, indicates that the heifers that first attained puberty were the last to cease luteal activity during nutritional restriction.

Implication

Identification of heifers that initiate puberty at a younger age may represent animals with the ability to continue estrous cycles with reduced nutrient intake.

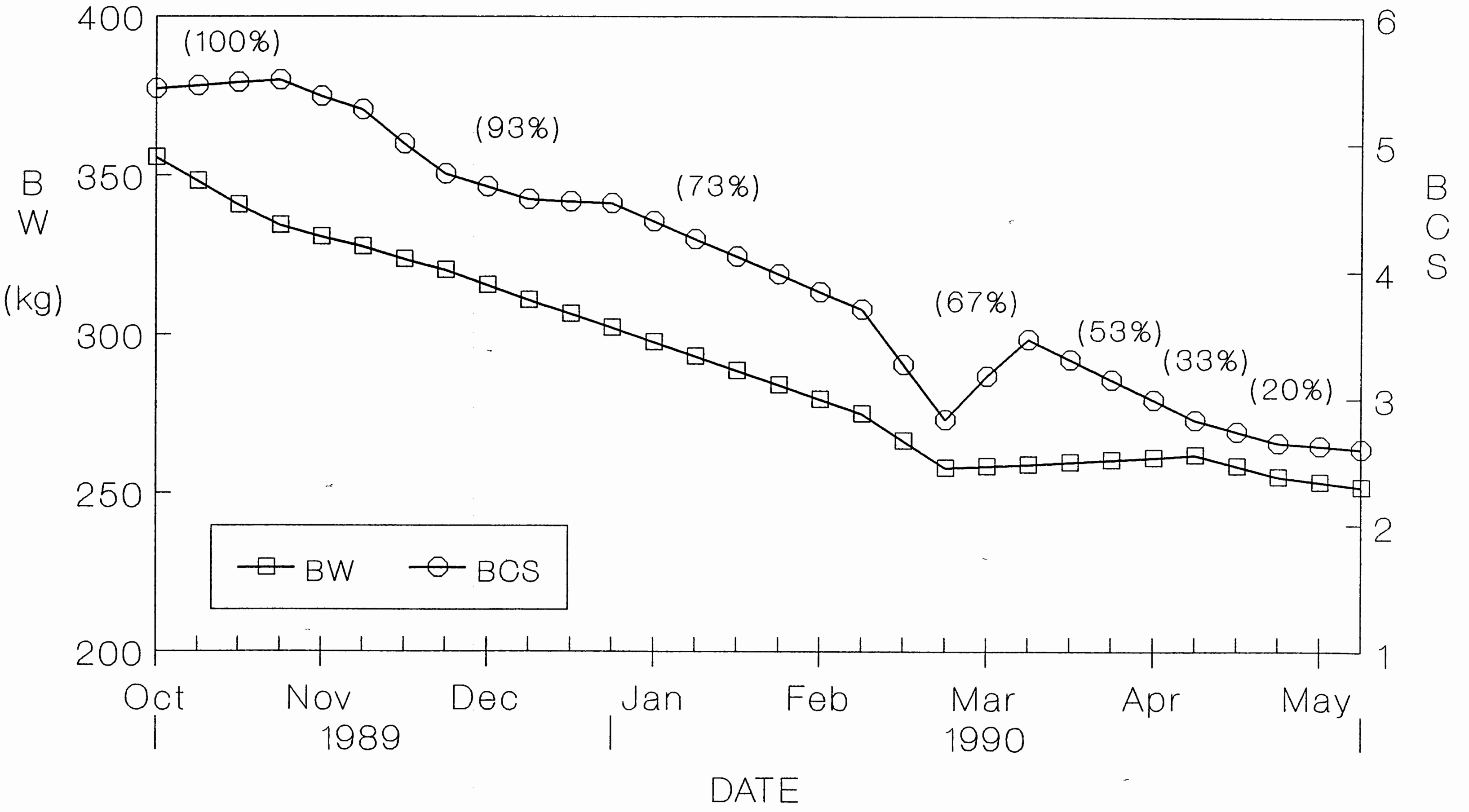

Figure 1. BW, BCS and percentage of heifers with luteal activity (in parentheses) during nutritional restriction.

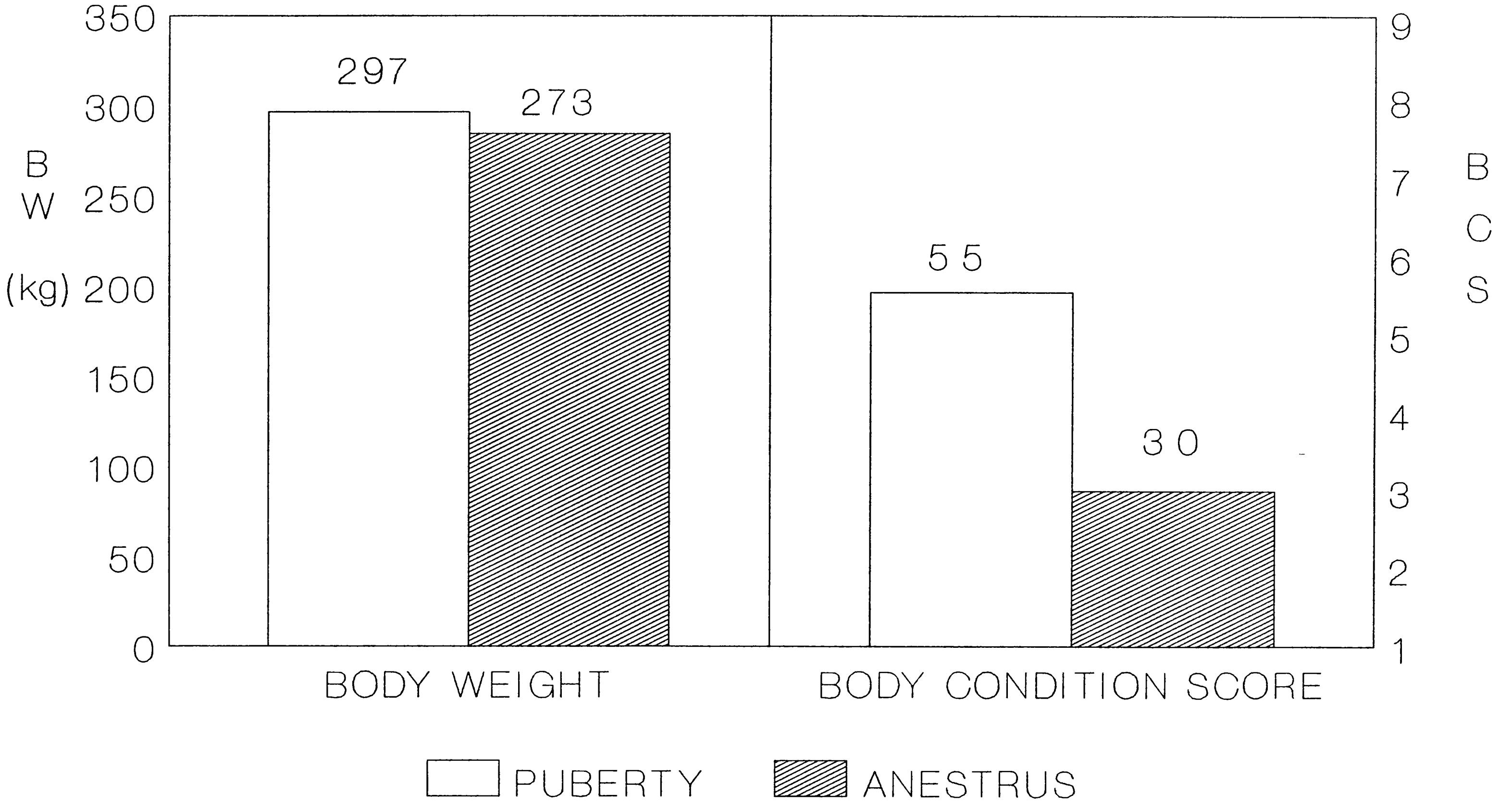

Figure 2. BW and BCS of heifers at puberty and at anestrus

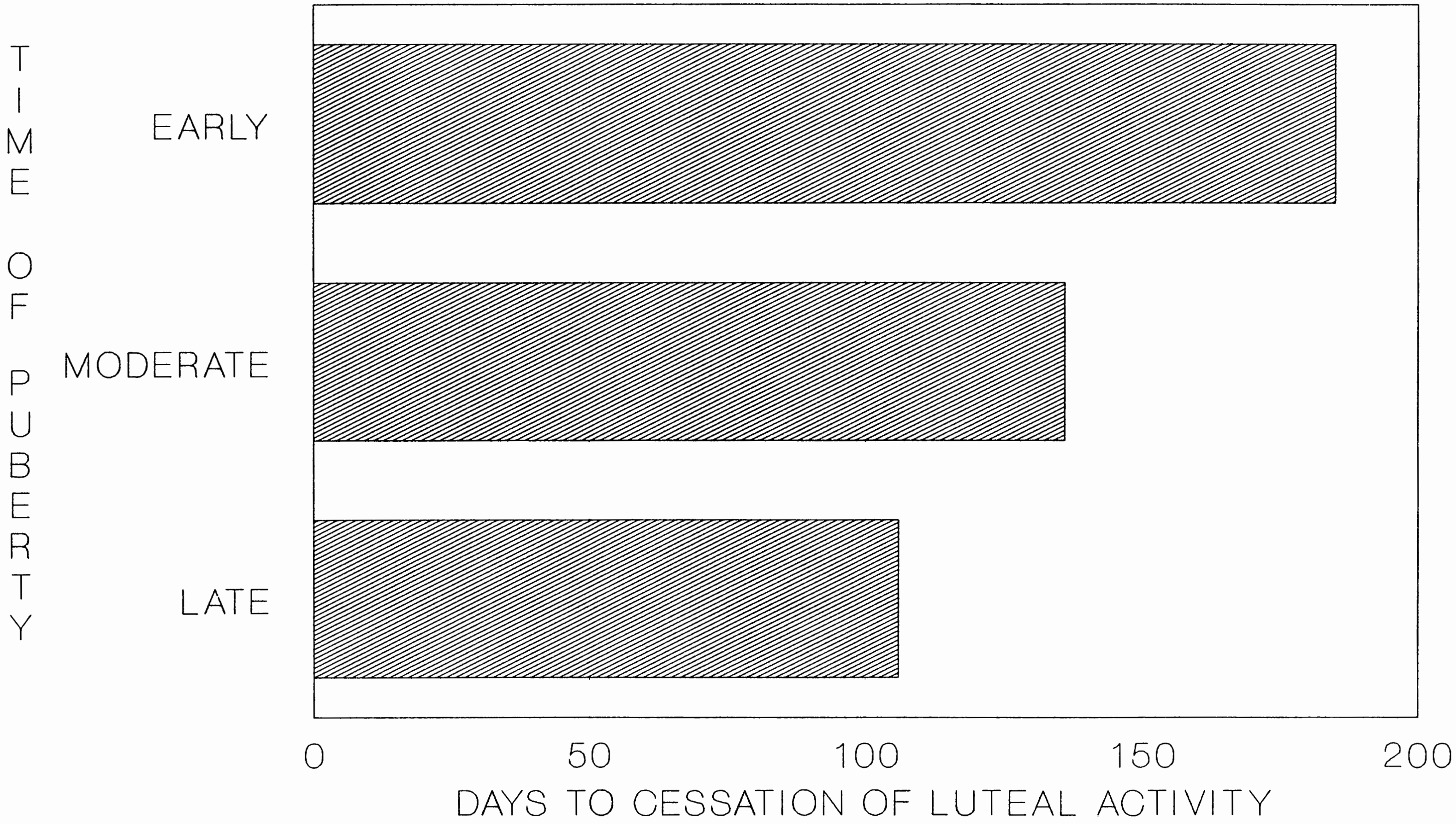

Figure 3. Relationship between time of puberty and days of nutritional restriction until the cessation of luteal activity.

Table 1. Body weight (BW) and body condition score (BCS) of heifers at initiation of nutritional restriction and at anestrus.

	Time of Puberty			
Characteristic	Early	Moderate	Late	Pooled S.E.
Initial BW, kg	354	352	362	11
Initial BCS	5.6	5.2	5.3	.3
Total BW loss to anestrus, kg	88	74	78	23
Daily BW loss to anestrus, kg	.47[a]	.58[ab]	.76[b]	.09
BCS loss to anestrus	2.9	2.0	1.8	.8

[ab] Means with different superscripts differ (P < .01)

Table 2. Spearman correlation coefficients between dates of birth, puberty and anestrus.

	Date at Puberty	Date at Anestrous
Date of birth	.01 (.99)[a]	-.29 (.30)
Date at puberty	-- --	-.49 (.06)

[a] Significances in parentheses

CHAPTER IV

INFLUENCE OF CDL (COBALT DEXTROSE LACTONE) ON OVARIAN ACTIVITY AND PLASMA GLUCOSE IN NUTRITIONALLY INDUCED ANESTROUS HEIFERS DURING RE-ALIMENTATION

Abstract

Fifteen nutritionally anestrus Angus x Hereford heifers were blocked in pairs and fed native grass hay *ad libitum* and 1.5 kg of a 30% CP supplement 5 days a week. One heifer in each pair received CDL (42 mg of cobalt per day) at the time that the protein supplement was administered. Concentrations of progesterone and glucose were determined in weekly blood samples. Blood samples were also obtained every 1 h for 6 h on Day 14 after initiation of re-alimentation to evaluate concentrations of glucose in plasma. Re-alimentation was associated with increased BW and BCS. No differences were found in BW or BCS gain between control and heifers fed CDL. Luteal activity occurred in half of the control heifers by day 122 of the experiment, while 50% of the CDL treated heifers did not initiate estrous cycles until 163 d ($P < .03$). Treatment

with CDL did not influence concentrations of glucose in plasma of heifers on day 14 or in weekly samples. Increased nutrient intake was associated with increased concentrations of glucose in plasma during refeeding.

Introduction

Reduced nutrient intake is associated with loss of BW which in turn is manifested in changes in BCS, decreased luteal activity and cessation of estrous cycles (Richards et al., 1989a). Estrous cycles in nonlactating cows can be maintained if BCS is 4 or greater, although this may differ depending on other factors such as breed, climate and age (Short et al., 1990).

Luteal activity can be reinitiated, after nutritional anestrus, by increased nutrient intake. Richards et al. (1989a) found that at the resumption of estrous cycles, cows weighed 53 kg more than at the onset of anestrus and had a body condition score of 4.6 compared to 3.1 at anestrus. These findings and those of Louw et al., (1988) and Imakawa et al., (1986a) suggest that greater body fat reserves are required to reinitiate estrus cycles than to maintain cycles in cows that are losing weight (Richards et al., 1989a).

Concentrations of glucose in plasma may influence reproductive performance in cattle. High demands for glucose occur during late pregnancy and early lactation in cows (Bickerstaffe et al, 1974; Baird et al., 1983) and animals with greater fertility had greater concentrations of glucose in blood compared with less fertile cows (Selk, 1986).

Progesterone synthesis in Holstein heifers can be increased by increasing glucose availability, both *in vivo* and *in vitro*, (Lynn et al., 1965). Concentrations of glucose in plasma can be increased by infusion of glucose into cows (Garmendia, 1986; McCaughey et al., 1988; Sano et al., 1991). Anestrous cows infused with glucose had increased concentrations of LH in serum (Garmendia, 1986). Conversely, McCaughey et al. (1988), working with Hereford-cross cows, reported that infusion of glucose did not alter concentration or LH in serum, frequency of LH pulses or duration of LH pulses.

CDL (Cobalt Dextrose Lactone), has been used to increase plasma glucose in beef cows (Bishop et al., 1991). Treatment with CDL increased concentrations of glucose in plasma of non-pregnant cows but did not alter reproductive performance when fed post partum.

Objectives of this study were to determine if the use of CDL can increase concentrations of glucose in plasma and hasten the initiation of ovarian activity in nutritional anestrous heifers during re-alimentation.

Materials and Methods

Nutritional anestrus was induced in fifteen Angus x Hereford heifers by feeding 3 kg of low quality hay per day. After normal luteal activity had ceased, heifers were re-alimented and blocked in pairs according to body weight (BW) body condition score (BCS) and duration of anestrus. Heifers were kept in a drylot with shade and were allowed *ad libitum* access to native grass hay and fed 1.5 kg of a 30% CP supplement 5 days per week. One heifer in each pair received CDL^{TM} (Cobalt Dextrose Lactone: .60% cobalt; Agro-K; Minneapolis, MN) at the time (0900 h) that the protein supplement was individually fed to animals. It was administered (7.04 g of CDL premix containing 42 mg of cobalt) in 100 g of soybean meal per day, 5 days per week. On the average, heifers received .14 mg of cobalt per kg of BW each day.

BW and BCS (BCS: 1 = emaciated, 9 = obese; Wagner et al., 1988) were determined every 14 days during re-alimentation. Feed and water were denied for 16 h prior to weighing. Blood samples were taken weekly at 0800 h before and after the onset of anestrus. Oxalic acid (1.25 mg) was added to each 10 ml sample and samples were cooled to 4 C. Samples were centrifuged (3000 x g for 20 min) within 4 h and plasma was decanted and stored at -20 C until progesterone and glucose concentrations were quantified. Blood samples were also obtained on Day 14 after initiation of re-alimentation. Commencing at 0800 h, blood samples were obtained at 1 h interval, beginning 1 h before feeding, and for 5 h after feeding the protein supplement.

Progesterone was determined by radioimmunoassay (Lusby et al., 1981). Cessation of ovarian luteal activity was indicated by concentrations of progesterone less than 1 ng/ml for more than 1 wk. Onset of ovarian luteal activity was considered to have occurred at the first of two successive samples when concentrations of progesterone were greater than 1 ng/ml. Glucose was quantified in all weekly plasma samples, and in samples taken on Day 14 of treatment, by an enzymatic colorimetric procedure (Glucose No. 510, Sigma Chemical Co., St. Louis, MO.).

Analyses of variance were used to evaluate effects of treatment on BW, BCS and days of refeeding to re-initiation of luteal activity (SAS, 1985). A simple logistic regression function ($E\{Y\} = [1 + \exp(-\beta_0 - \beta_1 X)]^{-1}$) was used to evaluate the relationship between day of refeeding and the percentage of heifers with luteal activity (Neter et al., 1989). Split-plot analyses of variance were used to analyze plasma glucose concentrations, in which treatment was the main plot and date or time of sample was the sub plot (SAS, 1985). A weighted regression of date of refeeding on plasma glucose concentrations was also performed (Neter et al., 1989).

Results and Discussion

Re-alimentation was associated with increased BW (2.1 ± .0% of the initial BW per week) and BCS (3.8 ± .0% of the initial BCS per week) of heifers. BW and BCS gains were similar ($P > .10$) for control and CDL treated heifers and the means for both treatments are shown in Figure 4.

At the onset of anestrus, heifers weighed 273 ± 8 kg and had a BCS of 3.0 ± .2. Feeding CDL tended to influence the BW ($P < .11$) and BCS ($P < .20$) at the re-initiation of estrous cycles. Estrous cycles were re-initiated in control heifers at 343 ± 10 kg and at a BCS of 4.1 ± .2. CDL treated heifers, were slightly heavier (365 ± 7 kg) and had a slightly greater BCS (4.5 ± .3) than control heifers at the re-initiation of cycles (Figure 5).

Heifers weighted 30% more and had 43% more BCS at the re-initiation of luteal activity as compared to at the onset of anestrus ($P < .001$). Richards et al. (1989a) found that restricted cows initiated anestrus with a BCS of 3.1 and a BW of 321 kg. After 63 d of rapid regain of weight, cows re-initiate luteal activity with a BCS of 4.6 and a BW of 374 kg. Similarly, Imakawa et al. (1986a) observed that restricted heifers became anestrus at a BW of 270 Kg and after 49 d of high energy feeding, heifers reinitiate luteal activity at a BW of 350 kg.

Luteal activity occurred in control heifers after 122 ± 14 d of refeeding, while the onset of luteal activity did not occur in CDL treated animals until 163 ± 6 d ($P < .03$; Figure 6). The two logistic regression functions, differed significantly ($P < .01$) in the intercept ($b_0 = -4.8 \pm .7$ and -17.5 ± 2.4 for control an CDL respectively), and in the slope ($b_1 = .04 \pm .01$ and $.11 \pm .02$ for control an CDL respectively), indicating that control heifers started luteal activity earlier than CDL treated heifers but the percentage of heifers with luteal activity increased more rapidly in CDL treated heifers than in control heifers. When multiparus lactating Hereford and Hereford x Angus cows, grazing native range pastures, were fed either protein supplement (control) or protein supplement plus CDL, diet did not influence luteal activity within 85 d postpartum (Bishop et al., 1991). In the present study, we do not know why days to initiation of luteal activity was greater for CDL treated than for control heifers.

Concentrations of glucose in acute samples on day 14 of refeeding were not influenced by CDL treatment (table 3). Time of day did not influence ($P > .10$) concentration of glucose in plasma.

Concentrations of glucose in weekly plasma samples during refeeding were not influenced ($P > .10$) by treatments (Figure 7). There was a significant increase in glucose concentrations during the refeeding period but the day x treatment interaction was not significant ($P > .10$). Glucose concentrations increased from an average of 59 mg% on day 0 to 69 mg% at the end of the refeeding period (P <

.001). The average increase in plasma glucose was .05 mg% for each day of refeeding. Richards et al. (1989b) found that re-alimentation, of nutritionally anestrous Hereford cows, was related to increased plasma glucose and re-initiation of normal estrous cycles. When pregnant, non lactating beef cows were fed CDL, concentrations of glucose in plasma were grater than in control animals, but CDL did no alter postpartum reproduction performance (Bishop et al., 1991).

Implication

Increased nutrient intake is associated with increased concentrations of glucose in plasma. Estrous cycles are re-initiated in nutritionally anestrous heifers at a greater BCS and BW than those at which anestrous occurs. CDL consumption did not influence concentrations of glucose during re-alimentation of nutritionally anestrous cows, however, the onset of luteal activity was delayed. Less feed may be needed to maintain estrous cycles in heifers, rather than to allow heifers to become nutritionally anestrus and then feed animals to re-initiate cycles.

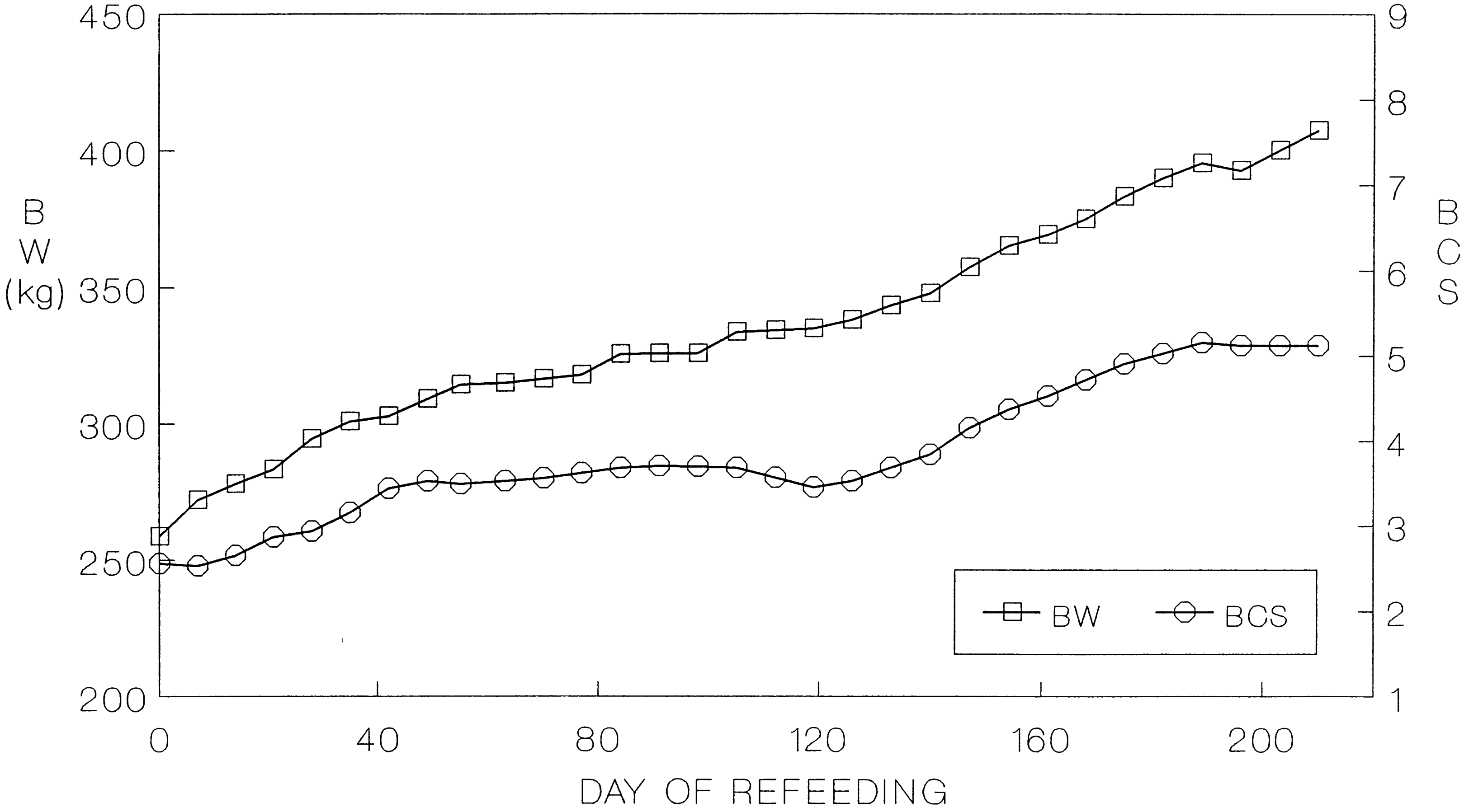

Figure 4. BW and BCS during re-alimentation of nutritional anestrous heifers.

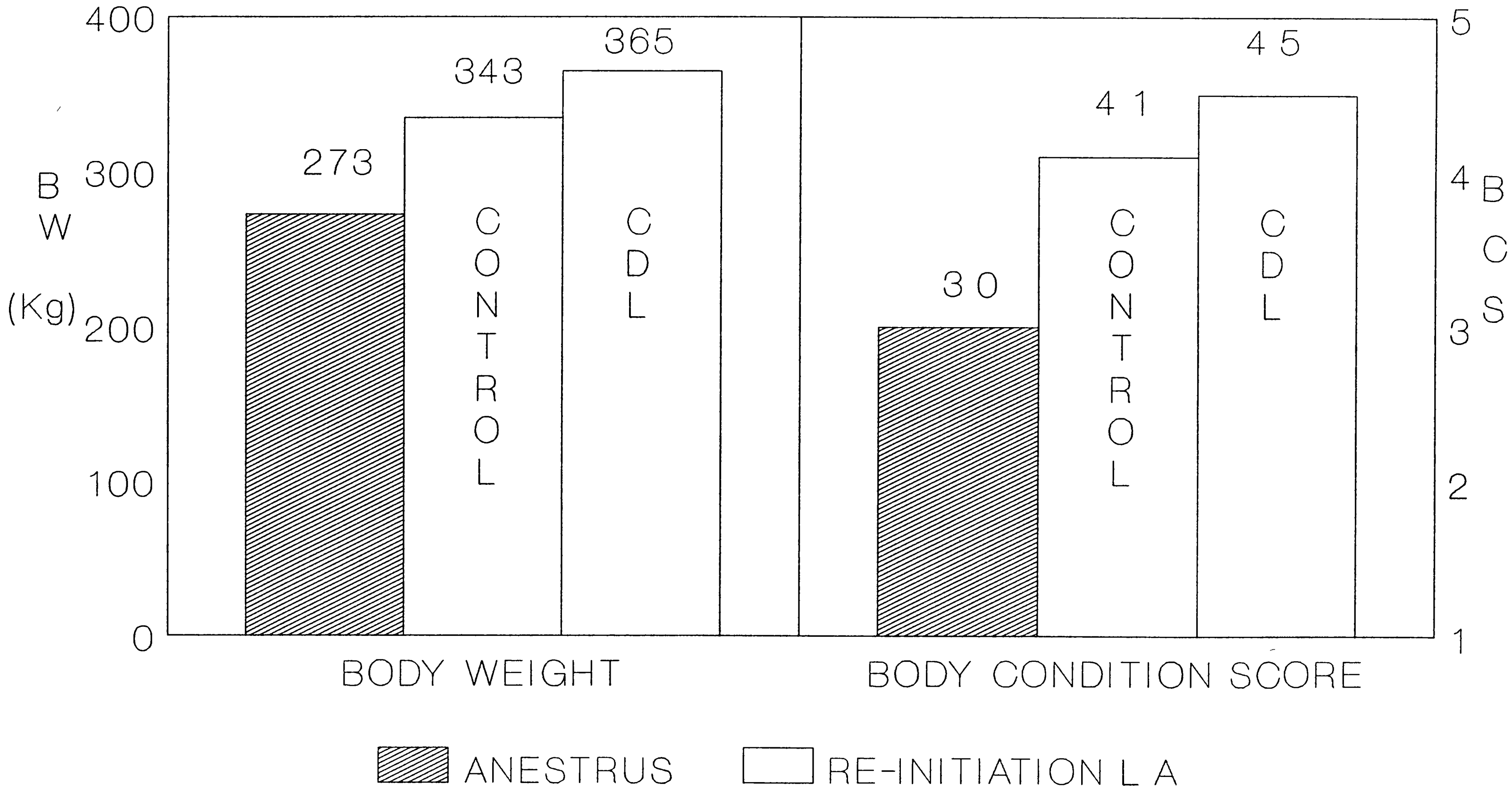

Figure 5. BW and BCS of heifers at anestrus and at re-initiation of luteal activity.

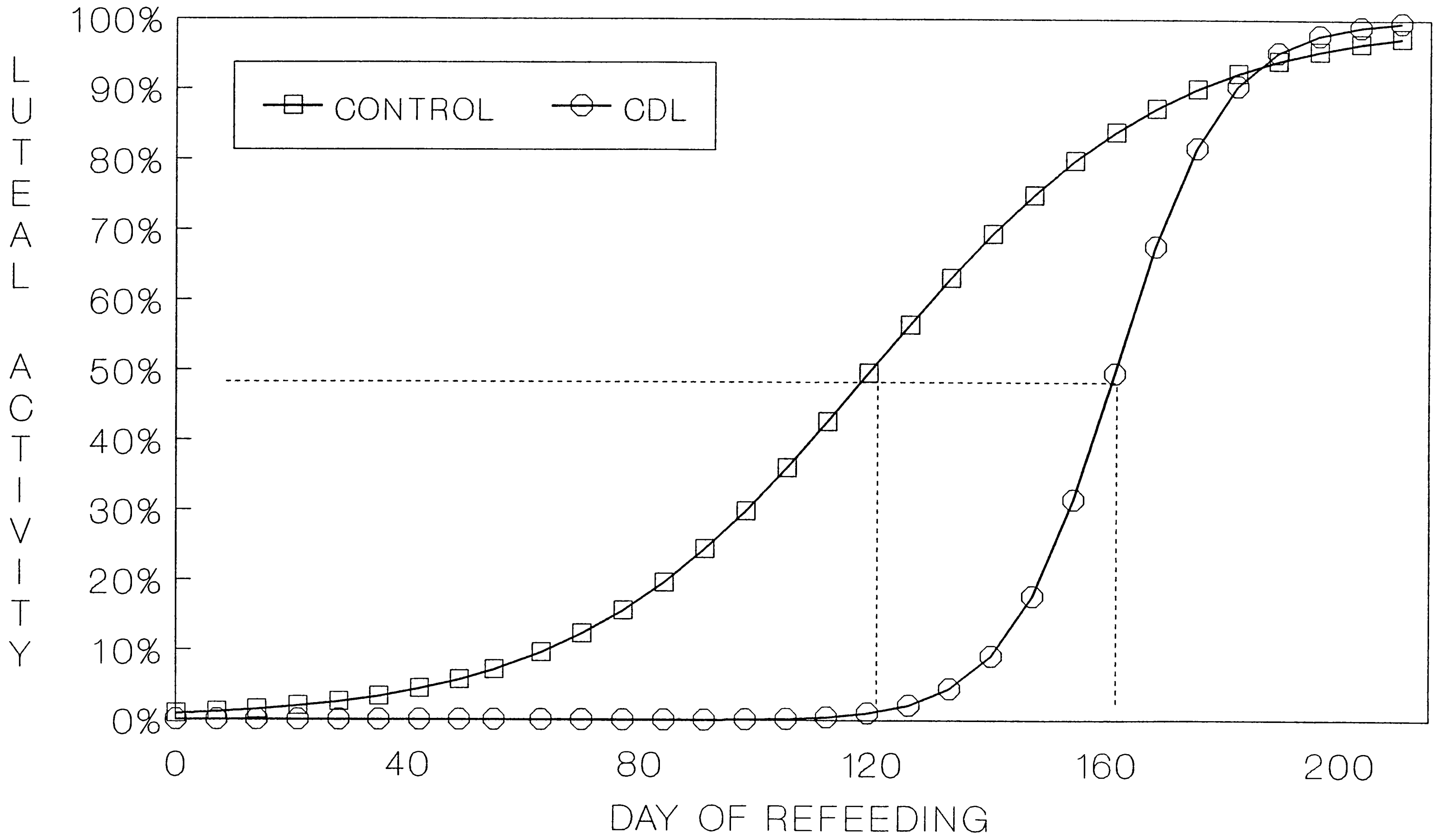

Figure 6. Logistic regression function between heifers with luteal activity and day of refeeding.

Table 3. Concentrations of glucose (mg%) in plasma of control and CDL heifers on day 14 of re-alimentation.

TREATMENT	TIME[a]						
	0	1	2	3	4	5	6
CONTROL	57.0	56.7	56.8	56.3	60.1	55.8	60.3
CDL	52.7	50.1	52.7	51.5	54.5	55.4	53.3

[a] Hours after first sample. Heifers were fed a protein supplement after the first sample (MSE = 41.1).

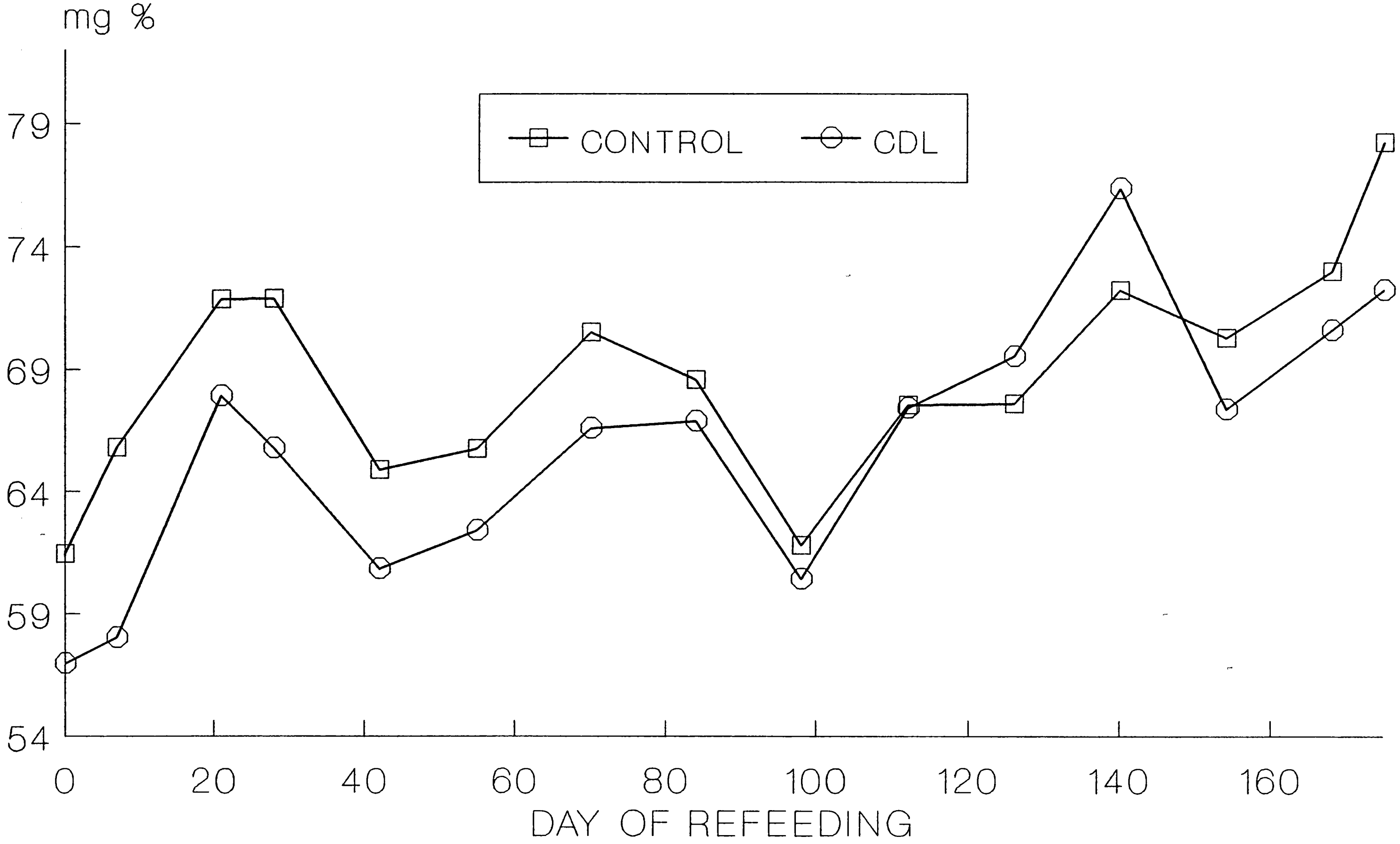

Figure 7. Concentrations of glucose in plasm during re-alimentation of nutritionally induced anestrous heifers.

CHAPTER V

SUMMARY AND CONCLUSIONS

Age at puberty is a major limiting factor for efficient beef production. Nutritional restriction may delay the onset of puberty and can cause anestrus in heifers that are exhibiting normal estrous cycles. The mechanism by which nutrition causes anestrus in cattle has not been established, but it has been demonstrated that body energy reserves control reproductive performance in cows (Selk et al., 1988; Spitzer et al., 1991).

Fifteen Angus x Hereford heifers were fed a complete diet from 8 mo until puberty. After all the heifers exhibited normal estrous cycles, nutritional anestrus was induced by feeding a limited hay diet. Blood samples were taken biweekly before puberty and weekly after puberty. Concentrations of progesterone were determined by radioimmunoassay. Onset of puberty was considered to have occurred at the first sample when concentrations of progesterone were greater than 1 ng/ml. Cessation of ovarian luteal activity was indicated by concentrations of progesterone less than 1 ng/ml for more than 1 wk.

Heifers attained puberty at a body weight (BW) of 297 ± 6 kg and a body condition score (BCS) of 5.5 ± .1. Nutritional restriction was associated with loss of BW, BCS and cessation of luteal activity. Estrous cycles ceased after diets of heifers were restricted for 154 ± 16 d. At that time, heifers weighed 273 ± 8 kg and had a BCS of 3.0 ± .2. Although heifers were 316 ± 21 d older at the onset of anestrus than at puberty, they weighted 7.5 ± .1% less ($P < .02$) and had 44.4 ± .1% less BCS ($P < .01$).

A Spearman's rank correlation coefficient was computed between date of puberty and date of cessation of luteal activity. The correlation of -.49 ($P < .06$) indicates that the heifers that first attained puberty were the last to cease luteal activity during nutritional restriction. These results indicate that the identification of heifers that initiate puberty at a younger age may represent animals with the ability to continue estrous cycles during reduced nutrient intake.

Fertile estrous cycles can be reinitiated, after nutritionally induced anestrus by increased nutrient intake. Resumption of luteal activity is associated with increased BW and BCS. Glucose may be the energy mediator for the resumption and maintenance of estrous cycles (Richards et al., 1989a, 1989b).

Fifteen nutritional anestrous Angus x Hereford heifers, were blocked in pairs and re-alimented. Heifers were fed native grass hay and 1.5 kg of a 30% crude protein supplement 5 d a week. One heifer in each pair received CDL (42 mg of cobalt per day) at the same time that the protein supplement was fed. Concentrations of progesterone and glucose were determined in weekly blood samples. Blood samples were also obtained every 1 h for 6 h on Day 14 after initiation of re-alimentation to evaluate concentrations of glucose in plasma.

Re-alimentation was associated with increased BW and BCS. Increases in BW and BCS gain were similar for control and heifers fed CDL. On the average, heifers weighted 30% more and had 43% more BCS at the re-initiation of luteal activity as compared to the onset of anestrus ($P < .001$). Luteal activity occurred in half of the control heifers at 122 d while CDL treated animals required 163 d ($P < .03$) to reinitiate luteal activity.

Concentrations of glucose in control and CDL heifers were similar during d 14 of feeding and in weekly plasma samples. Increased nutrient intake was associated with increased concentrations of glucose. Feeding CDL did not improve, and may have delayed, the re-initiation of estrous cycles of nutritionally anestrous heifers.

LITERATURE CITED

Adams, D.C., R.E. Short and V.W. Knapp. 1987. Body size and body condition effects on performance and behavior of grazing beef cows. Nutr. Rep. Int. 35:269.

Adashi, E.Y., A.J.W. Hsueh and S.S.C. Yen. 1981. Insulin enhancement of luteinizing hormone and follicle-stimulating hormone release by cultured pituitary cells. Endocrinology 108:1441.

Amakiri, S.F. 1974. Sweat gland measurement in some tropical and temperate breeds of cattle in Nigeria. Anim. Prod. 18:285.

Amakiri, S.F. and S.K. Onwuka. 1980. Quantitative studies of sweating rate in some cattle breeds in a humid tropical environment. Anim. Prod. 30:383.

Apgar, J., D. Aspros, J.E. Hixon, R.R. Saatman and W. Hansel. 1975. Effect of restricted feed intake on the sensitivity of the bovine corpus luteum to LH in vitro. J. Anim. Sci. 41(4):1975.

Arije, G.F. and J.N. Wiltbank. 1971. Age and weight at puberty in Hereford heifers. J. Anim. Sci. 33(2):401.

Armstrong, J.D. and J.H. Britt. 1987. Nutritionally-induced anestrus in gilts: Metabolic and endocrine changes associated with cessation and resumption of estrous cycles. J. Anim. Sci. 65:508.

Baird, G.D., J.G. Van Der Walt and E.N. Bergman. 1983. Whole-body metabolism of glucose and lactate in productive sheep and cows. British Journal of Nutrition 50:249.

Beal, W.E., R.E. Short, R.B. Staigmiller, R.A. Bellows, C.C. Kaltenbach and T.G. Dunn. 1978. Influence of dietary energy intake on bovine pituitary and luteal function. J. Anim. Sci. 46(1):181.

Beam, S.W. and D.W. Holcombe. 1990. Reproductive and hormonal responses in ewe lambs administered insulin during follicular growth. J. Anim. Sci. 60(Suppl. 1):178.

Bellows, R.A., O.O. Thomas, T.M. Riley, R.B. Gibson, N.M. Kieffer, J.J. Urick and O.F. Pahnish. 1967. Feed effects on puberty in beef heifers. J. Anim. Sci. 24:588(Abstr.).

Bergman, E.N., R.P. Brockman and C.F. Kaufman. 1974. Glucose metabolism in ruminants: comparison of whole-body turnover with production by gut, liver, and kidneys. Federation proceedings 33:1849.

Bickerstaffe, R., E.F. Annison and J.L. Linzell. 1974. The metabolism of glucose, acetate, lipids and amino acids in lactating dairy cows. J.Agric. Sci (Camb.) 82:71.

Bishop, D.K., R.P. Wettemann, K.S. Lusby and J.W. Castree. 1991. Concentrations of glucose in plasma and reproductive performance of beef cows fed CDL (cobalt). J. Anim. Sci. 69(Suppl. 1):43.

Bishop, D.K., R.P. Wettemann and C.M. O'Connell. 1990. Pulsatile infusion of GnRH initiates luteal activity in nutritional anestrous beef cows. J. Anim. Sci. 68(suppl. 1):416.

Brooks, P.H. and D.J.A. Cole. 1970. The effect of the presence of a boar on the attainment of puberty in gilts. J. Reprod. Fertil. 23:435.

Brooks, A.L., R.E. Morrow and R.S. Youngquist. 1985. Body composition of beef heifers at puberty. Theriogenology 24:235.

Bushmich, S.L., R.D. Randel, M.M. McCartor and L.H. Carroll. 1980. Effect of dietary monensin on ovarian response following gonadotropin treatment in prepuberal heifers. J. Anim. Sci. 51(3):692.

Cermak, D.L., T.Braden, J. Manns, G.D. Niswender and T.M. Nett. 1983. Contents of hypothalamic GnRH, pituitary FSH and LH, and pituitary receptors for GnRH and estradiol in postpartum suckled beef cows. J. Anim. Sci. 57(Suppl. 1):322.

Collier, R.J., S.G.Doelger, H.H. Head, W.W. Thatcher and C.J. Wilcox. 1982. Effects of heat stress during pregnancy on maternal hormone concentrations, calf birth weight and postpartum milk yield of Holstein cows. J. Anim Sci. 54(2):309.

Collier, R.J., R.M. Eley, A.K. Sharma, R.M. Pereira and D.E. Buffington. 1981. Shade management in subtropical environment for milk yield and composition in Holstein and Jersey Cows. J. Dairy Sci. 64:844.

Critser, J.K., T.M. Block, S. Folkman, and E.R. Hauser. 1987c. Effect of photoperiod on LH, FSH, prolactin and melatonin patterns in ovariectomized prepubertal heifers. J. Reprod. Fert. 81:29.

Critser, J.K., T.M. Block, B.W. Kirkpatrick, M.J. Lindstrom and E.R. Hauser. 1988. The effect of photoperiod on diurnal rhythms of serum gonadotropins, prolactin and melatonin in ovariectomized heifers. Domestic Animal Endocrinology 51(1):23.

Critser, J.K., M.M. Hinshelwood and E.R. Hauser. 1987a. The effect of exogenous melatonin administration on gonadotropin and prolactin patterns in ovariectomized estradiol-treated heifers exposed to increasing photoperiod. Theriogenology. 28(2):257.

Critser, J.K.; M.J. Lindstrom, M.M. Hinshelwood and E.R. Hauser. 1987b. Effect of photoperiod on LH, FSH and prolactin patterns in ovariectomized oestradiol-treated heifers. J. Reprod. Fert. 79:599.

Dale, H.E., A.C. Ragsdale and C.S. Cheng. 1959. Effect of constant environmental temperatures, 50 and 80 F., on appearance of puberty in beef calves. J. Anim. Sci. 18:1363.

Day, M.L., K. Imakawa, M. Garcia-Winder, D.D. Zalesky, B.D. Schanbacher, R.J. Kittok and J.E. Kinder. 1984. Endocrine mechanisms of puberty in heifers:Estradiol negative feedback regulation of luteinizing hormone secretion. Bio. Reprod. 31:332.

Day, M.L., K. Imakawa, P.L. Wolfe, R.J. Kittok and J.E. Kinder. 1987. Endocrine mechanisms of puberty in heifers. Role of hypothalamo-pituitary estradiol receptors in the negative feedback of estradiol on luteinizing hormone secretion. Bio. Reprod. 37:1054.

Day, M.L., K. Imakawa, D.D. Zalesky, R.J. Kittok and J.E. Kinder. 1986. Effects of restriction of dietary energy intake during the prepubertal period on secretion of luteinizing hormone and responsiveness of the pituitary to luteinizing hormone-releasing hormone in heifers. J. Anim. Sci. 62:1641.

Del Vecchio, R.P., D.A. Neuendorff, R.C. Stahringer and R.D. Randel. 1990. Progesterone, estrogen and 13,14-dihydro-15-keto-prostaglandin $F_{2}\alpha$ concentrations during the onset of puberty in dairy heifers. J. Anim. Sci. 68(suppl. 1):18.

Dinius, D.A., M.E. Simpson and O,B. Marsh. 1976. Effect of monensin fed with forage on digestion and the ruminal ecosystem of steers. J. Anim. Sci. 42:229.

Dodson, S.E., B.J. McLeod, W. Harseign, A.R. Peters and G.E. Lamming. 1988. Endocrine changes from birth to puberty in the heifer. J. Reprod. Fert. 82:527.

Donaldson, L.E. 1968. The pattern of pregnancies and life-time productivity of cows in a Northern Queensland beef cattle herd. Australian Vet. J. 44:493.

Donaldson, L.E., J.M. Basset and G.D. Thorburn. 1970. Peripheral plasma progesterone concentration of cows during puberty, oestrous cycles, pregnancy and lactation and the effects of undernutrition or exogenous oxytocin on progesterone concentration. J. Endocrinol. 48:599.

Dunn, T.G., and C.C. Kaltenbach. 1980. Nutrition and the postpartum interval of the ewe, sow and cow. J. Anim. Sci. 51(Suppl. 2):29.

Dunn, T.G., J. Rone, C.C. Kaltenbach, L.A. van der Walt, M.L. Riley and A.M. Akbar. 1974. Hormone changes during underfeeding of beef cows. J. Anim. Sci. 39:206(Abstr.).

Earle, D. 1976. A guide to scoring dairy cow condition. The Journal of Agriculture for the Farmers of Victoria 74(7):228.

Ferrell, C.L.. 1982. Effects of postweaning rate of gain on onset of puberty and productive performance of heifers of different breeds. J. Anim. Sci. 55:1272.

Finch, V.A., I.L. Bennett and C.R. Holmes. 1982. Sweating response in cattle and its relation to rectal temperature, tolerance of sun and metabolic rate. J. Agric. Sci. Camb. 99:479.

Flowers, B., T.C. Cantley, M.J. Martin and B.N. Day. 1989. Effect of elevated ambient temperatures on puberty in gilts. J. Anim. Sci. 67:779.

Foster, D.L., F.J.P. Ebling, A.F. Micka, L.A. Vannerson, D.C. Bucholtz, R.I. Wood, J.M. Suttie and D.E. Fenner. 1989. Metabolic interface between growth and reproduction. I. Nutritional modulation of gonadotropin, prolactin, and growth hormone secretion in the growth-limited female lamb. Endocrinology 125:342.

Frisch, R.E., D.M. Hegsted and K. Yoshinaga. 1977. Carcass components at first estrus of rats on high-fat and low-fat diets:Body water, protein, and fat. Proc. Natl. Acad. Sci. 74(1):379.

Frisch, R.E. and R. Revelle. 1970. Weight at menarche and an hypothesis of weight and adolescent events. Science 169:397.

Garmendia, J.C. 1986. Energy metabolites in blood, luteinizing hormone secretion and reproductive performance of beef cows. Ph.D. Thesis. Oklahoma State University, Stillwater.

Gatenby, R.M. 1986. Exponential relation between sweat rate and skin temperature in hot climates. J. Agric. Sci. Camb. 106:175.

Gombe, S. and W. Hansel. 1973. Plasma luteinizing hormone (LH) progesterone levels in heifers on restricted energy intakes. J. Anim. Sci. 37(3):728.

Gonzalez-Padilla, E., J.N. Wiltbank and G.D. Niswender. 1975. Puberty in beef heifers. 1. The interrelationship between pituitary, hypothalamic and ovarian hormones. J. Anim. Sci. 40:1091.

Grainger, G. and A.A. McGowan. 1982. The significance of precalving nutrition of the dairy cow. In: Conference on dairy production from pasture. Proceedings. pp. 135-171.

Grass, J.A., P.J. Hansen, J.J. Rutledge and E.R. Hauser. 1982. Genotype x environmental interactions on reproductive traits of bovine females. I. Age at puberty as influenced by breed, breed of sire, dietary regimen and season. J. Anim. Sci. 55(6):1441.

Gregory, K.E., D.B. Laster, L.V. Cundiff, R.M. Koch and G.M. Smith. 1978. Heterosis and breed maternal and transmitted effects in beef cattle II. Growth rate and puberty in females. J. Anim. Sci. 47(5):1042.

Gregory, K.E., L.A. Swinger, R.M. Koch, L.J. Sumption, J.E. Ingalls, W.W. Rowden and J.A. Rothlisberger. 1966. Heterosis effects on growth rate of beef heifers. J. Anim. Sci. 25:290.

Hansen, P.J., L.A. Kamwanja and E.R. Hauser. 1983. Photoperiod influences age at puberty of heifers. J. Anim. Sci. 57(4):985.

Harrison, L.M. and R.D. Randel. 1986. Influence of insulin and energy intake on ovulation rate, luteinizing hormone and progesterone in beef heifers. J. Anim. Sci. 63:1128.

Hauser, E.R. 1984. Seasonal effects on female reproduction in the bovine (*Bos taurus*). Theriogenology 21(1):150.

Hawk, H.W., W.J. Tyler and L.E. Casida. 1954. Some factors affecting age at puberty in Holstein-Friesian heifers. J. Dairy Sci. 37:252.

Hill, J.R.(Jr.), D.R. Lamond. D.M. Henricks, J.F. Dickey and G.D. Niswender. 1970. The effects of undernutrition on ovarian function and fertility in beef heifers. Biol. Reprod. 2:78.

Howland, B.E., R.L. Kirkpatrick, A.L. Pope and L.E. Casida. 1966. Pituitary and ovarian function in ewes fed on two nutritional levels. J. Anim. Sci. 25:716.

Huntington, G.B., R.L. Prior and R.A. Britton. 1981. Glucose and lactate absorption and metabolic interrelationships in steers changed from low to high concentrate diets. J. Nutr. 111:1164.

Imakawa, K., M.L. Day, M. Garcia-Winder, D.D. Zalesky, R.J. Kittok, B.D. Schanbacher and J.E. Kinder. 1986a. Endocrine changes during restoration of estrous cycles following induction of anestrous by restricted nutrient intake in beef heifers. J. Anim. Sci. 63:565.

Imakawa, K., M.L. Day, D.D. Zalesky, M. Garcia-Winder, R.J. Kittok and J.E. Kinder. 1986b. Influence of dietary-induced weight changes on serum luteinizing hormone, estrogen and progesterone in the bovine female. Biol. Reprod. 35:377.

Imakawa, K., R.J. Kittok and J.E. Kinder. 1983. The influence of dietary energy intake on progesterone concentrations in beef heifers. J. Anim. Sci. 56(2):454.

Imakawa, K., R.J. Kittok and J.E. Kinder. 1984. Luteinizing hormone secretion after withdrawal of exogenous progestogen in heifers fed three levels of dietary energy. J. Anim. Sci. 58(1):151.

Ingram, D.L. and L.E. Mount. 1975. Man and animals in hot environment. Springer Verlag New York Inc.

Izard, M.K.and J.G. Vandenbergh. 1982. The effects of bull urine on puberty and calving date in crossbreed beef heifers. J. Anim. Sci. 55(5):1160.

Jainudeen, M.R.and E.S.E. Hafez. 1987. Cattle and water buffalo. In: E.S.E. Hafez (Ed.) Reproduction in farm animals. pp 297-314. Lea & Febiger Philadelphia.

Johnson, H.D. 1965. Environmental temperature and lactation (with special reference to cattle). Int. J. Biometeor. 9(2):103.

Johnson, M.S., T.N. Wegner and D.E. Ray. 1987. Effect of elevating serum lipids on luteinizing hormone response to gonadotropin releasing hormone challenge in energy-deficient anestrous heifers. Theriogenology 27:421.

Jones, E.J., J.D. Armstrong and R.W. Harvey. 1991. Changes in metabolites, metabolic hormones, and luteinizing hormone before puberty in Angus, Braford, Charolais, and Simmental heifers. J. Anim. Sci. 69(4):1607.

Kaltenbach, C.C. and J.N. Wiltbank. 1962. Heterotic effects on age and weight at puberty in beef heifers. J. Anim. Sci. 21:662(Abs).

Kamwanja, L.A., K.K. Schillo, P.J. Hansen, E.R. Hauser and D.J. Dierschke. 1980. The influence of season on body weight, growth rate and feed consumption as related to puberty in heifers. J. Anim. Sci. 51(Suppl. 1):289.

Kinder, J.E., M.L. Day and R.J. Kittok. 1987. Endocrinology of puberty in cows and ewes. J. Reprod. Fert. Suppl. 34:167.

Lamond, D.R. 1970. The influence of undernutrition on reproduction in the cow. Animal Breeding Abstracts 38(3):359.

Laster, D.B., H.A. Glimp and K.E. Gregory. 1972. Age and weight at puberty and conception in different breeds and breed-crosses of beef heifers. J. Anim. Sci. 34:1031.

Laster, D.B., G.M. Smith, L.V. Cundiff and K.E. Gregory. 1979. Characterization of biological types of cattle(cycle II). II. Postweaning growth and puberty of heifers. J. Anim. Sci. 48:500.

Laster, D.B., G.M. Smith and K.E. Gregory. 1976. Characterization of biological types of cattle. IV. Postweaning growth and puberty of heifers. J. Anim. Sci. 43:63.

Lesmeister, J.L., P.J. Burfening and R.L. Blackwell. 1973. Date of first calving in beef cows and subsequent calf production. J. Anim. Sci. 36:1.

Levin, R.N. and R.E. Johnston. 1986. Social mediation of puberty: an adaptive female strategy? Behavioral and Neural Biology 46:308.

Little, W., C.B. Mallinson, D.N. Gibbons and G.J. Rowlands. 1981. Effects of plane of nutrition and season of birth on the age and body weight at puberty of British Friesian heifers. Anim. Prod. 33:273.

Louw, B.P., C.R. Thomas and A.W. Lishman. 1988. The influence of loss and gain of body mass on ovarian activity in beef cows. S. Afr. J. Anim. Sci. 18:1.

Ludri, R.S. 1983. Effect of hot-humid and cold climatic conditions on milk production, nutrient conversion efficiency and water requirement of cross-bred cows. Indian J. Anim. Sci. 53(8):812.

Lusby, K.S., R.P. Wettemann and E.J. Turman. 1981. Effects of early weaning calves from first-calf heifers on calf and heifer performance. J. Anim. Sci. 53:1193.

Lynn, J.E., W.E. Collins, E.K. Inskeep, W.H. McShan and L.E. Casida. 1965. Effects of gonadotropins, oxytocin and glucose on the bovine corpus luteum at the fourteenth day of the estrual cycle. J. Anim. Sci. 24:790.

MacNeil, M.D., L.V. Cundiff, C.A. Dinkel and R.M. Koch. 1984. Genetic correlations among sex-limited traits in beef cattle. J. Anim. Sci. 58(5):1171.

Madan, M.L. and H.D. Johnson. 1973. Environmental heat effects on bovine luteinizing hormone. J. Dairy Sci. 56:1420.

Matamoros, I.A., N.M. Cox and A.B. Moore. 1991. Effects of exogenous insulin and body condition on metabolic hormones and gonadotropin-induced follicular development in prepuberal gilts. J. Anim. Sci. 69(5):2081.

McBride, B.W. and J.M. Kelly. 1990. Energy cost of absorption and metabolism in the ruminant gastrointestinal tract and liver: a review. J. Anim. Sci. 68(9):2997.

McCann, J.P., D.L. Aalseth and J.R. Gavin III. 1990. Diverse metabolic actions of GH in sheep are dependent on body condition. J. Anim. Sci. 68(Suppl. 1):315.

McCann, J.P. and W. Hansel. 1986. Relationships between insulin and glucose metabolism and pituitary-ovarian functions in fasted heifers. Biol. Reprod. 34:630.

McCann, J.P. and T.J. Reimers. 1986. Effects of obesity on insulin and glucose metabolism in cyclic heifers. J. Anim. Sci. 62:772

McCartor, M.M., R.D. Randel and L.H. Carroll. 1979. Dietary alteration of ruminal fermentation on efficiency of growth and onset of puberty in Brangus heifers. J. Anim. Sci. 48:488.

McCaughey, W.P., L.M. Rutter and J.G. Manns. 1988. Effect of glucose infusion on metabolic and reproductive function in postpartum beef cows. Can. J. Anim. Sci. 68:1079.

McClure, T.J. 1968. Malnutrition and infertility of cattle in Australia and New Zealand. Australian Veterinary Journal 44:134.

McClure, T.J., C.D. Nancarrow and H.M. Radford. 1978. The effect of 2-Deoxy-D-glucose on ovarian function of cattle. Aust. J. Biol. Sci. 31:183.

McDowell, R.E., B.T. McDaniel, M.S. Barrada and D.H.K. Lee. 1961. Rate of surface evaporation from the normal body surface and with sweat glands inactivated under hot conditions. J. Anim. Sci. 20:380.

McGuire, M.A., R.J. Collier, F.C. Buonomo, D.K. Beede, M.A. DeLorenzo, C.J. Wilcox, G.B. Huntington and C.K. Reynolds. 1988. Effects of acute thermal stress and level of feeding on concentrations of somatotropin, insulin-like growth factors and thyroid hormones in plasma of Holstein cows. J. Anim. Sci. 66(suppl. 1): 511.

McLean, J.A. 1963. The regional distribution of cutaneous moisture vaporization in the Ayrshire calf. J. Agric. Sci. 61:275.

Menge, A.C., S.E. Mares, W.J. Tyler and L.E. Casida. 1960. Some factors affecting age at puberty and the first 90 days of lactation in Holstein heifers. J. Dairy Sci. 43:1099.

Miller, H.L. and C.W. Alliston. 1974. Influence of programmed circadian temperature changes upon levels of luteinizing hormone in the bovine. Biology of Reproduction 11:187.

Minton, J.E. 1986. Effects of heat stress on feed intake of beef cattle. Annu. Rep. Okla. Agric. Exp. Stn. 121:325.

Morris, C.A., R.L. Baker and G.L. Bennett. 1986. Some genetic and non-genetic effects on the first oestrus and pregnancy rate of beef heifers. Proceedings of the New Zeland society of Animal Production 46:71.

Morrison, S.R. and G.P. Lofgreen. 1979. Beef cattle responses to air temperature. Transactions of the ASAE. 22:861.

Moseley, W.M., M.M. McCartor and R.D. Randel. 1978. Effects of monensin on growth and reproductive performance of beef heifers. J. Anim. Sci. 45:961.

Moss, G.E., J.R. Parfet, C.A. Marvin, R.D. Allrich and M.A. Diekman. 1985. Pituitary concentrations of gonadotropins and receptors for GnRH in suckled beef cows at various intervals after calving. J. Anim. Sci. 60:285.

Mulinos, M.G. and L. Pomerantz. 1940. "Pseudo-hypophysectomy". A condition resembling hypophysectomy produced by malnutrition. J. Nutr. 19:393.

Neter, J., W. Wasserman and M.H. Kutner. 1989. Applied linear regression models (2nd Ed.). Richard D. Irwin, Inc.

NRC. 1976. Nutritional Requirements of Beef Cattle. (5th Rev. Ed.). National Academy of Sciences-National Research Council, Washington, DC.

Oxenreider, S.L. and W.C. Wagner. 1971. Effect of lactation and energy intake on postpartum ovarian activity in the cow. J. Anim. Sci. 33:1026.

Page, R.D., D.H. Keisler, R.L. Butcher, R.A. Dailey and E.K. Inskeep. 1987. Prepubertal and peripubertal changes in secretory patterns of LH and FSH in beef heifers. Animal Reproduction Science 14:85.

Patil, J.S. and B.R. Deshpande. 1979. Changes in body weight, blood glucose and serum proteins in relation to the appearance of post-partum oestrous in Gir cows. J. Reprod. Fert. 57:525.

Patterson, D.J., L.R. Corah, J.R. Brethour, M.F. Spire, J.J. Higgins, G.H. Kiracofe, J.S. Stevenson and D.D. Simms. 1991. Evaluation of reproductive traits in *Bos taurus* and *Bos indicus* crossbred heifers: effects of postweaning energy manipulation. J. Anim. Sci. 69(6):2349.

Pearce, G.P. and P.E. Hughes. 1987. The influence of boar-component stimuli on puberty attainment in the gilt. Anim. Prod. 44(2):293.

Pearce, G.P., P.E. Hughes and W.D. Booth. 1988. The involvement of boar submaxillary salivary gland secretion in boar-induced precocious puberty attainment in the gilt. Animal Reproduction Science 16(2):125.

Pennel, P.L., D.D. Zalesky, M.L. Day, M.W. Wolfe, T.T. Stumpf, S.M. Azzam, R.J. Kittok and J.E. Kinder. 1986. Influence of bull exposure on initiation of estrous cycles in prepubertal beef heifers. J. Anim. Sci. 63(Suppl. 1):129.

Peters, R.R. and H.A. Tucker. 1978. Prolactin and growth hormone response to photoperiod in heifers. Endocrinology 103:229.

Preston, T.R. and M.B. Willis. 1970. Genetic improvement. In: Intensive beef production. pp 105-165. Pergamon Press.

Ramirez, D.V. and S.M. McCann. 1963. Comparison of the regulation of luteinizing hormone (LH) secretion in immature and adult rats. Endocrinology 72:452.

Randel, R.D. 1990. Nutrition and postpartum rebreeding in cattle. J. Anim. Sci. 68(3):853.

Randel, R.D. and R.C. Rhodes III. 1980. The effect of dietary monensin on the luteinizing hormone response of prepuberal heifers given a multiple gonadotropin-releasing hormone challenge. J. Anim. Sci. 51:925.

Rasby, R.J., R.P. Wettemann, R.D. Geisert, J.J. Wagner and K.S. Lusby. 1991. Influence of nutrition and body condition on pituitary, ovarian, and thyroid function of nonlactating beef cows. J. Anim. Sci. 69(5):2073.

Rhodes III, R.C., M.M. McCartor and R.D. Randel. 1978. Effect of feeding protein-protected lipids upon growth and reproductive development of yearling heifers. J. Anim. Sci. 46:769.

Richards, M.W., J.C. Spitzer and M.B. Warner. 1986. Effect of varying levels of postpartum nutrition and body condition at calving on subsequent reproductive performance in beef cattle. J. Anim. Sci. 62(2):300.

Richards, M.W., R.P. Wettemann and H.M. Schoenemann. 1989a. Nutritional anestrous in beef cows: body weight change, body condition, luteinizing hormone in serum and ovarian activity. J. Anim. Sci. 67:1520.

Richards, M.W., R.P. Wettemann and H.M. Schoenemann. 1989b. Nutritional anestrus in beef cows: concentrations of glucose and nonesterified fatty acids in plasma and insulin in serum. J. Anim. Sci. 67:2354.

Riumallo, J. and J.V.G.A. Durnin. 1988. Changes in body composition in adolescent boys. European journal of clinical nutrition 42:107.

Roberson, M.S., R.P. Ansotegui, J.G. Berandinelli, R.W. Whitman and M.J. McInerney. 1987. Influence of biostimulation by mature bulls on occurrence of puberty in beef heifers. J. Anim. Sci. 64:1601.

Roberson, M.S., J.G. Berandinelli, R.P. Ansotegui and R.W. Whitman. 1983. Influence of prostoglandin $F_{2\alpha}$ and social interaction on induction of first estrous in beef heifers. J. Anim. Sci. 57(Suppl. 1):407.

Roberson, M.S., T.T. Stumpf, M.W. Wolfe, R.J. Kittok and J.E. Kinder. 1991a. Influence of direction of body weight change on pattern of gonadotropin secretion in ovariectomized beef heifers of equivalent body weight. J. Anim. Sci. 69(4):1616.

Roberson, M.S., M.W. Wolfe, T.T. Stumpf, A.S. Cupp, N. Kojima, L.A. Werth, R.J. Kittok and J.E. Kinder. 1990. Influence of body condition and restriction of dietary energy on secretion of gonadotropins in beef heifers. J. Anim. Sci. 68(suppl. 1):438.

Roberson, M.S., M.W. Wolfe, T.T. Stumpf, L.A. Werth, A.S. Cupp, N. Kojima, P.L. Wolfe, R.J. Kittok and J.E. Kinder. 1991b. Influence of growth rate and exposure to bulls on age at puberty in beef heifers. J. Anim. Sci. 69(5):2092.

Roy, J.H.B., C.M. Gillies, M.W. Perfitt and I.J.F. Stobo. 1980. Effect of season of the year and phase of the moon on puberty and on the occurrence of oestrus and conception in dairy heifers reared on high planes of nutrition. Anim. Prod. 31:13.

Rutter, L.M. and J.G. Manns. 1987. Hypoglycemia alters pulsatile luteinizing hormone secretion in the postpartum beef cow. J. Anim. Sci. 64:479.

Rutter, L.M., R.D. Randel, G.T. Schelling and D.W. Forrest. 1983. Effect of abomasal infusion of propionate on the GnRH-induced luteinizing hormone release in prepuberal heifers. J. Anim. Sci. 56(5):1167.

Sacco, R.E., J.F. Baker and T.C. Cartwright. 1987. Production characters of primiparous females of a five-breed diallel. J. Anim. Sci. 64:1612.

Sano, H., M. Nakai, T. Kondo and Y. Terashima. 1991. Insulin responsiveness to glucose and tissue responsiveness to insulin in lactating, pregnant, and nonpregnant, nonlactating beef cows. J. Anim. Sci. 69(3):1122.

SAS. 1985. SAS User's Guide: Statistics. SAS Inst., Inc., Cary, NC.

Scahms, D., E. Schallenberger, S. Gombe and H. Karg. 1981. Endocrine patterns associated with puberty in male and female cattle. J. Reprod. Fert., Suppl. 30:103.

Schillo, K.K., D.J. Dierschke and E.R. Hauser. 1982. Influence of month of birth and age on patterns of luteinizing hormone secretion in prepubertal heifers. Theriogenology 18(5):593.

Schillo. K.K., P.J. Hansen, L.A. Kamwanja, D.J. Diershke and E.R. Hauser. 1983. Influence of season on sexual development in heifers: Age at puberty as related to growth and serum concentrations of gonadotropins, prolactin, thyroxine, and progesterone. Biol. Reprod. 28:329.

Schleger, A.V. and H.G. Turner. 1965. Sweating rates in the field and their reaction to diurnal and seasonal changes. Aust. J. Agric. Res. 16:92.

Selk, G.E. 1986. The relationships of prepartum nutrition, body weight change, body condition score change, postpartum blood glucose and insulin with reproductive performance in beef cows. Ph.D. Thesis. Oklahoma State University, Stillwater.

Selk, G.E., R.P. Wettemann and K.S. Lusby. 1985. Plasma glucose and reproduction in postpartum range cows. J. Anim. Sci. 61(Suppl. 1):41.

Selk, G.E., R.P. Wettemann, K.S. Lusby, J.W. Oltjen, S.L. Mobley, R.J. Rasby and J.C. Garmendia. 1988. Relationships among weight change, body condition and reproductive performance of range beef cows. J. Anim. Sci. 66:3153.

Sen, K.K., S. Azhard and K.M.J. Menon. 1979. Evidence for the involvement of an energy-dependent process in gonadotropin-releasing hormone-stimulated luteinizing hormone release by rat anterior pituitary. Endocrinology 105:1158.

Short, R.E. and D.C. Adams. 1988. Nutritional and hormonal interrelationships in beef cattle reproduction. Can. J. Anim. Sci. 68:29.

Short, R.E. and R.A. Bellows. 1971. Relationships among weight gains, age at puberty and reproductive performance in heifers. J. Anim. Sci. 32:127.

Short, R.E., R.A. Bellows, R.B. Staigmiller, J.G. Berardinelli and E.E. Custer. 1990. Physiological mechanisms controlling anestrus and infertility in postpartum beef cattle. J. Anim. Sci. 68(3):799.

Siebert, B.D. and J.B.F. Field. 1975. Reproductive activity in beef heifers following post-weaning feeding on spear grass hay alone or with supplements. Australian J. Exp. Agri. and Anim. Hus. 15:12.

Spitzer, J.C., Morrison, D.G., R.P. Wettemann and W.C. Bridges (Jr.). 1991. Reproductive response of first-calf beef cows as affected by body condition at calving and postpartum weight gain. J. Anim. Sci. 69(Suppl. 1):42.

Spitzer, J.C., G.D. Niswender, G.E. Seidel,Jr. and J.N Wiltbank. 1978. Fertilization and blood levels of progesterone and LH in beef heifers on a restricted energy diet. J. Anim. Sci. 46(4):1071.

Staigmiller, R.B., B.G. England, R. Webb, R.E. Short and R.A. Bellows. 1982. Estrogen secretion and gonadotropin binding by individual bovine follicles during estrus. J. Anim. Sci. 55(6):1463.

Staigmiller, R.B., R.E. Short, R.A. Bellows and J.B. Carr. 1979. Effect of nutrition in response to exogenous FSH in beef cattle. J. Anim. Sci. 48(5):1182.

Stanisiewski, E.P., L.T. Chapin, N.K. Ames, S.A. Zinn and H.A. Tucker. 1988. Melatonin and prolactin concentrations in blood of cattle exposed to 8, 16 or 24 hours of daily light. J. Anim. Sci. 66:727.

Steel, R.G.D. and J.H. Torrie. 1980. Principles and Procedures of Statistics: A Biometrical Approach (2nd Ed.). McGraw-Hill Book Co., New York.

Stewart, T.S., C.R. Long and T.C. Cartwright. 1980. Characterization of cattle of a five-breed diallel. III. Puberty in bulls and heifers. J. Anim. Sci. 50:808.

Stryer, L. 1988. Integration of metabolism. In: Biochemistry. W.H. Freeman and Company. Third edition. New York. pp 627-645.

Tatman, W.R., M.B. Judkins, T.G. Dunn and G.E. Moss. 1990. Luteinizing hormone in nutrient-restricted ovariectomized ewes. J. Anim. Sci. 68(4):1097.

Thompson, L.H. and J.S. Savage. 1978. Age at puberty and ovulation rate in gilts in confinement as influenced by exposure to a boar. J. Anim. Sci. 47:1141.

Tucker, H.A. and R.P. Wettemann. 1976. Effects of ambient temperature and relative humidity on serum prolactin and growth hormone in heifers. Proc. Soc. Exp. Biol. and Med. 151:623.

van Houten, M., B.I. Posner, B.M. Kopriwa and J.R. Brawer. 1979. Insulin-binding sites in the rat brain: in vivo localization to the circumventricular organs by quantitative radiography. Endocrinology 105:666.

Vandenbergh, J.G.. 1967. Effect of the presence of a male on the sexual maturation of female mice. Endocrinology 81:345.

Vandenbergh, J.G. 1976. Acceleration of sexual maturation in female rats by male stimulation. Journal of reproduction and fertility 46:451.

Wagner, J.J., K.S. Lusby, J.W. Oltjen, J. Rakestraw, R.P. Wettemann and L.E. Walters. 1988. Carcass composition in mature Hereford cows: Estimation and effect on daily metabolizable energy requirement during winter. J. Anim. Sci. 66:603.

Walters, D.L., C.C. Kaltenbach, T.G. Dunn and R.E. Short. 1982. Pituitary and ovarian function in postpartum beef cows. I. Effect of suckling on serum and follicular fluid hormones and follicular gonadotropin receptors. Biol. Reprod. 26:640.

Ward, J.K., D. Richardson and W.S. Tsien. 1961. Volatile fatty acid concentrations and proportions in the gastrointestinal tract on full-feed beef heifers. J. Anim. Sci. 20:830.

Warnick, A.C., K.J. Senseman, T.A. Olson, A.C. Hammond and E.L. Adams. 1990. Puberty in Angus, Brahman, Hereford and Senepol heifers. J. Anim. Sci. 68(Suppl. 1):17.

Webley, G.E. and M.R. Luck. 1986. Melatonin directly stimulates the secretion of progesterone by human and bovine granulosa cells in vitro. J. Reprod. Fert. 78:711.

Webster's. 1988. Ninth new collegiate dictionary. Merriam-Webster Inc., Publishers Springfield, Massachusetts, U.S.A.

Wettemann, R.P. 1980. Postpartum endocrine function of cattle, sheep and swine. J. Anim. Sci. 51(Suppl. 2):2.

Wettemann, R.P. and H.A. Tucker. 1974. Relationship of Ambient temperature to serum prolactin in heifers. Proc. Soc. Exp. Biol. and Med. 146:908.

Wilcox, G.A., R.J. Pruitt, P.A. Momot and R.A. Pritchard. 1990. Effects of source of energy on age and weight at puberty of beef heifers. J. Anim. Sci. 68(Suppl. 1): 76.

Wiltbank, J.N., K.E. Gregory, L.A. Swiger, J.E. Ingalls, J.A. Rothlisberger and R.M. Koch. 1966. Effects of heterosis on age and weight at puberty in beef heifers. J. Anim. Sci. 25:744.

Wiltbank, J.N., C.W. Kasson and J.E. Ingalls. 1969. Puberty in crossbreed and straightbreed beef cattle on two levels of feed. J. Anim. Sci. 29:602.

Wiltbank, J.N., W.W. Rowden and J.E. Ingalls. 1959. The age and weight at puberty in Hereford heifers. J. Anim. Sci. 18:1562.

Yelich, J.V., R.P. Wettemann, K.S. Lusby, H.G. Dolezal and D.K. Bishop. 1991. Influence of growth rate on body composition of beef heifers at puberty. J. Anim. Sci. 69(Suppl. 1):41.

Zimmmerman, D.R., R. Carlson and B. Lantz. 1974. The influence of exposure to the boar and movement on pubertal development in the gilt. J. Anim. Sci. 39:230(Abstr.).

VITA

Jorge Antonio Vizcarra

Candidate for the Degree of

Master of Science

Thesis: FACTORS INFLUENCING REPRODUCTION OF BEEF HEIFERS: AGE AT PUBERTY, NUTRITIONAL ANESTRUS, GLUCOSE IN PLASMA AND CONSUMPTION OF COBALT

Major Field: Animal Science

Biographical:

Personal Data: Born in Montevideo, Uruguay; July 21, 1955, the son of Jacinto Antonio and Maria del Carmen Vizcarra.

Education: Received the Ingeniero Agronomo degree from the Facultad de Agronomia, Universidad de la Republica Oriental del Uruguay in July, 1981; completed the requirements for the Master of Science Degree Science at Oklahoma State University, December 1991.

Professional experience: Researcher, Instituto Nacional de Investigaciones Agricolas (INIA), 1981.

Professional Organizations: Association of Ingenieros Agronomos of Uruguay, American Society of Animal Science.