

The effects of ruminally undegradable protein, propionic acid and monensin on puberty and reproductive efficiency in beef heifers

by David Leon Lalman

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Animal Science
Montana State University
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Abstract:
Two hundred ten spring born crossbred beef heifers were used in two experiments conducted in consecutive years with a randomized complete block design. The objectives were to determine the effects of increasing the dietary intake of ruminally undegradable protein or propionic acid on the occurrence of puberty and to elucidate the mechanism of action for monensin on puberty in beef heifers. The experimental diets were fed for approximately 120 days beginning in mid-November and consisted of low quality grass hay and straw with: 1) .45 kg hd^-1 d^-1 supplement formulated to meet NRC (1984) recommendations for protein, vitamins, and minerals to obtain .4 kg gain per day (CON), 2) .5 kg supplement containing an additional 250 g hd^-1 d^-1 ruminally undegradable protein from blood meal and corn gluten meal (RUP) , 3) .45 kg supplement supplying 200 mg hd^-1 d^-1 monensin (MON), and 4) .45 kg supplement and 400 g hd^-1 d^-1 of a fifty percent water, fifty percent propionic acid mixture sprayed on the roughage mixture prior to feeding (PROP). The hay:straw ratio in each diet was adjusted biweekly as needed in order to maintain similar weight gains for heifers fed each diet. As planned, weight gain was similar ($P > .1$) for all treatments. MON fed heifers were 21 days younger at first estrus than RUP fed heifers ($P < .05$) with CON and PROP heifers being intermediate. RUP treated cattle were 7 and 8 kg heavier at puberty than CON or PROP treated cattle respectively ($P < .05$). PROP fed heifers were 6 kg heavier at puberty than MON fed heifers ($P < .1$). Heifers receiving RUP supplement required less TDN than did CON or PROP treated heifers ($P < .05$) to maintain same level of gain. MON fed heifers consumed more ruminally degradable protein than RUP fed heifers ($P < .05$). Increased dietary ruminally undegradable protein enhanced roughage utilization but increased weight at puberty. Increased ruminal propionate and additional protein flowing from the rumen had no effect on age at puberty compared to control animals. However, heifers fed RUP supplement were older and heavier at puberty than those fed MON. The conclusion can be drawn that RUP and weight gain do not solely mediate the effects of MON on sexual maturity in beef heifers.

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

Two hundred ten spring born crossbred beef heifers were used in two experiments conducted in consecutive years with a randomized complete block design. The objectives were to determine the effects of increasing the dietary intake of ruminally undegradable protein or propionic acid on the occurrence of puberty and to elucidate the mechanism of action for monensin on puberty in beef heifers. The experimental diets were fed for approximately 120 days beginning in mid-November and consisted of low quality grass hay and straw with: 1) .45 kg hd^{-1} d^{-1} supplement formulated to meet NRC (1984) recommendations for protein, vitamins, and minerals to obtain .4 kg gain per day (CON), 2) .5 kg supplement containing an additional 250 g hd^{-1} d^{-1} ruminally undegradable protein from blood meal and corn gluten meal (RUP), 3) .45 kg supplement supplying 200 mg hd^{-1} d^{-1} monensin (MON), and 4) .45 kg supplement and 400 g hd^{-1} d^{-1} of a fifty percent water, fifty percent propionic acid mixture sprayed on the roughage mixture prior to feeding (PROP). The hay:straw ratio in each diet was adjusted biweekly as needed in order to maintain similar weight gains for heifers fed each diet. As planned, weight gain was similar ($P > .1$) for all treatments. MON fed heifers were 21 days younger at first estrus than RUP fed heifers ($P < .05$) with CON and PROP heifers being intermediate. RUP treated cattle were 7 and 8 kg heavier at puberty than CON or PROP treated cattle respectively ($P < .05$). PROP fed heifers were 6 kg heavier at puberty than MON fed heifers ($P < .1$). Heifers receiving RUP supplement required less TDN than did CON or PROP treated heifers ($P < .05$) to maintain same level of gain. MON fed heifers consumed more ruminally degradable protein than RUP fed heifers ($P < .05$). Increased dietary ruminally undegradable protein enhanced roughage utilization but increased weight at puberty. Increased ruminal propionate and additional protein flowing from the rumen had no effect on age at puberty compared to control animals. However, heifers fed RUP supplement were older and heavier at puberty than those fed MON. The conclusion can be drawn that RUP and weight gain do not solely mediate the effects of MON on sexual maturity in beef heifers.

CHAPTER 1

INTRODUCTION

Replacement heifer development from weaning until they become a productive cow at two years of age represents one of the most important variables in the long term profitability of a ranch. Because heifers that conceive early in their first breeding season have more, heavier calves during their lifetime (Lesmeister et al., 1973), attainment of puberty before the first breeding season must be considered an important management goal.

In general, two factors determine the profitability of heifer development programs: 1) input costs and 2) reproductive performance. It is apparent that spring born heifers developed on a high plane of nutrition through their first winter achieve puberty at earlier ages, experience a greater number of cycles prior to the breeding season, and have a higher conception rate early in the breeding season. In order to achieve this desirable reproductive response, cattlemen often feed relatively large quantities of high cost harvested forages and grain during the winter months. The greatest advantage ruminant animals have over nonruminants is their ability to harvest and convert forages to an animal product that is useful for human consumption. If scientists

can develop methods to decrease the amount of expensive harvested feed required to optimize reproductive performance in cattle, the industry would realize a tremendous improvement in production efficiency. Consequently it would be advantageous for producers to minimize winter feed inputs for developing heifers and allow for a greater proportion of growth to occur during the growing season when cost of gains are cheapest. In order for such a system to be successful scientists must better understand the role that specific dietary elements play in either stimulating or inhibiting the physiological mechanism regulating attainment of puberty.

The objective of this study was to determine the effects of increasing the quantity of dietary ruminally undegradable protein (RUP) and propionic acid, independent of weight gain, on the occurrence of puberty and reproductive efficiency in yearling beef heifers. A second objective was to elucidate the mechanism of action for monensin on age and weight at puberty in beef heifers.

CHAPTER 2

LITERATURE REVIEW

Endocrine Regulation of Puberty

Puberty is the stage of maturation in which an individual becomes physiologically capable of sexual reproduction. The mechanisms which ultimately trigger this transition lack complete definition.

All neuroendocrine and endocrine organs related to reproduction are functional in the prepuberal female but lack integration (Foster et al., 1975; Trounson et al., 1977). The key to this integration appears dependent upon maturational changes in the hypothalamus. The most widely accepted model for the regulation of the puberal transition is called the Gonadostat Hypothesis. This theory suggests that sensitivity of the hypothalamo-pituitary axis to estradiol, as a negative stimulus to the release of gonadotropin secretion, is reduced during maturation. Decreased sensitivity of regulatory centers in the brain to estradiol allows increased frequency and amplitude of episodic secretion of luteotropic hormone (LH) which in turn stimulates the ovary and initiates follicle maturation and ovulation (Ramirez and McCann, 1963). Research reported by Day et al., (1987) supports the theory that there is a decline in the concentration of estradiol binding sites

at the hypothalamus and/or pituitary prior to puberty thereby decreasing the negative effect of estradiol on LH release. It is still unclear whether the change in hypothalamic sensitivity is due to changes in steroid concentrations or is a result of maturational changes in the hypothalamus.

Changes in chronic LH secretion have been linked to insulin release in non-lactating heifers (McCann and Hansel, 1986). The presence of insulin receptors located in the hypothalamus suggests a regulatory role for insulin in gonadotropin-releasing hormone (GnRH), and thus may affect LH secretion.

Although the effect insulin has on hypthalamo-pituitary centers and LH secretion remains vague, a direct effect of insulin on ovarian function is becoming more clear. Insulin has been shown to synergize with FSH to facilitate morphological differentiation of granulosa cells and enhance LH receptor binding (Amsterdam et al., 1988). From work in dairy heifers, it has been suggested that insulin availability may limit ovarian activity and responsiveness to gonadotropins (Butler and Canfield, 1989). Bailey (1989) fed steers hay supplemented with rumen undegradable protein, and a high concentrate diet. The circulating blood insulin was more than doubled in blood plasma of steers fed the high concentrate diet compared to controls. Many researchers have found that heifers fed relatively high concentrate diets reach sexual maturity sooner, possibly a function of higher insulin levels.

The interaction of insulin with the reproductive processes may be closely related to Insulin Like Growth Factor-1 (IGF-1). This hormone is produced predominantly in the liver and has an important role in muscle protein deposition and composition of gain (Anderson et al., 1988). Although not fully characterized in ruminants, nutritional status is thought to be a major factor controlling IGF-1 concentration and activity. Insulin Like Growth Factor-1 has been shown to amplify FSH action in bovine granulosa cells including enlargement of LH binding sites (Spicer et al., 1988). Plasma insulin and IGF-1 are closely related in that they are elevated in cattle fed diets relatively dense in protein or energy (Anderson et al., 1988; Breier et al., 1988; Elsasser et al., 1988; Houseknecht et al., 1988).

Importance of Early Puberty

It has been well documented that heifers conceiving early in their first breeding season have more as well as heavier calves at weaning throughout their lifetime (Burris and Priode, 1958; Lesmeister et al., 1973; Spitzer et al., 1975). In order to calve at 24 months of age, heifers must conceive at 14 - 15 months of age. Consequently, many heifers that conceive after 15 months are not desirable replacement females and represent a substantial expense to the beef industry. Wiltbank, (1970) suggested that breeding heifers 20 days sooner than the cow herd would improve their second breeding

season conception rate. Spitzer et al., (1975) found that heifers synchronized and bred 20 days earlier than the mature cows, then selected as replacements based on early conception had, at second breeding, higher conception rates and weaned calves 15 kg heavier compared to traditional managed heifers.

In order for heifers to respond to estrus synchronization management, they must have a functional corpus luteum. Therefore, a higher percentage of puberal heifers at the onset of any synchronization program generally results in a greater proportion of heifers synchronized and bred. Byerley et al., (1987) reported reduced pregnancy rates for heifers bred at the first (57%) compared to the third (78%) estrus. Therefore managers should strive to have heifers in their second or third cycle before the beginning of the breeding season, to improve synchronization results, increase pregnancy rates and overall lifetime production.

Factors Affecting Puberty

Age and weight at puberty are highly correlated factors (Laster et al., 1979) which are influenced by a number of environmental and genetic parameters. It is well documented that breed and heterosis influence age and weight at puberty (Preston and Willis, 1974; Gregory, 1984; Granger et al., 1989).

Short and Bellows (1971) have shown that postweaning growth has a marked effect on age at first estrus. Wiltbank

et al., (1985) fed heifers to reach two different target weights at the beginning of the breeding season; 272 kg (TW1) or 318 kg (TW2). More heifers in TW2 showed estrus and became pregnant in the first 20 days of the breeding season and more were pregnant at the end of the first breeding season. These differences were carried over into the second year. Additionally, each heifer exposed in TW2 weaned 43.4 kg more calf than those in TW1. Heifers in TW2 were fed 220 kg more corn and 100 kg less hay than TW1 heifers. Whether these results are, 1) a reflection of the effects body composition and/or growth rate has on puberty or 2) a function of the changed hormonal and metabolite profiles associated with different nutritional regimes, remains to be answered.

Because estrogen plays a major role in regulation of hypothalamic and pituitary hormones, adipose tissue could be involved in regulation of reproductive processes. Brooks et al., (1985) concluded that there is no critical body weight or percent body fat that mediates the attainment of puberty in beef heifers. However, Frisch (1975) suggested that a threshold for fat must be reached and maintained if puberty and normal cyclicity is to occur in women. Adipose tissue stores steroids and influences the amount and potency of estrogen circulating in the blood. These adipose tissues account for roughly one third of the total estrogen circulating in the blood which is derived from androgens converted into estrogen (Frisch, 1970).

Breier et al., (1988) found that steers treated with estradiol had increased basal plasma concentrations of IGF-1 at both high and low levels of energy intake. Ellenberger (1989) fed eight steers ad libitum from 240 to 510 kg live weight, gaining at 1.4 kg/d. Six other steers were diet restricted and grew at .37 kg/d from 240 to 307 kg, prior to ad libitum feeding of the same diet to a final weight of 510 kg. During realimentation, IGF-1 levels rose above those of control steers and remained higher at the final weight. Serum IGF-1 concentrations have also been shown to decrease as GH concentrations decreased in steers and heifers fed a low level of nutrition (Breier et al., 1988; Houseknecht et al., 1988). Breier (1988) concluded that decreased plasma concentrations of IGF-1 at a low level of nutrition may abolish the growth-promoting activity of circulating GH. Perhaps this relationship and the direct role IGF-1 may play in reproductive processes could in part explain the well documented incidence of lower reproductive capacity of cattle fed diets that result in relatively low weight gains or even weight loss.

In general, it is evident that growth rate, body composition, and composition of diet are factors which influence reproductive efficiency in beef cattle. Results reported by Short and Bellows (1971) and Wiltbank et al., (1985) on the occurrence of puberty, could be controlled by any of the three previously mentioned factors. Because these

three factors are highly correlated, weight gain must be experimentally controlled to study the influence that diet composition has on the attainment of puberty.

Some studies have demonstrated that a high energy intake may not enhance reproduction. Brooks et al., (1985) fed prepuberal heifers 120, 100 and 80 percent of NRC requirements for energy while maintaining 100% of NRC requirement for CP for all treatments. They reported a difference among energy intake treatments in cattle for mean weight and percent body fat at puberty but no differences in age at puberty. Growth hormone (GH) has been linked to mammary development and lifetime milk production in dairy and beef heifers (Waldo et al., 1989). Stelwagen and Grieve (1990) concluded that mammary glands contained more adipose tissue in animals fed high planes of nutrition, indirectly indicating an adverse dietary effect on mammogenesis. In addition, these researchers found that mammary DNA increased at a greater rate relative to body growth in heifers on the low plane of nutrition. Sejrsen et al., (1986) reported treatment with exogenous somatotropin around the time of puberty enhances the growth rate of mammary parenchymal tissue. These studies support an argument for an optimum, rather than maximum, growth rate, body fat composition and plane of nutrition to promote greater lifetime milk production.

Effect of Monensin on Reproduction in Cattle

It is evident that nutritional status of the animal influences reproductive capacity yet specific mechanisms and elements within a diet causing variation in reproduction are not well defined. Monensin is one member of a class of carboxylic polyether ionophore antibiotics originally used as anticoccidial feed additives for poultry. This "ionophore" is well known to improve feed efficiency and/or weight gain in beef cattle. Monensin has been shown to affect puberty in beef heifers in several ways; decrease age at puberty, decrease weight at puberty, and increase ovarian response to gonadotropins (Moseley et al., 1977; McCartor et al., 1979; Bushmich et al., 1980; Moseley et al., 1982). McCartor et al. (1979) demonstrated that heifers fed diets composed of 80% alfalfa hay, 20% concentrates and 200 mg monensin per day exhibited puberty 25 days earlier than controls and weighed 17.7 kg less. Mason and Randel (1982) fed mature beef cows 200 mg monensin per day and reported that post partum interval was shortened by 46 days when compared to controls. Hixon et al. (1982) reported that monensin shortened post partum interval of first calf beef heifers by 13.4 days. However Goehring et al. (1989) found that reproductive performance of cows fed a high or low energy diet supplemented with lasalocid, a similar ionophore, was not affected. However, cows receiving the low energy diet and lasalocid had increased milk production and weaned heavier calves.

Monensin fed at 200 mg $head^{-1}$ d^{-1} increased the capability of the pituitary to secrete LH upon multiple GnRH challenges in prepuberal heifers (Randel and Rhodes, 1980). Moreover, Bushmich et al. (1980) showed that heifers supplemented with monensin had larger corpora lutea (CL), more luteal progesterone and displayed an enhanced ovarian response to gonadotropins compared to controls.

Numerous ruminal effects have been identified and attributed to monensin when incorporated in beef cattle diets. According to Schelling (1984) these changes include:

1) modification of acid production
2) modified feed intake
3) change in gas production
4) modified digestibilities
5) change in protein utilization
6) modified rumen fill and rate of passage
7) other ruminal modes of action

The most obvious and extensively studied effect of ionophores is increased ruminal propionic acid as a percent of total VFA's (Bergen and Bates, 1984). Since propionate is thought to be more efficiently utilized by the animal than other VFA's (Blaxter and Wainman, 1964), it has been concluded that approximately 20% more metabolizable energy was available to the host when the diet was supplemented with monensin (Rowe et al., 1981).

McCartor et al. (1979) conducted a study in which it was

shown that heifers with elevated ruminal propionate reached puberty at a substantially younger age and lighter weight. Rutter et al. (1983) concluded that heifers abomasally infused with 200g propionate per day had an enhanced ability to respond to a GnRH challenge with both higher concentrations and longer periods of LH release compared to heifers infused with water. These researchers switched treatments after 21 days of infusion so that the control heifers received the propionate infusion and the propionate heifers received the water infusion. Twenty four hours after this switch another series of blood samples was taken. Heifers initially receiving propionate infusions were found to have maintained the enhanced LH response to a GnRH infusion, indicating a possible lasting response.

In another study heifers were fed protein-protected lipid and were found to have lower total ruminal concentrations of volatile fatty acids (VFA), were fatter, gained faster, and were older at puberty when compared to controls (Rhodes et al., 1978). These results suggest that decreased ruminal VFA concentration could have a negative effect on puberty. However, the protein protected lipid diet would supply additional protein available for digestion in the small intestine. Therefore these results could be confounded with ruminal escape protein.

Infusion of propionate into ruminants increases concentrations of glucose and insulin (Sartin et al., 1985;

Istasse et al., 1987). Collectively these studies imply a strong relationship between ruminal fermentation and the mechanisms governing the onset of puberty in heifers. However a study designed to relate increased propionate absorption with measurements of circulating hormone levels has not been conducted. Similarly, a study illustrating a physiological mechanism linking increased propionate and reproductive performance in heifers remains to be published at this time.

Highly digestible fiber supplements have been found to produce similar IGF-1 concentrations and growth rates as supplements high in starch (grain supplement, Houseknecht et al., 1988). Although not reported, one would expect heifers receiving supplements high in fiber to have lower ruminal and serum propionate concentrations. These experiments may indicate that the form of supplemental dietary energy and increased propionate concentration may not be critical to triggering reproductive processes.

Monensin has been shown to decrease ruminal ammonia nitrogen production (Chalupa, 1980). This suggests a change in enzyme activity regarding deamination and proteolyses. Faulkner et al. (1985) found that monensin reduced microbial protein synthesis and increased diet protein escape in steers. Poos et al. (1979) reported decreased bacterial nitrogen reaching the abomasum of steers although more dietary protein reached the abomasum. Essential and branched chain amino acids in plasma increase as amount of protected protein

increase in the diet (Kung et al., 1984). Miner and Petersen (1988) concluded that supplementation of pregnant winter-grazing beef cows with soybean meal and a ruminally undegradable protein (RUP) source enhanced ruminal fermentation characteristics that may make more nutrients available to the animal. In addition, Petersen et al. (1987) demonstrated that RUP supplementation increased milk production, calf weaning weights and decreased the post-partum interval of two year old beef cows when compared to a ruminally degradable protein source. Similarly, Wiley et al. (1991) reported a shorter post-partum interval when first calf beef heifers were fed RUP. These studies suggest a positive reproductive response when beef females are fed protein that escapes ruminal degradation.

Based on this literature it is possible that the affect monensin has on age and weight at puberty in beef heifers could be a result of increased propionic acid or increased RUP. If researchers could determine how these specific dietary elements affect puberty, insight into the mechanism mediating puberty and the ability to manipulate the timing of puberty could be enhanced.

CHAPTER 3

MATERIALS AND METHODS

Experiment 1.

This study was conducted at the Montana State University Livestock Teaching and Research Center, Bozeman, Mt. One hundred weanling Angus, Hereford and Angus x Hereford heifers with an average weight of 249 ± 1.5 kg were utilized in a complete randomized block design to evaluate the effect of four nutritional supplements on the age and weight at puberty, and reproductive performance. On November 8, 1989 the heifers were blocked by weight and randomly assigned to nutritional treatments within weight block. Four pens were allotted to each treatment with either six or seven heifers per pen.

The experimental diets (Table 1) were fed for 114 days beginning November 9, 1989 and consisted of low quality grass hay and straw with: 1) .45 kg supplement formulated to meet NRC (1984) requirements for protein, vitamins, and minerals in order to obtain .4 kg gain per day (Con); 2) .5 kg supplement containing an additional 250 g ruminally undegradable protein (RUP); 3) .45 kg supplement including 200 mg Monensin (Mon); 4) .45 kg supplement and 400 g of a fifty percent water, fifty percent propionic acid mixture sprayed on the roughage mixture prior to feeding (Prop). Each diet was mixed individually and

fed at approximately 1300 h ad libitum as a complete ration. The hay:straw ratio in each diet was adjusted bi-weekly as needed to maintain ad libitum feed intake and similar ADG among treatments.

TABLE 1. FORMULATION OF SUPPLEMENTS

Ingredient	TREATMENT[a]			
	CON	RUP	MON	PROP
	% DM			
Beet pulp	38.7	3.17	13.7	13.7
Blood meal	---	61.17	---	---
Corn gluten meal	---	10.98	---	---
Soybean meal	34.74	---	64.97	65.0
Dicalcium phosphate	2.03	2.16	3.41	3.41
Calcium sulfate	5.53	4.3	1.47	1.47
Calcium carbonate	---	---	5.21	5.21
Potassium chloride	7.84	8.19	---	---
Trace mineral salt	11.0	9.88	11.04	11.04
Vitamin A (1000 IU/d)	20	20	20	20
Monensin (mg/d)	---	---	200	---
Propionic acid (g/d)	---	---	---	200

[a]CON = Control, RUP = Ruminally undegradable protein, MON = Monensin, PROP = Propionic acid

Potter et al. (1986) and Raun et al. (1976) have reported improved performance and feed efficiency of cattle fed high roughage diets containing monensin. Because our diets consisted of primarily low quality roughages we expected the RUP, MON, and PROP cattle to be more efficient in roughage utilization (i.e. maintain similar weight gains on a lower hay:straw ratio). Therefore, we designed these supplements to 1) maintain similar weight gains with ad libitum intake, and 2) minimize confounding effects of different protein and energy intake. Consequently, the Con supplement was designed

to provide less crude protein on a percentage basis due to the expected higher protein intake from a greater hay:straw ratio.

Nutrient intake was measured by mean pen intake of hay, straw and supplement. Crude protein (CP) analyses (A.O.A.C., 1980) and neutral detergent fiber (NDF) analyses (Van Soest and Wine, 1967) of forage and supplement were used to calculate predicted CP and TDN intake per animal.

In order to estimate propionic acid losses due to volatilization, on d 95, samples of CON and PROP diets were collected at 2 hour intervals until the daily feed was consumed. These samples were prepared and analyzed using gas chromatography by the method described by Erwin et al., 1961. Peak area was measured using a planimeter to determine relative propionate concentrations in the feed. From Figure 1 it is evident that no volatilization of propionate was occurring during the time period that was sampled and that there was almost no propionate in the CON diet.

Water was supplied by automatic water troughs equipped with electrical heating elements. Water temperature was monitored and thermostats were adjusted weekly to minimize pen effects on water temperature and intake.

The heifers were weighed bi-weekly at approximately 1000 h before the afternoon feeding. Initial and final weights were an average of two weights measured on consecutive days.

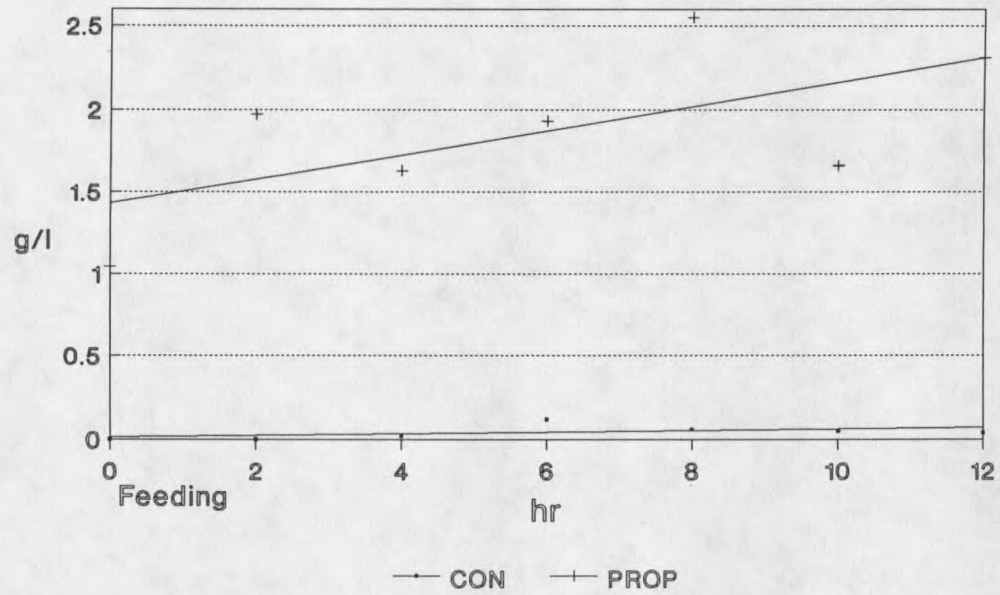


Figure 1. Relative propionic acid concentrations in PROP and CON diets over a twelve hour sampling period.

Heifers were observed twice daily for approximately one hour for estrous activity beginning December 15, 1989 and continuing through June 6, 1990. Beginning March 5, 1990 when supplement feeding was discontinued, heifers were managed as a contemporary group at which time two sterile marker bulls were maintained with the heifers to aid in estrous detection. Heifers were determined to be in behavioral estrous when they stood to be mounted by a bull or another heifer. If a heifer did not stand to be mounted but exhibited other signs of sexual activity or displayed at least one well defined paint mark along the back and tail-head area, she was recorded and considered to be in estrus. Seven to nine days following

estrus a 10 ml blood sample was collected by venipuncture of a tail or jugular vein for determination of serum progesterone (P4) concentration.

Blood samples were allowed to clot and centrifuged at 1000 x g at 4 c for 30 minutes. Serum was decanted and stored at -25 c until assayed for P4 (analysis conducted at LARRL, Miles City, MT). Progesterone concentrations were determined by solid-phase RIA provided by commercially available kits[1]. Limit of sensitivity for the progesterone RIA was 40 pg ml^{-1}, and the inter- and intra-assay coefficients of variation were 3.3 and 6.3 % for a sample containing 15 ng ml^{-1} and 2.5 and 10.8% for a sample containing 1 ng ml^{-1}. Based on serum P4 concentrations, puberal estrus was defined in retrospect as estrous behavior followed by serum P4 concentrations > 1.0 ng/ml 7 to 9 days later. Heifers not puberal prior to the breeding season but exhibiting behavioral estrus during the AI period were determined to be puberal when inseminated.

Weight at puberty was determined by interpolation using pre and post estrus weights (assuming a linear rate of gain) which were taken every 14 days during the feedlot period and every 28 days thereafter. Each heifer was classified as puberal (1) or non puberal (0) prior to May 21. Similarly heifers were classified as receiving AI service (1) or not receiving service (0).

Beginning May 1, 1990, heifers were bred by artificial

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[1]Diagnostic Products Corp., Los Angeles, CA.

insemination (AI) to an Angus bull by a trained technician 12 hours following standing estrous. On June 6, 1990 the AI period was terminated and 3 intact Hereford bulls were turned in with the heifers for an additional 24 days. Pregnancy was determined by rectal palpation at a minimum of 60 days after the end of the breeding season.

Experiment 2.

Experiment 2 was conducted similarly to Experiment 1 with these modifications. On November 10, 1990, 110 weanling heifers were allotted to treatments and pens, with either 6 or 7 heifers per pen. The feeding period began on November 13, 1990 and continued through March 18, 1991 for a total treatment period of 125 days.

Blood samples were collected from all heifers every 5th day beginning February 1, 1991 and continuing through May 2, 1991. Serum was analyzed for progesterone concentration similar to Experiment 1, only the analysis was conducted by the MSU Animal and Range Sciences Department Physiology Lab. Puberty criteria consisted of greater than 1 ng/ml serum progesterone on two consecutive bleeding dates. Heifers not puberal prior to the breeding season but exhibiting behavioral estrus during the AI period were considered to be puberal at that time. Weight at puberty was determined as in Experiment 1.

Because observation of behavioral estrus ended on May 21

both years, observed means for age and weight at puberty are biased downward in varying degrees, depending upon the percentage puberal by May 21. To reduce this bias in comparing means for treatments and other classes varying in percentage puberal, means for age and weight at puberty were adjusted as reported by Dickerson and Laster (1975).

Statistical Analysis

Age and weight at puberty, initial and breeding weights, feedlot (treatment period) and overall (initiation of study through first day of breeding season) ADG, blood metabolites and nutrient intake were analyzed using the General Linear Models procedure of SAS (SAS, 1988). The statistical model for age and weight at puberty, initial and breeding weights, feedlot and overall ADG and blood metabolites included the fixed effects of treatment, weight block, year and the interactions of treatment * weight block and treatment * year. If the interactions were not significant for a specific variable they were taken out of the model and the reported data are from analyses by the reduced model. Nutrient intake was analyzed by pen with treatment and year as the independent variables in the model. Nutrient intake is reported as the mean intake per animal in each pen. Least square means were compared using linear contrasts.

For Experiment 2 a weighted least squares procedure (SAS, 1988) was used to analyze mean P4 concentrations for up to

three consecutive bleeding dates post-puberty for each animal. Treatment, weight block, and treatment * weight block interaction were included in the statistical model.

Data for pregnancy rate and percent puberal prior to breeding were pooled across experiments (i.e., years) and analyzed by Chi-square procedures with CON, RUP, MON and PROP as factors (SAS, 1988). Results of Experiment 1 and Experiment 2 were pooled with year included in the model.

CHAPTER 4

RESULTS AND DISCUSSION

The experimental heifers weighed 249 ± 1.5 kg in mid November at the initiation of the study (Table 2). Pooled mean initial weights among treatments were very similar ($P > .1$). Likewise, there were no differences among heifers fed each dietary treatment for breeding weight, average daily gain during the supplementation period, or overall ADG ($P > .1$). Year had no effect on overall ADG or ADG during supplementation. There was a treatment * weight block interaction for feedlot ADG ($P < .05$). However there was no pattern to the ranking of values for ADG that could be biologically explained. Mean weight at the beginning of the breeding season was 300 kg. Both years heifers experienced some weight loss during the period between the end of supplementation period and beginning of the breeding season. This loss is probably due to low dry matter intake of lush immature grass, thus reducing ruminal fill. Considering this weight loss and the moderate rate of gain during the supplementation period, the overall growth rate of these heifers was marginal at best. Several researchers have reported improved reproductive performance with faster growth rates than the heifers on this study experienced (Fleck et

al., 1980; Lemenager et al., 1980; Wiltbank et al., 1985). However slower developmental weight gains has been shown to decrease adipose accretion in mammary tissue and increase lifetime milk production in dairy heifers when compared to animals gaining at a faster rate (Sejrsen et al., 1982; Stelwagen, 1990). Therefore it is evident that opportunity exists to develop management systems that minimize expensive feed inputs (i.e., develop heifers at a moderate rate) while optimizing reproductive performance.

TABLE 2. THE EFFECT OF RUMINALLY UNDEGRADABLE PROTEIN, PROPIONIC ACID OR MONENSIN ON WEIGHT CHANGE OF DEVELOPING BEEF HEIFERS.

	Treatment[a]				
Measurement	CON	RUP	MON	PROP	SE[b]
No. of Heifers	46	49	49	48	
	kg				
Initial wt	250.5	249.8	249.2	249.5	1.5
Breeding wt[c]	300.7	299.1	301.9	300.5	2.4
Feedlot ADG	.50	.54	.52	.51	.02
Overall ADG	.37	.36	.37	.36	.01

[a]CON = Control, RUP = Ruminally undegradable protein, MON = Monensin, PROP = Propionic acid
[b]Standard error of estimate
[c]May 1 weight

Two CON, 3 RUP and 4 PROP fed heifers from Experiment 1 were excluded from all analyses because they were determined to be puberal prior to the initiation of the study in November. Likewise, 4 CON, 1 RUP, 3 MON and 1 PROP fed heifers from Experiment 2 were excluded from all analyses because they were determined to be puberal prior to February

1, 1991.

Means for unadjusted age and weight at puberty were 376 d and 305 kg for the heifers cycling before May 21 during both years. These values are similar to those reported by Greer (1983) and Short and Bellows (1971) for Bos taurus heifers raised in Montana. The interaction of treatment * year for age at puberty approached significance (P = .09). This interaction was a result of CON heifers becoming puberal twenty days earlier in Experiment 2 compared to Experiment 1. RUP, MON and PROP fed heifers did not change rank relative to each other. One contributing factor to the interaction could be due to relatively more CON heifers becoming puberal on day 1, 5 and 10 of the study. However there was no obvious biological interpretation of this intercation. Diet composition changed age and weight at puberty independent of heifer weight gain (Table 3). The 10 day difference in age at puberty between CON and RUP fed heifers approached significance (P < .1). RUP fed heifers were 17 days older at puberty than heifers fed MON (P < .05).

Adjusting the means for age and weight at puberty to account for May 21 truncation of the distribution had no effect on ranking of treatments for age or weight at puberty (Table 4). However the difference between RUP and MON fed heifers for age at first estrus was magnified to 21 days (P < .005). Adjustment of weight at puberty did not significantly change comparisons among treatments. The nine day difference

in adjusted age at puberty between CON and MON fed heifers approached significance ($P < .1$). Moseley (1982), and McCartor (1979) reported decreased age at puberty in beef heifers fed monensin by 14 and 24 days respectively when compared to controls. However heifers used in the studies of Moseley (1982) and McCartor (1979) gained at a faster rate (1.1 and .63 kg/d respectively) compared to our heifers. Also experimental diets were fed for a longer period of time (203 and 157 days respectively) compared to our study of 120 d. Consequently it is tempting to hypothesize that producers who develop their heifers at a lower rate of gain could benefit from incorporating monensin in their replacement heifer rations. Additionally, in many areas, high quality forage is available for grazing 8 months or more of the year. In these circumstances it may not be practical or feasible for cattleman to feed supplements for extended periods (150 to 200 d). Further research is needed to determine the minimum length of monensin supplementation required to elicit an economically significant response from yearling spring-born heifers. Additional questions arise as a result of this research. When does the mechanism mediating the initiation of sexual maturation respond to monensin supplementation? Could this mechanism respond to monensin supplementation by 120 days?

TABLE 3. THE EFFECT OF RUMINALLY UNDEGRADABLE PROTEIN, PROPIONIC ACID OR MONENSIN FED TO BEEF HEIFERS ON AGE AND WEIGHT AT PUBERTY.

	Treatment[a]				
Measurement	CON	RUP	MON	PROP	SE[b]
Age (d)	376[cd]	386[d]	369[c]	376[cd]	4
Adj.[e] Age (d)	384[cd]	396[d]	375[c]	385[cd]	5.7
Wt (kg)	301[c]	308[d]	302[c]	300[c]	2.5
Adj.[e] Wt (kg)	302[c]	309[d]	303[cd]	301[c]	3.5

[a]CON = Control, RUP = Ruminally undegradable protein, MON = Monensin, PROP = Propionic acid
[b]Standard error of estimate
[cd]Means within a row with uncommon superscripts differ (P<.05)
[e]By restoring reduction in mean expected because of truncated distribution of observed age at puberty. See Materials and Methods.

The percentage of heifers puberal prior to May 21 or percent serviced during the first 21 days of the breeding season (Table 4) was similar for each nutritional treatment. Moseley et al. (1977) reported that 92% monensin fed heifers reached puberty compared to only 58% of control fed heifers although weight gain was not reported. Numerically, fewer cattle receiving the RUP supplement (64%) were serviced during the first 21 days of the breeding season compared to animals receiving the CON supplement (76%). Percentage of heifers pregnant in the fall was not affected by treatment in Experiment 1 (Table 5).

In Experiment 2, treatment had no effect (P > .1) on first luteal phase mean serum progesterone concentrations (Table 5).

TABLE 4. THE EFFECT OF RUMINALLY UNDEGRADABLE PROTEIN, PROPIONIC ACID OR MONENSIN FED TO BEEF HEIFERS ON PERCENT PUBERAL PRIOR TO MAY 21 AND PERCENT SERVICED DURING FIRST 21 DAYS OF BREEDING SEASON.

	Treatment[a]			
Measurement	CON	RUP	MON	PROP
	%			
Puberal prior to May 21	86	82	90	86
Bred during 1st 21 days	76	64	79	80
Preg. rate[b]	87	77	80	76

[a]CON = Control, RUP = Ruminally undegradable protein, MON = Monensin, PROP = Propionic acid
[b]Experiment 1 only

TABLE 5. THE EFFECT OF RUMINALLY UNDEGRADABLE PROTEIN, PROPIONIC ACID OR MONENSIN ON FIRST LUTEAL PHASE MEAN SERUM PROGESTERONE CONCENTRATIONS[a].

	Treatment[b]				
	CON	RUP	MON	PROP	SE[c]
P4[d] (ng/ml)	5.13	4.97	5.57	5.82	.45

[a]Experiment 2 only
[b]CON = Control, RUP = Ruminally undegradable protein, MON = Monensin, PROP = Propionic acid
[c]Standard error of estimate
[d]Progesterone

Nutrient intake exceeded NRC (1984) requirements necessary to achieve the targeted .4 kg gain per day during the supplementation period (Table 5). Total dry matter (DM) intake was similar for each treatment group. However amount of hay fed to maintain similar rates of gain did vary ($P < .05$). As expected heifers receiving the CON supplement required more hay ($P < .001$) and less straw ($P < .01$) than heifers receiving either RUP or PROP diets. Numerically, MON

fed heifers required 382 g/d less hay than did CON fed heifers. There was a treatment * year interaction ($P < .01$) for straw intake (Appendix Figure 2). This interaction was due to the PROP heifers consuming less straw during Experiment 2 than in Experiment 1. Heifers fed PROP were less efficient in Experiment 2 in utilizing roughage for gain than in Experiment 1. From the available information there is no explanation for this interaction, however, as expected PROP supplemented animals still required more straw than CON or MON fed heifers in both experiments to maintain the same rate of gain.

TABLE 6. THE EFFECT OF RUMINALLY UNDEGRADABLE PROTEIN, PROPIONIC ACID OR MONENSIN FED TO BEEF HEIFERS ON MEAN DAILY NUTRIENT INTAKE.

Nutrient[b]	Treatment[a]				
	CON	RUP	MON	PROP	SE[c]
	g/d				
Total DM	7660	7448	7605	7735	192
Hay	6786[d]	5378[e]	6404[d]	5868[e]	172
Straw	457[g]	1599[h]	787[i]	1254[j]	82
TDN	4045[d]	3734[e]	3985[de]	4068[d]	98
CP	570[f]	739[d]	608[e]	589[ef]	12
RDP	339[ef]	318[f]	370[d]	359[de]	7
RUP	231[h]	421[g]	238[h]	230[h]	5

[a]CON = Control, RUP = Ruminally undegradable protein, MON = Monensin, PROP = Propionic acid
[b]Total DM = Total dry matter, TDN = Total digestible nutrients, CP = Crude protein, RDP = Ruminally degradable protein, RUP = Ruminally undegradable protein
[c]Standard error of estimate
[def]Means within a row with different superscripts differ ($P < .05$)
[ghij]Means within a row with different superscripts differ ($P < .01$)

Cattle receiving the RUP supplement were most efficient in energy utilization since they required less ($P < .1$) TDN to gain .5 kg per day than did cattle receiving other

experimental supplements. By design RUP fed heifers had greater CP ($P < .05$) and RUP ($P < .01$) intake. Heifers fed MON required more hay than straw to achieve similar gains than was expected. As a result roughage CP and ruminally degradable protein (RDP) intake was greater than was estimated prior to the study. Consequently, MON fed heifers consumed 38 g/d more CP than did heifers fed the CON diet ($P < .05$), while consuming 31 g/d and 52 g/d more RDP than heifers consuming CON and RUP diets respectively ($P < .05$).

Blood metabolite concentrations (urea nitrogen, total protein, glucose, and cholesterol) can be used to assess nutritional status and evaluate the metabolic fate of dietary components (Table 6). These blood metabolite measurements have been used clinically for diagnosis of metabolic dysfunction (Kaneko, 1989). All serum metabolite concentrations observed in our study were within the normal range of healthy animals as reported by Kaneko (1989).

Table 7. THE EFFECT OF RUMINALLY UNDEGRADABLE PROTEIN, PROPIONIC ACID OR MONENSIN FED TO BEEF HEIFERS ON BLOOD METABOLITES.

	Treatment[a]				
Metabolite	CON	RUP	MON	PROP	SE[b]
	mg/dl				
Urea nitrogen	9.8[c]	11.5[d]	10.5[e]	9.4[c]	.3
Total protein	6	6	6	6	.05
Glucose	74.3	76.2	75.8	75.6	.8
Cholesterol	101.8[c]	90.8[d]	102.1[c]	94.5[d]	2

[a]CON = Control, RUP = Ruminally undegradable protein, MON = Monensin, PROP = Propionic acid
[b]Standard error of estimate
[cde]Means within a row with different superscripts differ ($P < .05$)

Treatment * year interactions existed for blood urea nitrogen (BUN), glucose, and cholesterol (Appendix Figures 3, 4 and 5). An explanation for biological causes of these interactions is difficult. The apparent cause of the treatment * year interaction for glucose concentration was due to a change in rank for PROP fed heifers. In Experiment 1 this group had the second lowest value while in Experiment 2 they were the highest. This interaction can partially be explained by the greater hay:straw ratio (lower straw intake) in Experiment 2 for PROP treated heifers. More hay relative to straw would provide more glucogenic substrate and thus increase serum glucose concentrations. Glucose is a highly regulated metabolite in ruminant animals, thus it would require a dramatic change in metabolism or diet to affect serum glucose concentration. No explanation other than analyses sensitivity is evident for the BUN treatment * year interaction. BUN was higher ($P < .05$) for heifers fed RUP and MON supplements. These results would suggest that escape protein in the RUP and possibly in the MON treatments may have been in excess of needs for growth, and thus contributed to the elevated serum BUN. However the treatment * year interaction for cholesterol appears to be primarily due to lower serum cholesterol for RUP treatment in Experiment 2 relative to Experiment 1. RUP heifers exhibited a proportionally greater increase in straw intake in Experiment 2 than all other treatments. The more diluted diet would be

expected to produce lower serum cholesterol concentrations. Cholesterol concentration was higher ($P < .05$) in serum from CON and MON fed heifers. The greater hay:straw diet these animals received may have provided more fatty acids and fatty acid precursors to increase cholesterol synthesis. O'Kelly and Spiers (1990) found that ruminal bacteria in steers supplemented with monensin had an increased lipid content with an associated increase in the circulating levels of cholesterol. Because cholesterol is the precursor to steroid hormone synthesis, this study implies another possible mechanism for the effect monensin has on reproductive processes in cattle. Wiley et al. (1991) reported lower cholesterol concentration found in cows supplemented with RUP. These researchers suggested that increased amino acids may have stimulated ovarian cytochrome P-450 enzymes and enhanced the synthetic rate of steroid hormones from cholesterol, thus reducing serum cholesterol concentration. If the supply of cholesterol is rate limiting for steroidal synthesis and the stimulatory steroid surge required for LH release, then an increased cholesterol concentration would stimulate the puberal process, although this mechanism is highly speculative.

Total protein and glucose concentrations were not affected by treatment.

CHAPTER 5

CONCLUSION

An explanation for the response due to monensin supplementation in this study is speculative at best because the specific mechanism triggering puberty in the beef heifer is still unclear. Nevertheless the conclusion can be drawn that additional protein flowing from the rumen and weight gain do not solely mediate the effects of monensin on sexual maturity in beef heifers. According to Davison (1984) and Donoho (1984), 36 to 50% of monensin is absorbed by ruminants. Armstrong and Spears (1988) concluded that monensin alters metabolism in ruminants independent of ruminal microbial metabolism. Our study may support these findings in that additional dietary ruminal escape protein or propionic acid did not reduce age at puberty compared to the control fed heifers.

Increasing the quantity of RUP consumed by heifers fed a low quality roughage diet improved their ability to utilize dietary energy for weight gain. Perhaps there is a limiting amino acid for growth that was provided by the RUP supplement enabling heifers to utilize fewer energy resources to sustain the same level of growth. However, additional RUP had a negative effect on age and weight at puberty in this study.

Much of the current literature has demonstrated that protein deficiency is detrimental to reproductive performance in beef heifers. Could there be a threshold level of dietary protein that when surpassed has a deleterious effect on reproduction?

It is evident from this and other work that age and weight at puberty in the beef heifer can be manipulated, independent of weight gain, by changing diet composition. In order to reduce unnecessary feed inputs and thus decrease the cost of developing productive heifers, more research is needed to identify specific dietary elements that mediate the timing of puberty and reproductive efficiency.

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APPENDICES

APPENDIX A

FIGURES

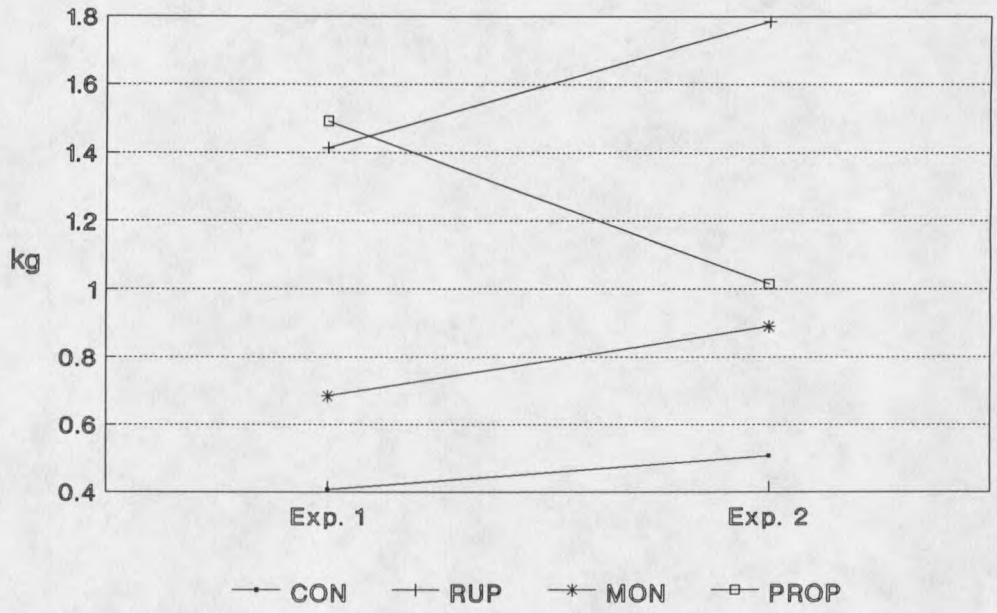


Figure 2. The effect of experiment and treatment on straw intake.

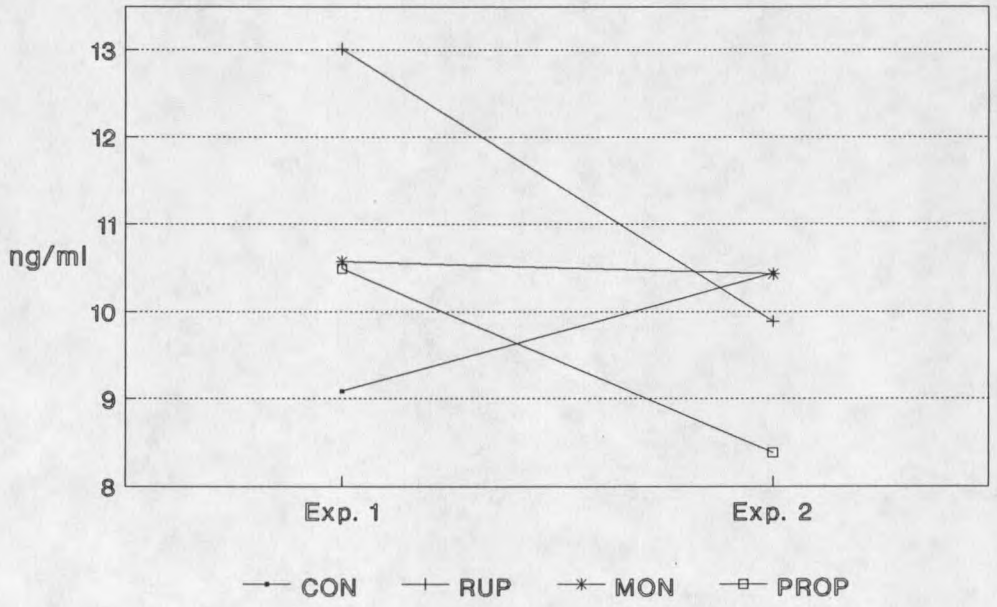


Figure 3. The effect of experiment and treatment on serum BUN concentrations.

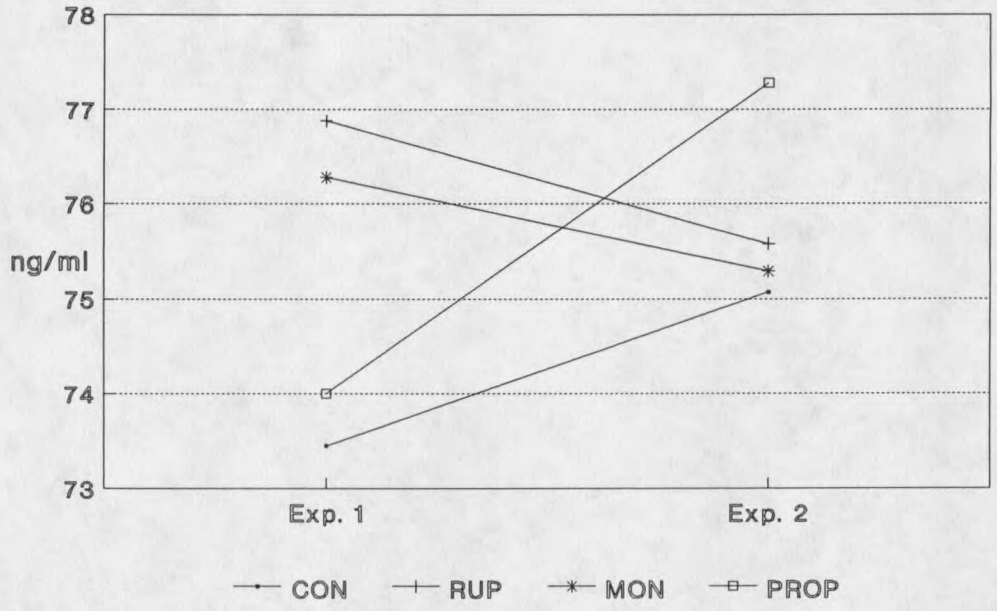


Figure 4. The effect of experiment and treatment on serum glucose concentrations.

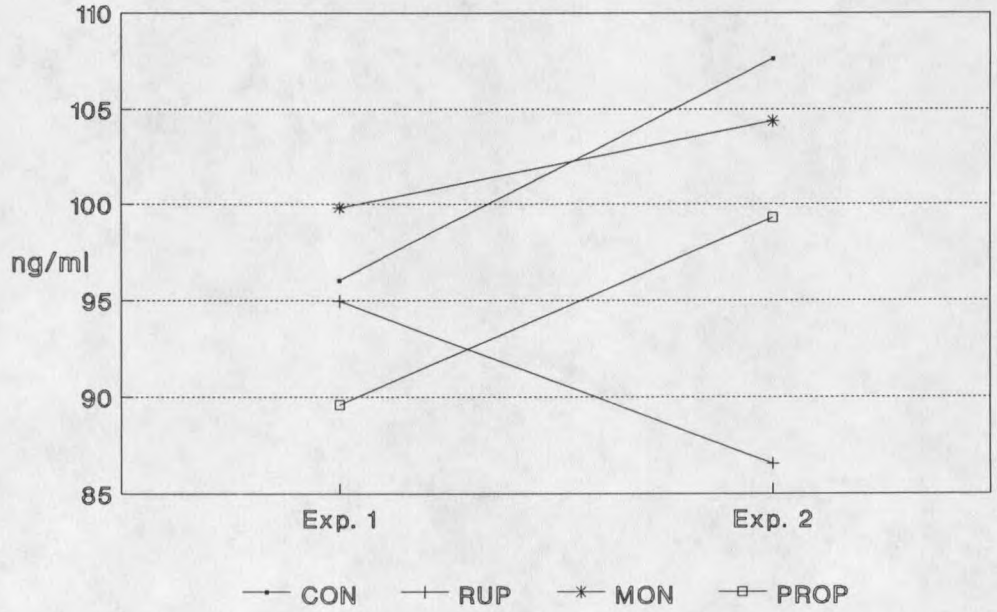


Figure 5. The effect of experiment and treatment on serum cholesterol concentrations.

APPENDIX B

ANOVA TABLES

Table 8. Least-Squares Analyses of Variance for Initial Weight, Breeding Weight, Feedlot ADG and Overall ADG.

	Initial Weight			Breeding Weight			Feedlot ADG			Overall ADG		
Source	df	Mean square	P	df	Mean square	P	df	Mean square	P	df	Mean square	P
Treatment	3	14.33	.93	3	62.98	.87	3	.013	.3	3	.0008	.9
Block	3	29378.35	<.01	3	16773.81	<.01	3	.014	.29	3	.044	<.01
Year	1	361.37	.06	1	16230.47	<.01	1	.013	.27	1	.011	.16
Trtmt*Block	9	54.06	.84	9	103.5	.94	9	.022	.04	9	.006	.43
Error	175	100.26		175	269.2		175	.01		175	.005	

Table 9. Least-Squares Analyses of Variance for Age and Weight at Puberty.

	Age			Weight		
Source	df	Mean square	P	df	Mean square	P
Treatment	3	1893.13	.03	3	580.68	.08
Block	3	533.39	.48	3	15588.92	<.01
Year	1	1370.01	.15	1	19139.13	<.01
Trtmt*Year	3	1389.77	.1	-	-	-
Error	153	642.15		156	255.29	

Table 10. Least-Squares Analyses of Variance for Dry Matter, Hay and Straw Intake.

	Dry Matter			Hay			Straw		
Source	df	Mean square	P	df	Mean square	P	df	Mean square	P
Treatment	3	118110.09	.75	3	3035282.6	.08	3	2031655.5	<.01
Year	1	370953.51	.27	1	562500.6	<.01	1	19992.18	.55
Trtmt*Year	3	716547.35	.09	3	422827.2	.18	3	272886.42	<.01
Error	24	294682.33		24	237860.7		24	53445.02	

Table 11. Least-Squares Analyses of Variance for Total Digestible Nutrients, Crude Protein, Ruminally Degradable Protein and Ruminally Undegradable Protein.

	TDN			CP			RDP			RUP		
Source	df	Mean square	P	df	Mean square	P	df	Mean square	P	df	Mean square	P
Treatment	3	188245.8	.03	3	46216.8	<.01	3	4192.05	<.01	3	70959.3	<.01
Year	1	53628.1	.15	1	7861.3	<.01	1	6802.15	<.01	1	3527.8	<.01
Trtmt*Year	3	163847.2	.1	3	5166.1	.23	3	648.55	.23	3	342.5	.22
Error	24	76998.35		24	3854.8		24	417.97		24	216.01	

Table 12. Least-Squares Analyses of Variance for Blood Urea Nitrogen, Total Protein, Glucose and Cholesterol.

	BUN			Total Protein			Glucose			Cholesterol		
Source	df	Mean square	P	df	Mean square	P	df	Mean square	P	df	Mean square	P
Treatment	3	37.55	<.01	3	.03	.84	3	33.55	.31	3	1497.51	<.01
Block	3	15.76	<.01	3	.06	.67	3	49.88	.15	3	699.02	.02
Year	1	47.96	<.01	1	2.48	<.01	1	19.93	.4	1	905.45	.04
Trtmt*Block	9	5.11	.12	9	.22	.04	9	63.46	.02	9	299.32	.15
Trtmt*Year	3	46.71	<.01	3	.49	<.01	3	56.61	.12	3	964.22	<.01
Error	172	3.17		172	.11		172	27.64		172	200.35	

Table 13. Least-Squares Analyses of Variance for Mean First Luteal Phase Progesterone Concentration.

	Progesterone		
Source	df	Mean Squares	P
Treatment	3	8.72	.50
Block	3	1.62	.93
Trtmt*Block	9	11.35	.42
Error	67	10.96	

Table 14. Observed Values Used in Chi-Square Analysis of Percent Puberal Prior to May 21, Percent Serviced First 21 Days of Breeding Season and Percent Pregnant for Experiment 1.

	% Puberal	% Non-Puberal	% Serviced	% Not Serviced	% Pregnant	% Open
CON	86.00	14.00	76.00	24.00	87	13
RUP	82.00	18.00	64.00	36.00	77	23
MON	90.38	9.62	78.85	21.15	80	20
PROP	85.71	14.29	79.59	20.41	76	24
P-Value		.68		.25		.84

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