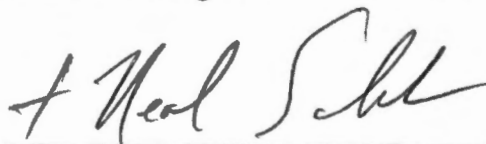


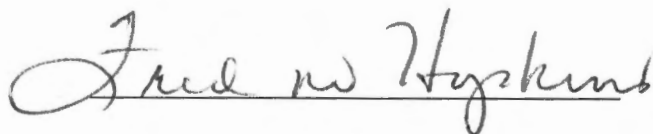
To the Graduate Council:

I am submitting herewith a thesis written by Timothy M. Towns entitled "Reproductive Performance in Cycling Beef Cows Experiencing Nutritional Restriction". I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Animal Science.

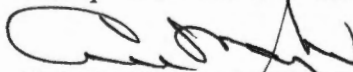


F. Neal Schrick, Major Professor

We have read this thesis
and recommend its acceptance:



Accepted for the Council:



Interim Vice Provost and
Dean of The Graduate School

**REPRODUCTIVE PERFORMANCE IN CYCLING BEEF COWS
EXPERIENCING NUTRITIONAL RESTRICTION**

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Timothy M. Towns

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ABSTRACT

The effect of weight loss during the breeding season on reproductive performance was assessed in 150 beef cows. Cows were sorted by calving date, body condition score (BCS; mean = 5.5 ± 0.5), BW (mean = 510 ± 8 kg), age, and breed. Restricted (**RES**) cows were fed to lose 5% BW from d -30 to d 0 (start of breeding season) and an additional 10% BW from d 0 to d 60 (end of breeding season). Control (**CON**) cows were fed to maintain BW. All cows reinitiated cyclicity (progesterone ≥ 1 ng/mL) prior to start of the breeding season. Estrus was synchronized and cows were inseminated at estrus and 12 h later. Bulls were placed with each group after the synchronization period through the breeding season. Pregnancy was determined at d 30, 60, and 150. Measurements for BW, BCS, and blood samples for progesterone, insulin, nonesterified fatty acids (NEFA), and urea nitrogen (BUN) were collected weekly from d -30 to d 60. Body weight of **RES** cows decreased 56.9 kg; whereas, **CON** cows increased 10.8 kg from d -30 to d 60. Insulin decreased throughout the experimental period in **RES** cows (d -30, 0.33 ± 0.02 ng/mL; d 60, 0.24 ± 0.02 ng/mL; $P < 0.05$). Concentrations of NEFA (d -30, 0.77 ± 0.12 mEq/dL; d 60, 0.95 ± 0.12 mEq/dL; $P < 0.05$) and BUN (d -30, 20.4 ± 0.9 mg/dL; d 60, 29.1 ± 0.9 mg/dL; $P < 0.05$) increased in **RES** cows. Neither estrous response (86.3 vs. 88.3%), estrous interval (2.5 vs. 2.6 days), nor conception rates (68.3 vs. 76.5%) differed between **RES** and **CON** cows, respectively. Pregnancy rates were similar on d 30 (58.9 vs. 67.5%), d 60 (89.0 vs. 93.5%), and d 150 (91.8 vs. 96.1%) between **RES** and **CON** cows, respectively. Crown-rump length did not differ between **RES** and **CON** embryos on d 45 in year 1 (25.7 ± 0.6 vs. 26.9 ± 0.6 mm) or d 30 in year 2 (11.5 ± 0.2 vs. 10.8 ± 0.2 mm, respectively). Calves from **RES** cows had lower BW

than **CON** at the end of the breeding season (145.4 ± 2.9 vs. 176.8 ± 2.9 kg; $P < 0.05$).

In conclusion, cows which had reinitiated estrous cyclicity but were losing weight during the breeding season did not have reduced reproductive performance. These results suggest lower pregnancy rates associated with poor nutrition may be more related to failure of animals to reinitiate postpartum cyclicity rather than inability to establish and maintain pregnancy.

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I. INTRODUCTION

The primary goal of beef cow/calf producers is a live calf every 365 days. Therefore, optimum reproductive efficiency of the cow herd is essential for producers to achieve this goal. Many factors contribute to decreases in reproductive performance, including reduced nutrition. Wiltbank and co-workers (1962) reported cows that lost weight during the postpartum interval (PPI) had a longer return to estrus and lower pregnancy rates compared to cows that maintained body weight. Similarly, Richards et al. (1986) observed cows that calved in thin body condition ($BCS \leq 4$) and losing weight during the postpartum period had lower pregnancy rates than similarly maintained cows that calved in good body condition ($BCS \geq 5$). Causes of reduced pregnancy rates in cows losing weight after calving may include ovulation failure, decreased fertilization rates, and embryo mortality. While the exact mechanisms causing reproductive failure are not known, the overall effects of reduced pregnancy rates in cattle experiencing nutritional stress have been reported (Wiltbank et al., 1962; Dunn et al., 1969; Rakestraw et al., 1986; Richards et al., 1986; Selk et al., 1988).

Failure to establish pregnancy due to reduced nutrition increases the calving interval and results in economic losses to beef producers. A study performed by Teague and Schrick (1999) revealed economic differences between calves born the first 30 days, second 30 days, and final 30 days of the calving season. Calves born during the first 30 days brought \$38.25 more per head than calves born during the second 30 days, and \$79.02 more than calves born during the final thirty days. Therefore, reduced reproductive efficiency and resultant delays in rebreeding have a significant economic impact for beef producers in Tennessee.

The majority of beef cows in Tennessee are rebred during lactation. Previous research examining the effects of undernutrition on reproductive efficiency has differed in the type of nutritional restriction, animal model, and typically, has not specifically determined the effects of nutritional restriction on the cyclic, lactating beef cow. The typical beef cow will not experience a decrease in energy or protein intake alone, but will have an overall decline in nutrition resulting from decreases in both. Therefore, this experiment was designed to study the effects of weight loss due to decreased nutrition during the breeding period on reproductive efficiency in **cycling**, lactating beef cows.

II. LITERATURE REVIEW

The Effect of Undernutrition on Reproductive Performance

Decreased nutrition and subsequent loss of body weight in cattle reduce reproductive efficiency by decreasing pregnancy rates, increasing postpartum and calving intervals, and in severe cases, inducing nutritional anestrus (Wiltbank et al., 1962; Richards et al., 1986; Schrick et al., 1992; Burns et al., 1997).

Nutritional status of cattle both pre-calving and postpartum has been shown to adversely affect return to estrus and subsequent pregnancy rates. Wiltbank and co-workers (1962) subjected 88 multiparous cows to either high or low energy diets before and after calving to lose (Low) or maintain body weight and BCS (High). Body weight and BCS were recorded monthly and return to estrus and pregnancy rates were determined. Cows fed the high energy diet before calving had a higher rate of return to estrus than those fed the low energy diet, regardless of the diet fed after calving. These results indicate that prepartum nutrition has a more profound effect on the postpartum interval than does postcalving nutrition. Conception rates were lower in cows *fed the low energy diet after calving* (77 and 20% in low energy group vs. 95 and 95% in high energy groups) regardless of prepartum nutrition, and was mostly attributed to a failure to return to estrus. However, pregnancy rates were still reduced in the low energy group beyond those cows that failed to return to estrus. These results suggest undernutrition may affect some other facet of reproductive performance such as fertilization or embryonic development.

Dunn et al. (1969) subjected 240 pregnant heifers to either high or low energy diets prepartum, then either low, moderate, or high energy diets after calving. Only the group

fed the low energy diet postcalving lost body weight (28 kg). Sixty-four percent of cows fed the low energy diet postpartum were pregnant after 120 days compared to 72% in the moderate group and 87% in the high group. Prepartum energy intake also affected pregnancy rate during the first 80 days postpartum as 41% of heifers fed low energy diet prepartum were pregnant while 47% of heifers fed high energy prepartum were pregnant. Energy intake prior to calving also affected return to estrus. At 60 days after calving, 69% of cows fed the high-energy prepartum diet had exhibited estrus, compared to 44% in the low-energy group.

Rakestraw and co-workers (1986) used 166 mature Hereford cows to measure the effect of postpartum body weight and BCS loss on subsequent pregnancy rates. Lactating cows were allotted to 1 of 3 treatments. **MM** cows were fed to maintain BW from calving through breeding, **LM** cows were fed to lose 10% of BW from calving until breeding and then maintain BW through the 8-wk breeding season, and the **ML** cows were fed to maintain BW from calving until breeding and then lose 10-15% of BW during the breeding season. Cows in maintenance groups were given access to pasture and protein supplement while cows in low groups were not given protein supplement. Postpartum nutrition affected return to estrus as only 37% of **LM** cows were cycling (progesterone > 1ng/mL) at the beginning of the breeding season compared to 64% in **MM** and 42% in **ML**. This study was done over a 3-yr period and BW loss differed between years. In year 1, **ML** cows had reduced pregnancy rates (50%) compared to **MM** (79%) and **LM** (88%). In year 2, **ML** and **LM** cows had reduced pregnancy rates compared to **MM** (65% and 53% vs. 87%, respectively). In year 3, pregnancy rate did

not differ between groups. This study indicated the negative effects of postpartum BW loss on reproductive performance.

More evidence of the negative effect of postpartum undernutrition on reproductive performance was demonstrated by Richards et al. (1986). Three hundred fifty-five multiparous beef cows in a 3-year study were allotted to 4 different nutritional regimens. The maintain (**M**) group was fed to maintain postpartum BW through the postpartum period, while the high (**H**) and low (**L**) groups were fed to gain .45 kg/d or lose .68 kg/d, respectively, from calving through the postpartum period. The low-flush (**LF**) group was fed to lose 0.45 kg/d until 2 wk. prior to the breeding season, then were supplemented with 4-6 kg/d of ground corn and corn silage ad libitum through the first 30 days of the breeding season. Postpartum nutritional regiment had no effect on return to estrus. However, cows that calved at $BCS \geq 5$ returned to estrus sooner than cows calving at $BCS \leq 4$. Within cows calving at $BCS \leq 4$, a lower percentage of cows losing weight (**L**) had shown estrus by 20, 40 and 60 days post-calving than cows that maintained or gained weight during the postpartum period (**M, H, LF**). Cumulative pregnancy rate at d 60 were also decreased in cows calving at $BCS \leq 4$ and losing weight (**L**) compared to $BCS \leq 4$ and maintaining weight (**M, H, LF**) (68% vs. 92%, 92%, and 85%, respectively). *No differences in PPI or pregnancy rates were observed in cows that calved at $BCS \geq 5$ regardless of postpartum nutritional management, suggesting that BCS at calving has a greater effect on pregnancy rates than does postpartum nutrition, although post-calving nutritional management profoundly influences reproductive performance of cows calving in thin body condition ($BCS \leq 4$).* Calf weights were also compared among treatment groups. Calves from cows that maintained (**M**) or gained weight (**H, LF**) during the

postpartum period posted higher adjusted 205 d weights than calves from cows losing weight (**L**), (197, 195, and 194 kg vs. 182 kg, respectively).

Rutter and Randel (1984) similarly reported a negative effect of postpartum nutrient level on the interval to first estrus. In this experiment, 3 diets were used: cows were fed either 90% (**L**), 100% (**M**), or 110% (**H**) of NRC recommendations for nutrient intake. Eighty-eight percent of cows that maintained BCS post-calving (**M** and **H**) had shown estrus by d 40, compared to only 36% of cows losing BCS (**L**).

Selk and co-workers (1988) examined the relationship between prepartum nutrition and subsequent reproductive performance. In this study, 45-78 mature Hereford cows were evaluated each year for five years to determine the effect of prepartum nutrition on subsequent pregnancy rates. Cows were allotted to 1 of 4 treatments: **M** cows were fed to maintain body weight from November until calving in March-April; the remaining 3 groups were fed to lose 5% of BW from November until 8 wk prior to calving and then either maintain BW (**LM**); lose an additional 5% BW (**LL**); or gain 5% BW (**LG**) the final 8 wk before calving. Pregnancy rate of **M** cows were higher than the **LM**, **LL**, and **LG** cows (71% vs. 42%, 51%, and 58%, respectively). Body condition scores before calving and at the start of the breeding season were the most determining factors of subsequent pregnancy rates.

Rae et al. (1993) examined the relationship between BCS at pregnancy determination (60-100 days following bull removal) and pregnancy rates of over 3000 beef cows in Florida. Cows having BCS at weaning of ≤ 4 had pregnancy rate of 59% while cows at BCS ≥ 5 had pregnancy rate of 90%. Body condition is a reliable indicator of nutritional

status of cattle, and these results indicate a strong relationship between nutrition and establishment of pregnancy.

Severe nutrient restriction has been shown to cease estrous cyclicity. Richards et al. (1989) fed mature, non-lactating beef cows (avg. BCS of 5.5) to maintain BW or lose 1% BW/wk until cessation of cyclicity. After 30 wk, 10 of 11 restricted cows ceased luteal activity with 24% reduction in initial BW. Similarly, Schrick and co-workers (1992) fed mature, lactating beef cows to lose 1 kg BW/d. Cows in this study became anestrus after 13 weeks of energy restriction and a loss of 19% BW. Imakawa et al. (1986) reported cessation of estrous cyclicity at 20% BW loss after restricting beef heifers to 50% energy requirement for 26 weeks.

Reduced nutrition has adverse effects on reproductive performance. Increased calving interval and delays in rebreeding due to undernutrition are mostly attributed to increases in the postpartum interval. However, decreases in pregnancy rate have been shown beyond that of failure to return to estrus in undernourished cows (Wiltbank et al., 1962). Pregnancy rates are dependent upon follicular growth and development, ovulation of the dominant follicle, fertilization, luteal function, uterine environment, maternal recognition of pregnancy and normal embryonic development. These factors are all associated with normal estrous cyclicity preceding breeding.

The Estrous Cycle

The bovine estrous cycle consists of four phases during a 18-24 day period (as reviewed by Garverick and Smith, 1993). Estrus (d 0) is the period of sexual receptivity to the male and lasts only 12-18 hours. It is characterized by high levels of estrogen and

culminates with the ovulation of the dominant follicle following the LH surge. After ovulation, the estrous cycle enters the metestrus phase (d 1-5) characterized by the formation of the corpus luteum (CL) due to the luteinization of granulosa and theca cells. This phase is associated with rising levels of progesterone from the growing CL. Following metestrus, the longest phase of the cycle occurs known as diestrus. Diestrus (d 5-18) is the period associated with high progesterone and a mature CL. During diestrus, estradiol concentrations are low and LH pulsatility is characterized by high amplitude and low frequency. At the end of diestrus, luteolysis occurs due to the release of prostaglandin $F_{2\alpha}$ from the uterus and its feedback mechanism with oxytocin from the corpus luteum (Silvia et al., 1991). Proestrus which is characterized by the regression of the CL and declining progesterone, follows. Estradiol also increases during proestrus concomitantly with the growth and development of the ovulatory follicle. The pattern of LH activity also changes during proestrus with the pulses having low amplitude but high frequency.

The Effects of Undernutrition on the Estrous Cycle

Variation of the estrous cycle length in underfed beef heifers receiving a diet containing 85% of the NRC requirement for energy and protein has been reported (Hill et al., 1970). Variation in estrous cycle length was greater in underfed heifers (22.3 days; SD = 4.3) than controls (20.2 days; SD=1.8). However, others have seen no variation in estrous cycle length in energy restricted versus control beef heifers (Spitzer et al., 1978) or beef cows (Schrack et al., 1990b).

Experiments measuring the effect of energy restriction and weight loss on progesterone and LH secretion have also resulted in conflicting data. During the estrous cycle of energy restricted cows, progesterone has been reported to increase (Donaldson et al. 1970; Rone, 1975; McCann and Hansel, 1986), decrease (Hill et al., 1970; Gombe and Hansel, 1973; Apgar et al., 1975; Beal et al., 1978; Imakawa et al., 1983; Knutson and Allrich, 1988), or remain unchanged (Corah et al., 1974; Spitzer et al., 1978; Kazmer et al., 1985; Harrison and Randel, 1986; Schrick et al., 1990b). Similarly, LH may be increased (Gombe and Hansel, 1973; Dunn et al., 1974), decreased (Apgar et al., 1975; McCann and Hansel, 1986; Richards et al., 1989a), or remain the same (Hill et al., 1970; Rone, 1975; Spitzer et al., 1978; Kazmer et al., 1985; Knutson and Allrich, 1988; Schrick et al., 1990b) during the estrous cycle of energy restricted heifers or cows. Results are obviously conflicting regarding the effect of nutritional restriction on progesterone and LH concentrations due to differences in experimental design and animal model.

Oogenesis, Folliculogenesis, and Ovulation

Oocytes develop from primordial germ cells in the fetal ovary (Picton et al., 1998). Primordial germ cells migrate to the urogenital ridge where they remain and are referred to as oogonia. These oogonia undergo many mitotic divisions to form the finite pool of oocytes. Oogonia then enter meiosis I and become arrested at the diplotene stage before birth and then are referred to as oocytes (Picton et al., 1998). The population of oocytes at birth is only about 130,000 due to oocyte atresia (Erickson, 1966b).

Follicular development begins with the formation of primordial follicles which consist of only one layer of squamous pre-granulosa cells which are not endocrine responsive (Picton et al., 1998). Growth of the oocyte initiates with growth of the primordial follicle where it increases in size from 30 μm to 120 μm in diameter. Once follicle growth is completed with the maturation of the dominant follicle, the oocyte then resumes meiosis and is competent for fertilization.

Follicle growth in cattle occurs in two to three waves during the estrous cycle (Roche and Boland, 1991). During each follicular wave, follicles are recruited for growth and one is selected as the dominant follicle which will either ovulate or undergo atresia (as reviewed by Garverick and Smith, 1993). Follicular recruitment occurs with a rise in FSH which initiates growth of the recruited follicles. Growth of these follicles is dependent on LH. The factor(s) that causes selection of the dominant follicle is not understood but secretion of inhibin by the dominant follicle inhibits FSH and causes atresia of other recruited follicles. The dominant follicle that results from the first follicular wave during the luteal phase of the estrous cycle cannot ovulate but rather regresses because of the lack of a LH surge which is suppressed by high concentrations of progesterone. The dominant follicle that results from the follicular wave at the end of the luteal phase will undergo ovulation. Regression of the corpus luteum by prostaglandin $\text{F}_{2\alpha}$ (d 18 of estrous cycle) results in rapid decline in progesterone production. This removes the inhibition of estradiol by progesterone. Estradiol concentrations rise and LH frequency increase, causing ovulation of the dominant follicle (reviewed by Haresign et al., 1983). The LH surge causes the oocyte to resume meiosis,

which results in the expulsion of a polar body and arrest at metaphase II of meiosis, capable of fertilization.

The Effects of Undernutrition on Oogenesis, Folliculogenesis, and Ovulation

Undernutrition has been shown to affect follicular development. Perry and co-workers (1991) reported a decrease in appearance rate of small and large follicles in lactating, beef cows following postpartum energy restriction and a decrease in appearance rate of large follicles following prepartum energy restriction. Hill et al. (1970) reported a decrease in follicle populations in energy and protein restricted heifers after 10-12 days of undernutrition. Results from Burns et al. (1997) revealed beef cows on a restricted energy diet had smaller diameter ovulatory follicles and decreased follicular growth of large follicles in the two estrous cycles preceding either anestrus or formation of subfunctional corpus lutea. Fazio et al. (1999) found a strong tendency for a greater follicular population in good conditioned cows (BCS 5-6) vs. thin conditioned cows (BCS of 3-4). In contrast, Schrick et al. (1990a) found no effect of energy restriction on follicle number, maximum follicle size, or days to appearance of ovulatory follicles during the period from d 16 of estrous cycle prior to and until d 11 of cycle during which cows became anestrus. Nolan et al. (1998) found greater follicle populations in beef heifers on low energy diet compared to high energy diet after administration of superovulatory regime.

Greer and co-workers (1992) proposed that undernutrition reduces the probability of normal oocyte development in cattle. A recent study performed in our laboratory tested the effects of body condition score on developmental competence of immature oocytes *in*

vitro (Fazio et al., 1999). Body condition scoring has been utilized as a successful method for determining nutritional status in cows (Randel, 1990). Ovaries were collected post-mortem from thin (BCS 3-4) and good (BCS 5-6) conditioned cows. Oocytes were collected from follicles and underwent *in vitro* maturation, fertilization, and culture. The results of this experiment determined that lowered body condition score had no subsequent effect on oocyte development and competence. However, metabolic profiles of these animals suggested that body condition and weight were being maintained; therefore, the effect of weight loss was not tested.

Britt (1992) suggested that loss of body weight can affect fertility several weeks after loss has occurred. It is estimated that premature antral follicles require sixty days for development to the ovulatory stage. Thus, follicles that begin growth during periods of negative energy balance may be exposed to negative metabolic conditions that leaves the follicle dysfunctional. Erickson (1985) suggested that the growing oocyte was the most susceptible to negative effects of environmental toxins or stress. This susceptibility would adversely affect oocyte quality, progesterone secretion, and ultimately fertility. Kendrick et al. (1999) examined the effects of energy restriction on oocyte quality in lactating dairy cows. Oocytes were removed from follicles > 2 mm in diameter *in vivo* via transvaginal ultrasound-guided aspiration. They found cows fed a high energy diet and in positive energy balance produced more good quality oocytes than cows fed a low energy diet in negative energy balance. Nolan and co-workers (1998) compared oocyte quality and development in superovulated beef heifers receiving either a high energy diet (BW gain 0.25 kg/head/d) or low energy diet (BW loss 1.3 kg/head/d). There was no

difference in morphological grade of oocytes or cleavage rate between control and restricted heifers.

Effects of undernutrition on ovulation can be seen with increases in the postpartum interval which is a delay to the first ovulation after parturition. A delay to first ovulation has been reported by Wiltbank et al. (1962), Spitzer et al. (1978), and Perry et al. (1991).

Development of the Corpus Luteum

The primary function of the corpus luteum is the production of progesterone which is the hormone responsible for maintaining pregnancy (Sawyer, 1995). Development of the corpus luteum begins with the luteinization of theca and granulosa cells prior to ovulation (Donaldson and Hansel, 1965). Luteinization of these cells is caused by the preovulatory surge of luteinizing hormone (LH). Luteinization transforms theca cells to small luteal cells and granulosa cells to large luteal cells (Donaldson and Hansel, 1965). Fitz et al. (1982) found that small luteal cells contain LH receptors and increase progesterone synthesis with administration of LH. Large luteal cells do not contain LH receptors and therefore are not responsive to LH (Fitz et al., 1982). Concentrations of these cells change throughout the lifespan of the corpus luteum. Small luteal cells are more predominant during early CL development (d 4 of the estrous cycle) while large luteal cells are more numerous in the mature CL (d 15). Large luteal cells have receptors for $\text{PGF}_{2\alpha}$ which allows for luteolysis at d 18 of the estrous cycle.

Luteolysis occurs at d 18 of the estrous cycle in cattle. Increasing estrogen production from growing follicles increases oxytocin receptors in the uterus (Silvia et al., 1991). Tonic release of oxytocin from the pituitary binds to the oxytocin receptors and causes a

release of $\text{PGF}_{2\alpha}$ from the uterus. Prostaglandin $\text{F}_{2\alpha}$ binds to the large luteal cell and causes the release of oxytocin. Oxytocin released from the CL then enters a feedback mechanism, releasing additional $\text{PGF}_{2\alpha}$ from the uterus which results in luteolysis of the CL. Four to five pulses of $\text{PGF}_{2\alpha}$ are needed for complete regression of the corpus luteum.

The Effect of Undernutrition on the Corpus Luteum

Undernutrition has been shown to adversely affect corpus luteum development. Decreased weight of the corpora lutea of undernourished beef cows has been reported (Hill et al., 1970; Burns et al., 1997). In contrast, Imakawa et al. (1983) found no effect of energy restriction on corpus luteum weight. Spitzer et al. (1978) found no difference in corpus luteum volume between energy restricted and control beef heifers. Schrick et al. (1992) reported that lactating beef cows experiencing energy restriction developed subfunctional corpora lutea in the estrous cycle preceeding nutritional anestrus with decreased progesterone production, but corpus luteum weight and size, and LH receptor number were similar as was *in vitro* production of progesterone. Burns et al. (1997) reported non-lactating beef cows experiencing severe energy restriction either developed a subfunctional corpus luteum prior to anestrus or had a functional corpus luteum prior to anestrus.

Fertilization, Embryonic Development, Maternal Recognition of Pregnancy, and Fetal Attachment

Once the oocyte has been expelled from the ruptured follicle, it is captured by the infundibulum of the oviduct. It then proceeds down the oviduct through the ampulla to the ampulla-isthmus junction (AIJ). Upon insemination and movement of sperm through the uterus to the AIJ, fertilization occurs. After fertilization, the 1-cell embryo travels through the isthmus and reaches the uterus at day 5 of embryonic development as a morula stage embryo (16-32 cells). Morula embryos then undergo compaction and form blastocysts between days 7-9 of embryonic development. Blastocyst embryos then hatch from the zona pellucida and become filamentous (Garverick and Smith, 1993). It has been suggested that the majority of reproductive failure due to embryo mortality occurs during the time period from insemination until day 14 of embryonic development (Dunne et al., 2000).

Maintenance of pregnancy is dependent on prevention of luteolysis by $\text{PGF}_{2\alpha}$ and oxytocin and is termed maternal recognition of pregnancy. This is accomplished by bovine interferon-tau ($\text{bIFN-}\tau$), a product produced by the conceptus, that prevents regression of the corpus luteum (as reviewed by Thatcher et al., 1995). Interferon-tau binds to the uterine epithelium and prevents $\text{PGF}_{2\alpha}$ pulses from the uterus; thereby, rescuing the corpus luteum and maintaining pregnancy.

The Effect of Undernutrition on Establishment of Pregnancy

Most research has focused on the effects of reduced nutrition on pregnancy rates, fertilization rates, follicular development and luteal function. Differences in fertilization

rates have been reported in beef heifers consuming an energy and protein restricted diet (Hill et al., 1970). Heifers were fed either a maintenance or restricted diet (85% NRC requirement for energy and protein) beginning d 4 after mating. Heifers were slaughtered on either days 3, 8, or 18 and ova recovered. Fertilization rates were lower for restricted heifers compared to controls. However, significant differences in fertilization rates were observed between days 3 and 18, suggesting that mechanisms occurring during this time frame may be influenced by nutritional stress. Conversely, Spitzer et al. (1978) reported no reduction in fertilization rates in energy restricted versus control beef heifers, leading them to hypothesize that reduced pregnancy rates observed in energy restricted heifers were the result of embryonic loss occurring after day 4.

A reduction in dietary intake has also been beneficial to embryo development in cattle. Nolan and co-workers (1998) found the percentage of embryos reaching blastocyst increased in energy restricted versus beef heifers receiving high energy intake following superovulation. In sheep, pregnancy rates on d 8 were not decreased in ewes fed low dietary energy for 14 days prior to synchronized breeding. However, a significant proportion of embryos recovered from restricted ewes were at earlier stages of development (morula and early blastocyst), while controls were 100% expanded blastocyst (Abecia et al., 1997).

Other experiments have been conducted to study the effects of excess dietary protein on embryonic development. Data from these experiments implicate excess dietary protein in reducing embryo quality (Butler, 1998). Endometrial tissue collected from cows receiving excess dietary protein released higher amounts of prostaglandin $F_{2\alpha}$ during culture. Increased uterine concentrations of prostaglandin $F_{2\alpha}$ have been

negatively associated with embryonic development and resulted in embryonic mortality (Schrick et al., 1993; Buford et al., 1996; Hockett et al., 1998; Seals et al., 1998; Lemaster et al., 1999).

III. MATERIALS AND METHODS

Experimental Design

Spring-calving, multiparous Angus, Hereford and crossbred beef cows were utilized to determine the effect of undernutrition on reproductive performance during 2 production years (1999, n = 85; 2000, n = 84). Cows were randomly allotted by weight, BCS, calving date, age, and breed to either a low nutrition (**RES**) or a control (**CON**) group.

All cows calved from January through March, except 6 cows which were integrated into the spring calving herd after elimination of the fall-calving herd in 1999. **RES** cows were fed to lose 5% of their body weight (BW) during the first 30 days of the experiment, 5% during the second thirty days, and 5% during the final thirty days of the experiment (Figure 1). Fifteen percent loss in BW was targeted to achieve adequate nutrient restriction without ceasing estrous cyclicity. Nutritional anestrus has been initiated after 19-25% loss in BW (Imakawa et al., 1986; Richards et al., 1989; Schrick et al., 1992). **CON** cows were fed to maintain or gain BW and body condition (BCS) throughout the experiment. **RES** cows were restricted by limited grazing using temporary fencing and limited access to grass hay before sufficient pasture growth. Body weight and BCS were maintained in **CON** cows by ad libitum access to pasture and grass hay as well as supplementation with corn silage. The loss or maintenance of BW was controlled by pasture management on a weekly basis after analysis of BW loss or gain of previous week.

Weight, BCS, and blood samples were collected weekly for the duration of the experiment. Weight and BCS measurements were taken on consecutive days at the initiation and end of experiment. Body condition was scored according to the 1996 NRC

Nutritional Restriction Weekly Blood Samples, BW, and BCS

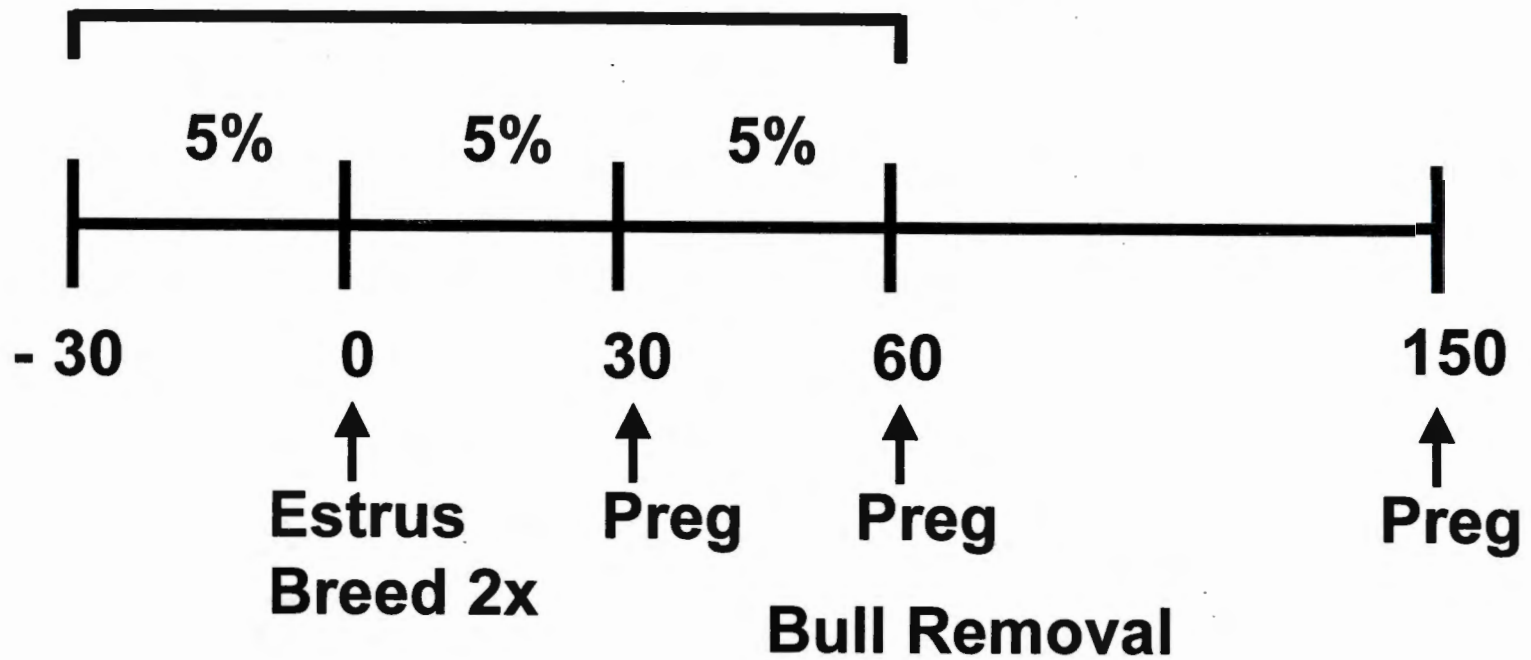


Figure 1. Schematic of Experimental Design

Nutritional Requirements for Beef Cattle (BCS, scale 1-9; NRC, 1996). Calf weights were taken every 30 days in year 2.

Cows were maintained on respective nutritional regimens for 30 days prior to the breeding season. All cows were cycling ($P_4 \geq 1.0$ ng/mL) at the beginning of the breeding season. Synchronization of estrus was achieved using the Select Sync protocol. In brief, cows were administered a 2 ml injection of GnRH (100 µg; Cystorelin; Merial; Iselin, NJ) intramuscularly on d -9 (d 0; start of breeding season). A 25 mg intramuscular injection of $PGF_{2\alpha}$ (Lutalyse; Pharmacia Animal Health; Kalamazoo, MI) was administered on d -2. Cows were observed for estrus with the aid of KMAR patches for 1 hour at 7:00 AM and 5:00 PM each day beginning at $PGF_{2\alpha}$ administration. Cows were bred via artificial insemination at onset of estrus and 12 h later by experienced technicians.

Angus and Gelbvieh bulls which had fulfilled the requirements of the breeding soundness examination were placed into **RES** and **CON** groups (2 per trt) for the remaining 60 days of the breeding season. Bulls were alternated between **RES** and **CON** groups on d 30 of the breeding season. Pregnancy confirmation and crown-rump length were determined by ultrasonography (7.5 MHz; Aloka, Corometrics Medical Systems; Wallingford, CT) at d 30, 60, and 150.

Blood Collection, Radioimmunoassays and Spectrophotometry

Blood samples were collected weekly via jugular venipuncture and placed immediately on ice. After collection, blood samples were centrifuged at 2000 x g for 30 minutes. Serum was then decanted and stored at -20°C until assayed for insulin, progesterone, non-esterified fatty acids (NEFA), and blood urea nitrogen (BUN).

Radioimmunoassays (Coat-A-Count; Diagnostic Products Corporation; Los Angeles, CA) were performed to determine concentrations of insulin and progesterone. Progesterone and insulin assays were performed as described by Seals et al. (1998) and Fazio et al. (1999), respectively. Sensitivity of the insulin assay was 0.05 ng/tube (200 µL sample volume) with intra- and inter-assay coefficients of variation (CV) of 3% and 10%, respectively. Progesterone assay sensitivity was 0.02 ng/tube (100 µL sample volume). Intra and inter-assay CV's for progesterone assays were 7% and 9%, respectively.

Spectrophotometry assays were used to determine NEFA and BUN concentrations. NEFA concentrations were determined with a NEFA-C kit (Wako Pure Chemical Industries, Osaka, Japan) as described by Fazio et al. (1999) with a sensitivity of 125 mEq/mL (50 µL sample volume) and an intra-assay CV of 9% and inter-assay CV of 4%. Blood urea nitrogen concentrations were determined using a urea nitrogen kit (Sigma Diagnostics, St. Louis, MO) as described by Fazio et al. (1999). Blood urea nitrogen assay sensitivity was 15 mg/dL (5 µL sample volume) and the intra and inter-assay CV's were 5% and 6%, respectively.

Concentrations of progesterone were evaluated to determine estrous cyclicity of females by initiation of the breeding season. Cows were considered cyclic when P_4 concentrations ≥ 1.0 ng/mL. Cows which did not meet this criterion were excluded from analysis.

Insulin, NEFA, and BUN assays were performed to quantify and verify nutritional restriction. Decreases in insulin concentrations during nutritional restriction are necessary to increase fatty acid oxidation to meet the animal's metabolic requirements during a fasted state (McCann and Hansel, 1986). The mobilization of fat tissue to meet metabolic requirements results in increased NEFA concentrations in blood (Emery et al., 1992).

Severe nutrient restriction results in increases in BUN concentrations. Increased BUN concentrations are the result of muscle tissue breakdown being used to provide energy to meet metabolic demands (Ellenberger et al., 1989) or excess crude protein in the diet (Canfield et al., 1990).

Statistical Analysis

Comparisons between RES and CON for body weight, body condition, insulin, non-esterified fatty acids, urea nitrogen, and embryo crown-rump length were determined by analysis of variance using the MIXED procedure (SAS, 1996). Body weight, body condition, crown-rump length and assay data were analyzed using a randomized block split plot design for repeated measures. Estrous response, pregnancy rates, and conception rates were analyzed using chi square analysis. Proc LIFEREG was used to analyze interval to estrus following administration of $PGF_{2\alpha}$.

IV. RESULTS

Body Weight, Body Condition, and Calf Performance

Restricted cows lost 56.9 kg, while CON cows gained 10.8 kg during the experimental period. At the start of the breeding season, BW was lower in RES versus CON cows (Figure 2A, $P < 0.05$). Similarly, BW at d 60 was lower in RES versus CON cows (Figure 2A, $P < 0.05$). At the end of the experimental period, body condition decreased 1.0 BCS unit in RES cows, and increased 1.0 BCS unit in CON cows. Body condition was lower in RES cows compared to CON at the initiation of the breeding season and at d 60 (Figure 2B, $P < 0.05$).

The loss of BW and BCS in RES cows also affected calf gain. In year 1, weaning weight was lower in RES compared to CON calves (Figure 3A, $P < 0.05$). In year 2, birth weight and on-test weight (d -30) were similar for RES and CON calves (Figure 3B). However, body weight was lower on d 30, d 60, and at weaning in RES versus CON calves (Figure 3B, $P < 0.05$).

Endocrine and Metabolic Profiles

Restricted and CON cows had similar serum insulin concentrations at the initiation of the experiment (Figure 4A). Insulin concentrations of CON cows were similar on d -30 and d 60 (Figure 4A), while insulin was lower on d 60 in RES cows versus d -30 (Figure 4A, $P < 0.05$). Non-esterified fatty acid concentrations were not different between RES and CON cows on d -30 (Figure 4B). Restricted cows NEFA concentrations were higher on d 60 compared to d -30 (Figure 4B, $P < 0.05$). Concentrations of NEFA in CON cows decreased during the experimental period (Figure 4B, $P < 0.05$). Serum NEFA

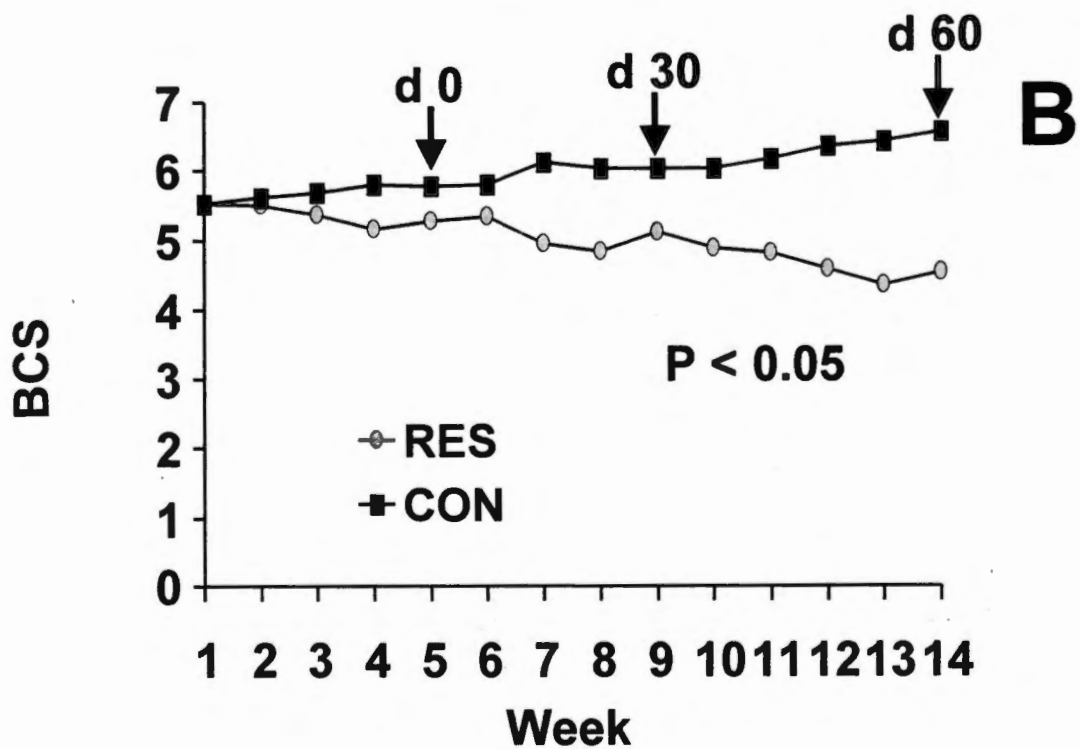
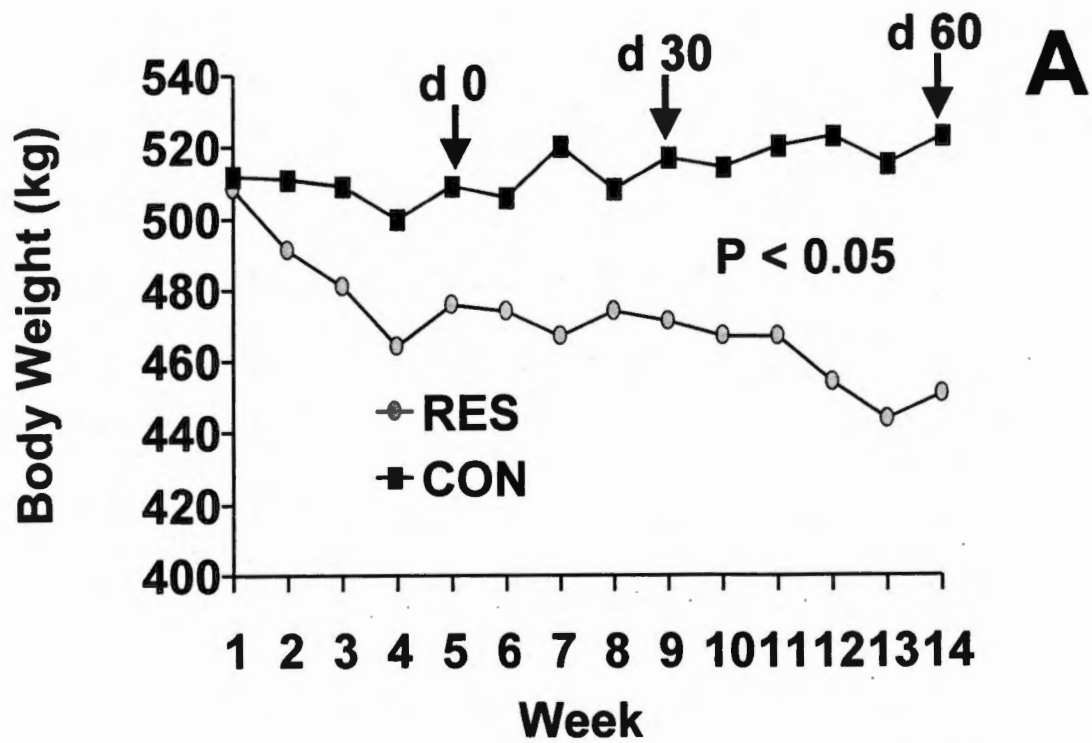


Figure 2. Body weight (A) and BCS (B) of RES and CON cows collected during experimental period. Significant differences are noted on days 0, 30, and 60.

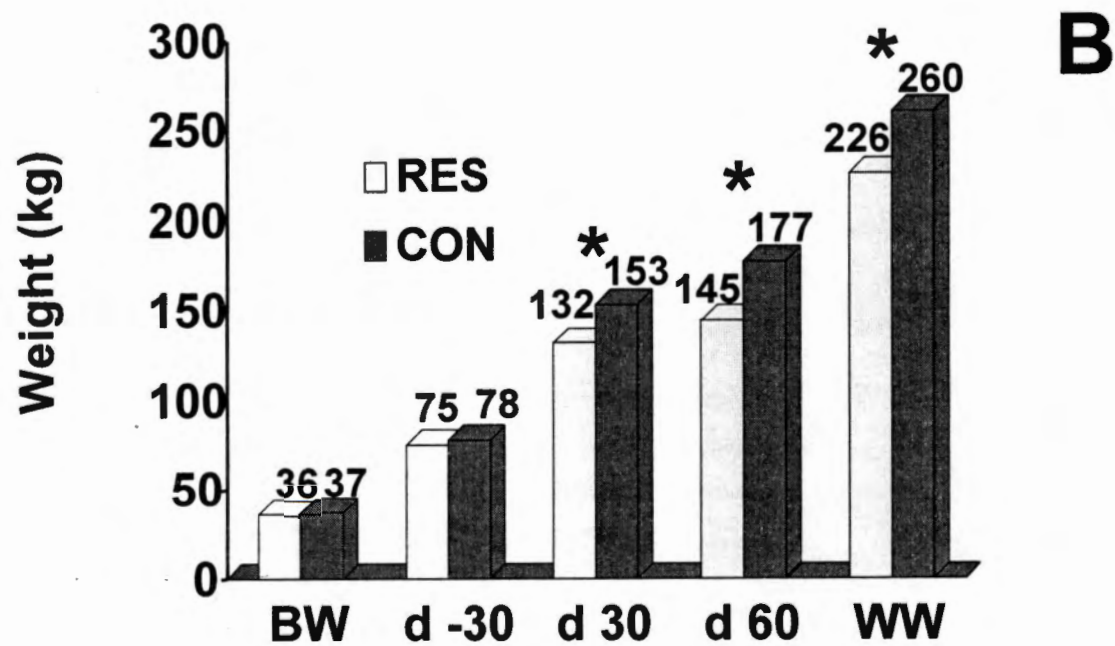
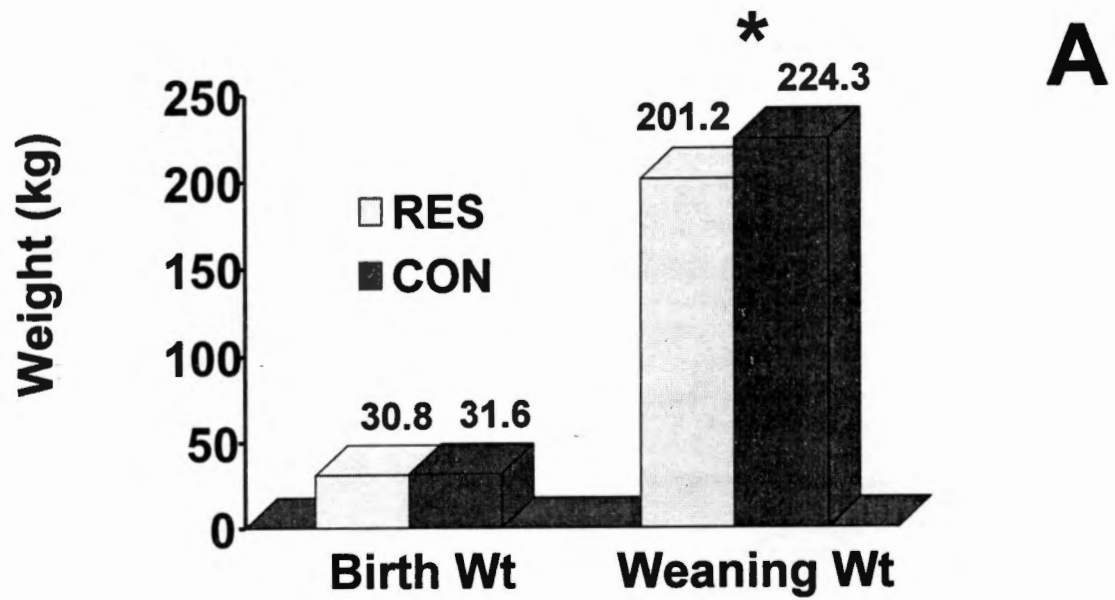


Figure 3. Body weight of **RES** and **CON** calves collected during Year 1 (A) and Year 2 (B). Means with (*) differ ($P < 0.05$).

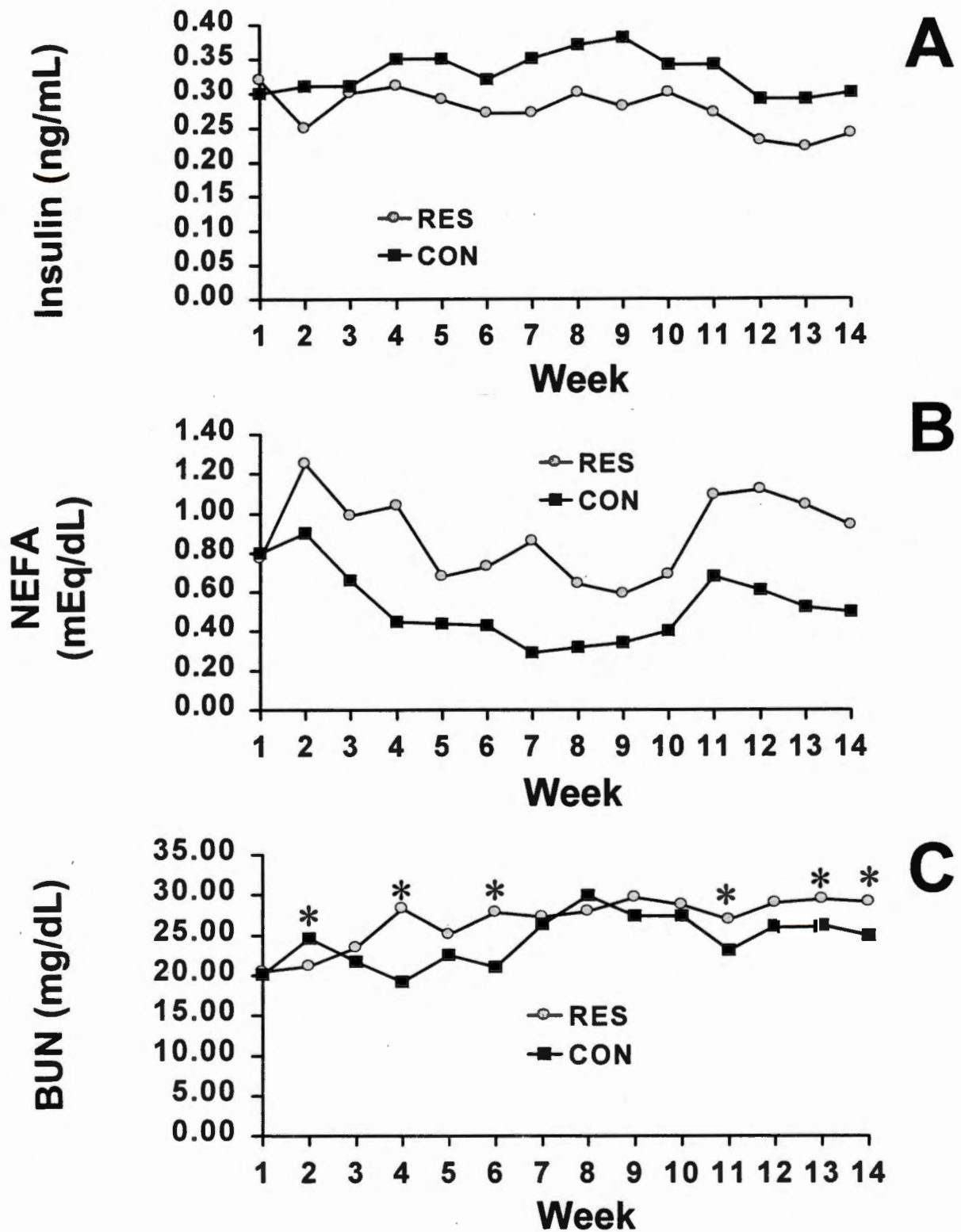


Figure 4. Serum concentrations of insulin (A), NEFA (B) and BUN (C) for RES and CON collected during experimental period. Means with (*) differ between CON and RES ($P < 0.05$). Insulin concentrations increased from d -30 to d 60 in RES ($P < 0.05$) and NEFA and BUN increased in RES from d -30 to d 60 ($P < 0.05$).

concentrations were higher in **RES** cows compared to **CON** on d 60 (Figure 4B, $P < 0.05$).

Blood urea nitrogen concentrations were similar on d -30 in **RES** and **CON** cows (Figure 4C). Concentrations of BUN in **RES** and **CON** animals increased throughout the experimental period (Figure 4C). However, BUN concentration was higher on d 60 in **RES** cows compared to **CON** (Figure 4C, $P < 0.05$).

Reproductive Performance

The response to estrous synchronization did not differ between **RES** (86.3%) and **CON** cows (88.3%; $P = 0.71$; Figure 5A). Likewise, the time interval from estrous synchronization to first observed estrus was similar for **RES** (2.5 days) and **CON** (2.6 days; $P = 0.45$; Figure 5B) groups.

No difference was observed in conception rates between **RES** and **CON** cows (68.2 vs. 76.4%, respectively; $P = 0.29$; Figure 6A). Pregnancy determination on d 30 revealed no difference in pregnancy rates between **RES** (58.9%) and **CON** cows (67.5%; $P = 0.27$; Figure 6B). Similarly, **RES** and **CON** cows did not differ in cumulative pregnancy rates on d 60 (89.0 vs. 93.5%, respectively; $P = 0.33$; Figure 7A) or d 150 (91.7 vs. 96.1%, respectively; $P = 0.26$; Figure 7B). Crown-rump length of embryos from A.I. pregnancies was collected on d 45 in year 1 and d 30 in year 2. Crown-rump length of embryos did not differ between **RES** and **CON** embryos in year 1 (25.7 ± 0.6 vs. 26.9 ± 0.6 mm, respectively; $P > 0.05$; Figure 8A) or year 2 (11.5 ± 0.2 vs. 10.8 ± 0.2 mm, respectively; $P > 0.05$; Figure 8B).

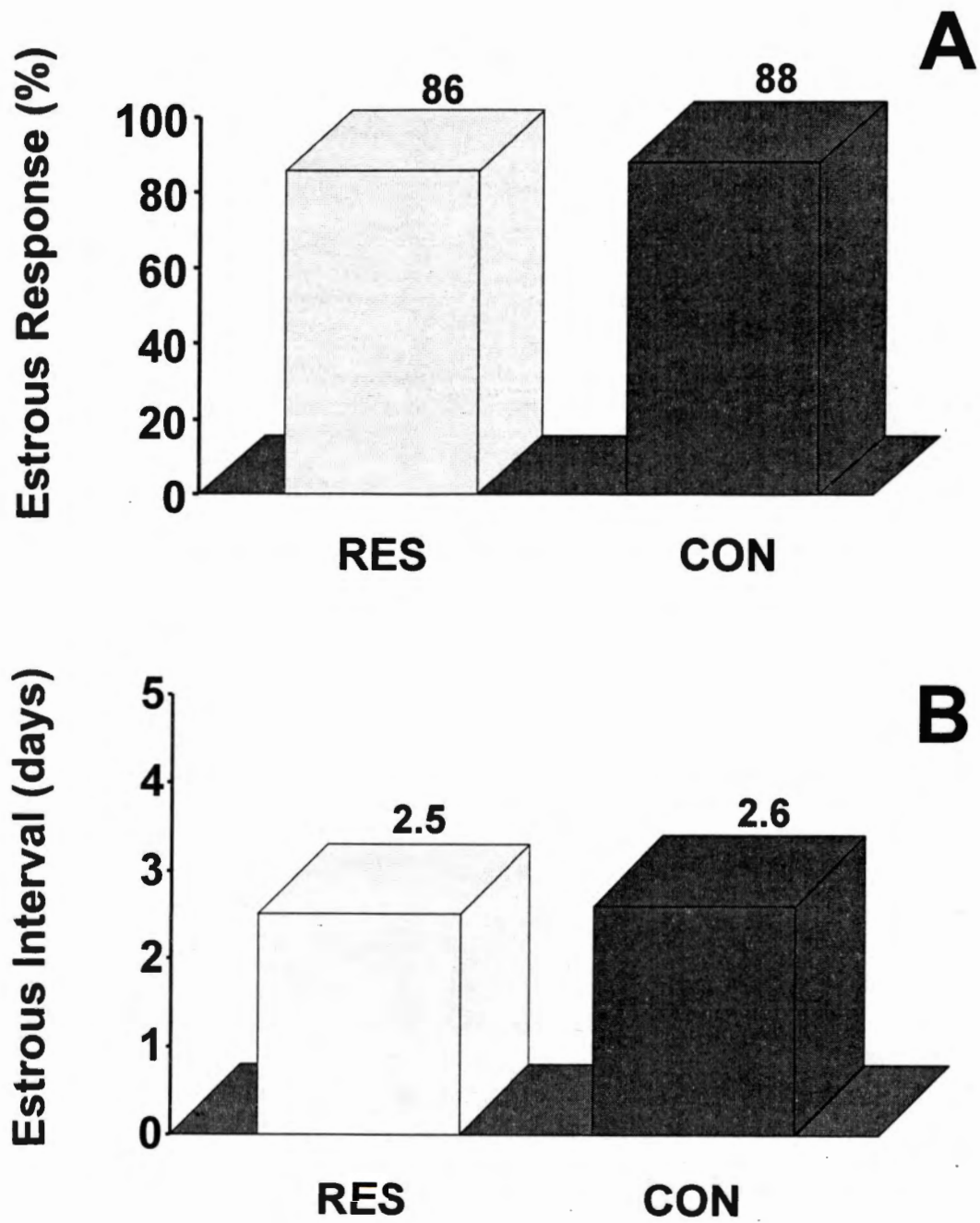


Figure 5. Estrous response (A; $P = 0.71$) and estrous interval (B; $P = 0.45$) collected from RES and CON cows.

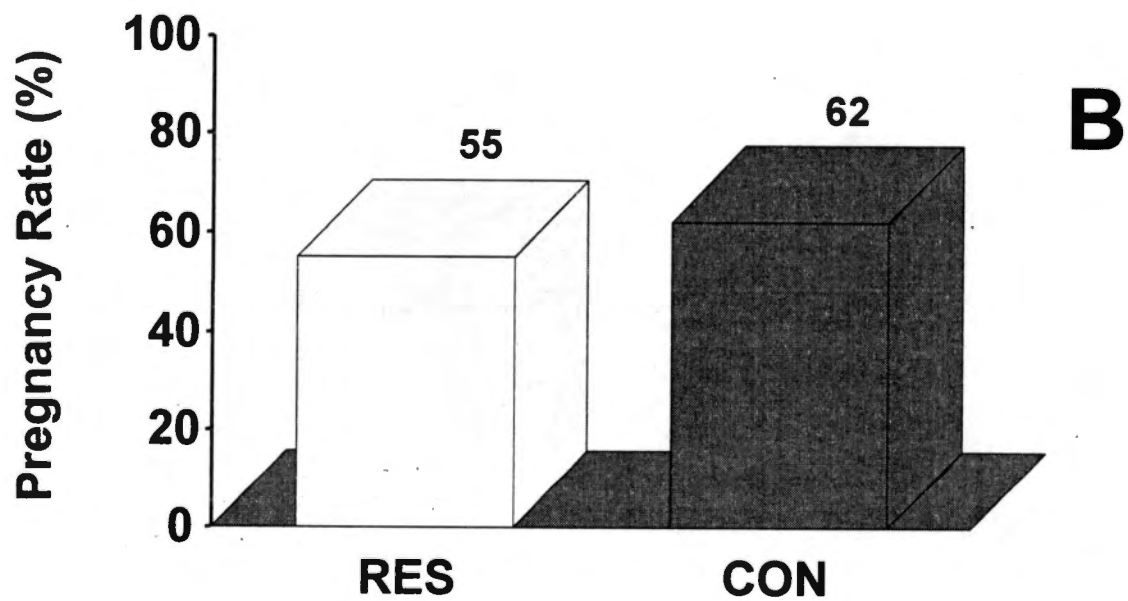
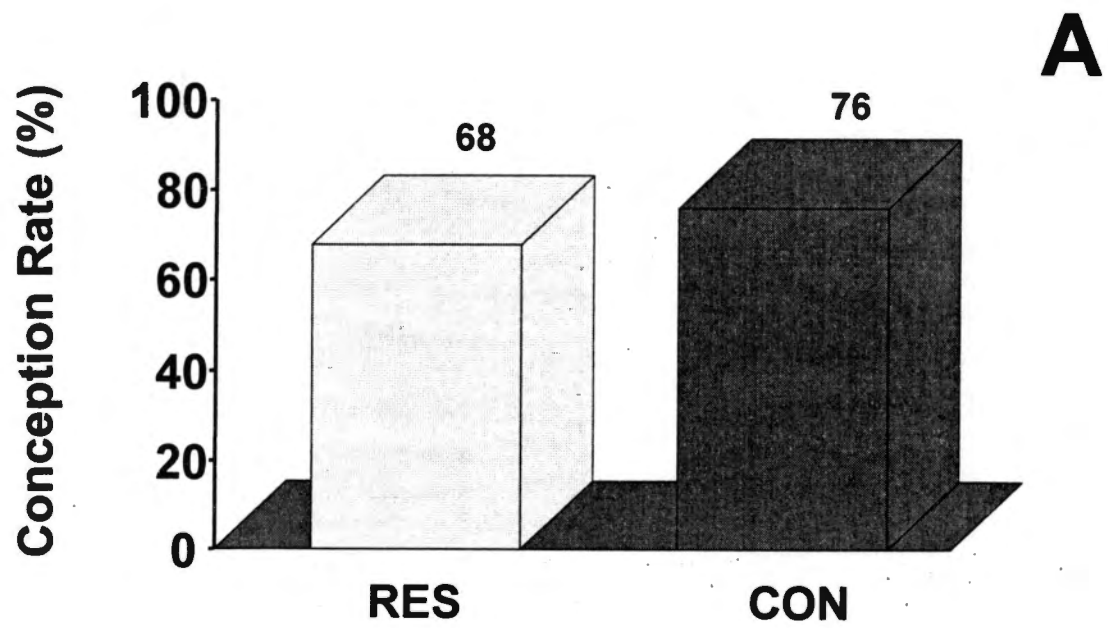


Figure 6. Conception rates (A; $P = 0.29$) and d 30 pregnancy rates (B; $P = 0.57$) collected from RES and CON cows.

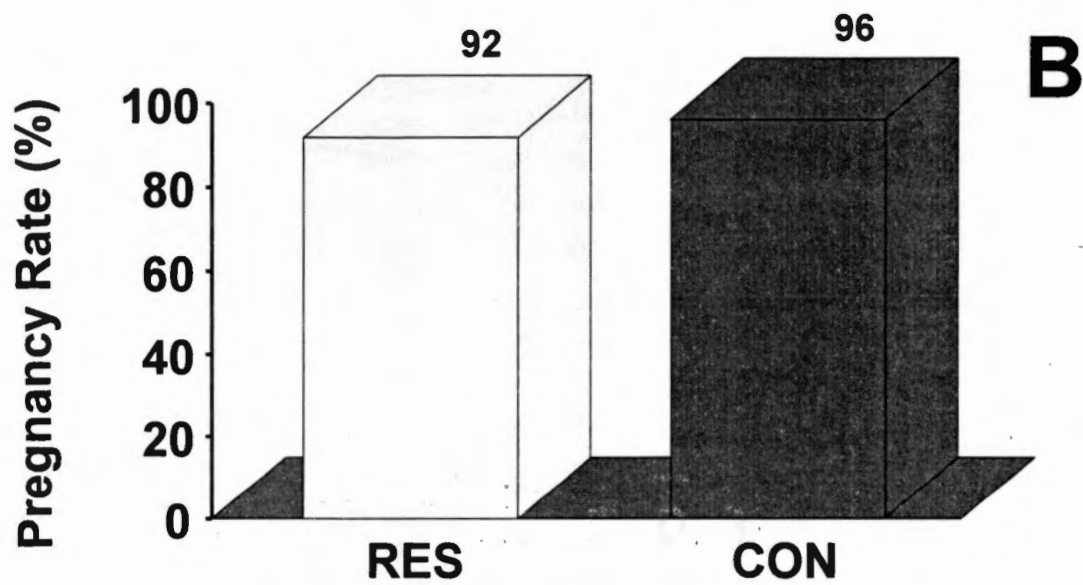
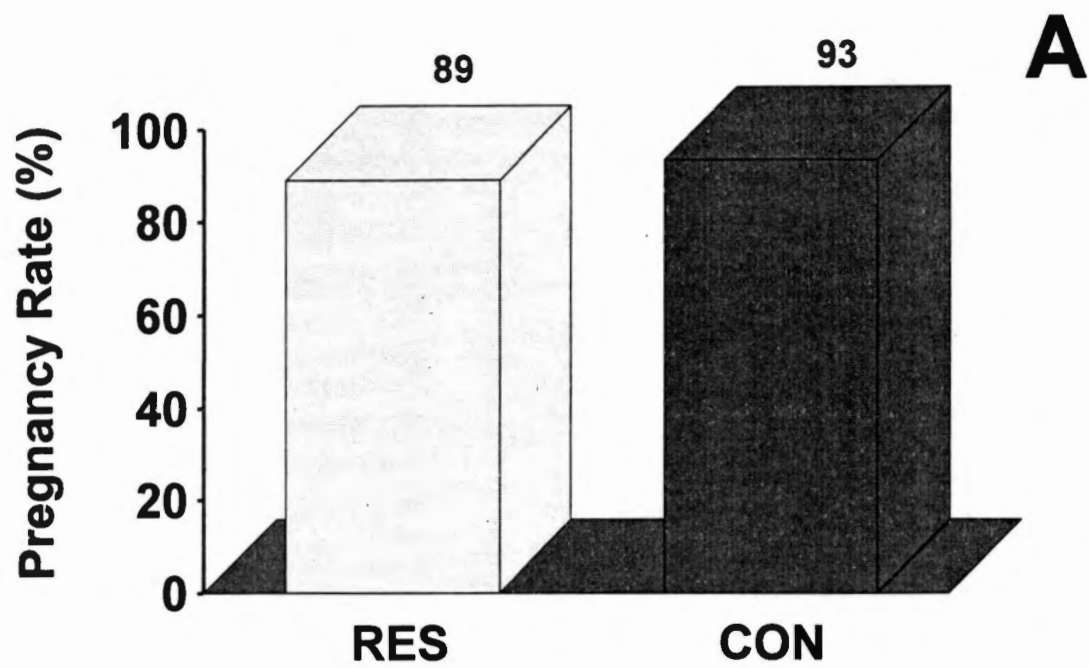


Figure 7. Pregnancy rates of **RES** and **CON** cows collected on d 60 (A; $P = 0.33$) and d 150 (B; $P = 0.26$).

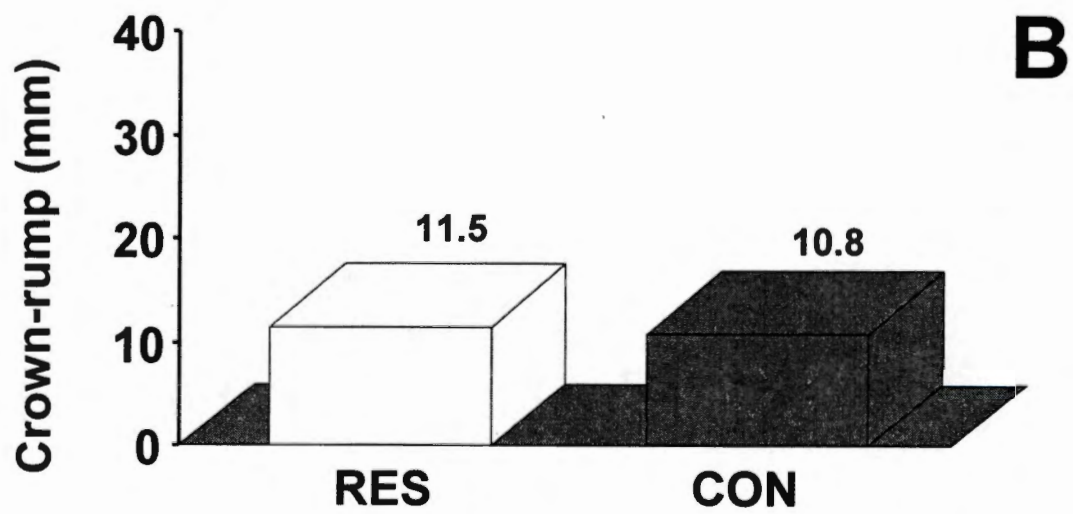
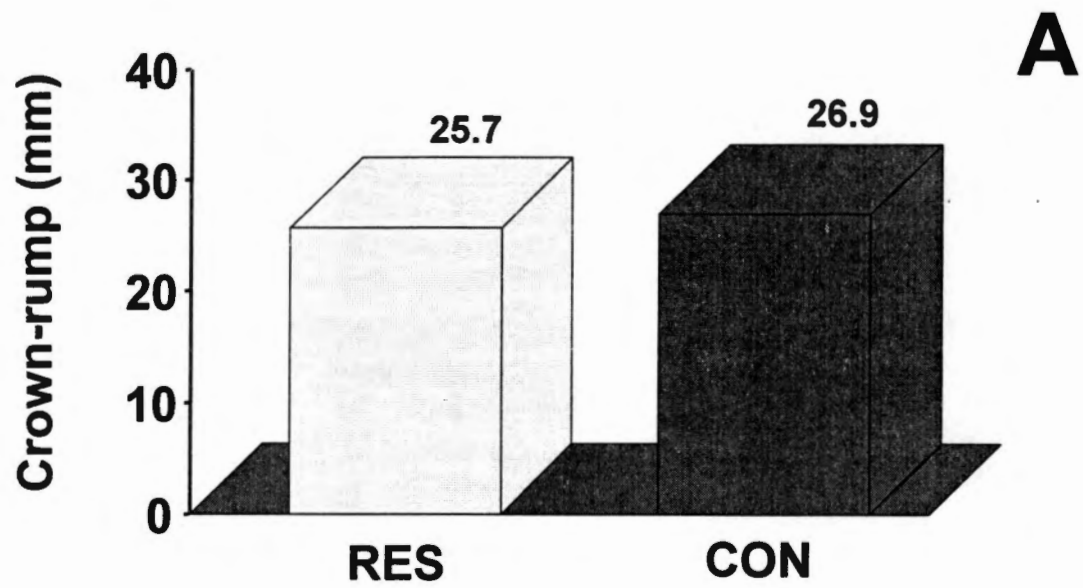


Figure 8. Crown rump length of **RES** and **CON** embryos collected on d 45 in year 1 (A; $P > 0.05$) and at d 30 in year 2 (B; $P > 0.05$)

In year 1, one cow from **CON** and **RES** groups experienced fetal loss between d 30 and 60. However, the **RES** cow was confirmed pregnant on d 150 from a subsequent natural service mating. In year 2, one cow from **RES** and **CON** animals lost embryos, but only the **CON** cow was able to establish another pregnancy by d 150. No year effects were observed on estrous response and interval, conception rates, or pregnancy rates.

V. DISCUSSION

Body Weight, Body Condition, and Calf Performance

Body weight of **RES** cows decreased 11% (56.9 kg) during the experimental period. While this did not achieve the targeted loss of 15%, the 11% decrease in BW is an acceptable loss capable of achieving nutritional restriction. Rakestraw and co-workers (1986) similarly managed mature, lactating beef cows to lose 10% BW from calving to the initiation of the breeding season or lose 10% of BW during the sixty day breeding season; whereas, Dunn et al. (1969) achieved a loss in BW of 28 kg in energy-restricted beef heifers. Less severe body weight loss has been used to establish nutritional restriction as in Selk et al. (1988) who achieved prepartum BW losses of 5 and 10%. Our objective to lose 15% BW during the 90 day experimental period was to obtain substantial nutrient restriction without ceasing estrous cyclicity, as has been achieved by BW losses of 19% (Schrack et al., 1992), 20% (Imakawa et al., 1986), and 24% (Richards et al., 1989).

Body condition score similarly decreased in **RES** cows consistent with the reduction in weight loss. However, **CON** cows' BCS increased 1 unit, while gaining only 10.8 kg. A 1 unit change in body condition contains 55 kg of BW (NRC, 1996). This discrepancy is probably due to subjective technician observation. Weight, BCS, and blood samples were collected from **RES** before collection of data from **CON** cows. This order may have biased BCS measurements from **CON** cows. Alternating the order in which groups are worked and observed, as well as, observations by more than one technician may be useful to alleviate bias in future studies.

Further evidence of the nutritional stress imposed on **RES** cows is the subsequent growth performance of suckled calves. In year 1, calf BW was taken at weaning and revealed a significant decrease in average daily gain (ADG) of **RES** calves compared to **CON** even though **RES** cows were restored to normal nutritional management at the conclusion of the experiment. In year 2, calf weights were taken on d -30, d 30, d 60, and at weaning. Body weight was significantly lower in **RES** calves after sixty days of feed restriction and continued to be lower throughout the experiment and at weaning. These results concur with those of Richards et al. (1986) who reported a decrease in 205 d weights of calves from beef cows losing weight compared to calves from beef cows gaining or maintaining BW during the postpartum period.

Endocrine and Metabolic Profiles

Insulin concentrations decreased throughout the experimental period in **RES** cows. These results are consistent with past research (McCann and Hansel, 1986; Richards et al., 1989; Schrick et al., 1990; Schrick et al., 1992) that reported decreases in insulin concentrations in animals experiencing nutritional restriction are necessary for the induction of fatty acid oxidation which is necessary to provide energy to meet metabolic demands.

Similarly, the increase in serum non-esterified fatty acid concentrations in **RES** cows during the experimental period confirms the mobilization of body fat reserves to serve as an alternate energy source during nutritional restriction (Emery et al., 1992). In contrast, Schrick et al. (1990) reported no increase in NEFA concentrations following 30 days of energy restriction in cycling, beef cows. Consequently during the last three weeks of the

experiment, concentrations of urea nitrogen in **RES** cows increased more dramatically, evident of a more severe nutrient restriction. Schrick et al. (1990) reported similar increases in BUN concentrations following energy restriction. This increase in urea nitrogen levels is indicative of the breakdown of muscle tissue to provide amino acids for gluconeogenesis to provide energy for metabolic use (Ellenberger et al., 1989).

Reproductive Performance

The objective of this experiment was to determine the effect of decreasing body weight on pregnancy rates in cows that have resumed estrous cyclicity by the beginning of the breeding season. This study was designed to establish a reduction in body weight and BCS due not only to a restriction in energy or protein alone, but due to restrictions of both. Previous studies have varied in the type of nutritional restriction (energy vs. protein restriction), animal model (cow vs. heifer), and physiological state (lactating vs. non-lactating). Past research has neglected to delineate whether reduced pregnancy rates due to undernutrition are the result of a failure to establish and maintain pregnancy or failure to reinitiate estrous cyclicity.

All cows had reinitiated cyclicity by the beginning of the breeding season as cows had recorded progesterone concentrations ≥ 1 ng/mL. Nutritional restriction did not affect response to synchronization as estrous data and time interval from prostaglandin $F_{2\alpha}$ administration to onset of estrus did not differ between **RES** and **CON** cows. Previous studies have reported a negative impact of undernutrition on the percentage of cows that return to estrus and subsequent pregnancy rates (Wiltbank et al., 1962; Dunn et al., 1969; Rakestraw et al., 1986). However, these studies imposed nutritional restriction

prepartum and/or from calving until the initiation of the breeding season. These studies have clearly demonstrated the importance of pre- and postpartum nutrition on cows' ability to reinitiate cyclicity postpartum. Consequently, conception and pregnancy rates have been decreased in these experiments and are no doubt the result of the cows' inability to establish postpartum cyclicity.

No difference was observed in conception rate between **RES** and **CON** cows. This is in contrast to Wiltbank et al. (1962) who reported significantly lower conception rates in beef cows receiving a low energy diet versus cows receiving a high energy diet after calving. Furthermore, pregnancy rates did not differ between **RES** and **CON** cows on d 30, d 60, or d 150. These are also in disagreement with results reported by Wiltbank and co-workers (1962), Dunn et al.(1969), and Rakestraw et al. (1986) who found decreased pregnancy rates after nutritional restriction. Likewise, no difference was observed in embryo crown-rump length in either year 1 or year 2. However, in contrast to previous studies, all cows in the current experiment had reinitiated cyclicity by the beginning of the breeding season.

Results from this study are in agreement with those of Richards et al. (1986) and Rae et al. (1983) who suggested BCS at calving has a greater impact on pregnancy rates than does postpartum nutrition. Richards and co-workers (1986) reported no difference in PPI or pregnancy rates in beef cows that calved with $BCS \geq 5$, regardless of nutritional treatment; while Rae et al.(1983) reported pregnancy rates of 90% in beef cows that calved at $BCS \geq 5$. Our study similarly subjected cows with $BCS \geq 5$ (mean = 5.5) at calving to nutritional restriction and found no differences in estrous response, conception or pregnancy rates.

VI. CONCLUSIONS

Results from this study indicate that nutritional restriction during the breeding season does not reduce reproductive performance of cows losing weight. While these results seem to contradict those of past research, all cows in the current experiment reinitiated estrous cyclicity by the beginning of the breeding season. Prior research has confirmed the negative impact of nutritional restriction on return to estrus and subsequent pregnancy rates and the importance of body condition at calving on subsequent pregnancy rates. The results of the current study suggest that the reduction in pregnancy rates associated with poor nutrition are more resultant of a failure to reinitiate estrous cyclicity, rather than a failure to establish and maintain pregnancy.

These results have the potential to benefit beef producers that encounter harsh winters, poor hay quality, or drought conditions that result in losses of feed resources. Feed resources must be made available prior to calving to assure proper body condition at calving ($BCS \geq 5$). This should allow for re-initiation of estrous cyclicity prior to the breeding season. If feed resources are scarce during the breeding season, cows should still be able to establish and maintain pregnancy if cows have reinitiated estrous cyclicity. Creep feeding calves to minimize losses in calf gain would be more cost efficient than purchasing extra feed to maintain cows and thus, support calf performance.

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VITA

Timothy Mark Towns was born May 16, 1976 in Gallatin, Tennessee. He attended Trousdale County High School in Hartsville, TN from 1981 until graduation in May 1994. Tim enrolled at the University of Tennessee, Knoxville in the fall of 1994, majoring in Animal Science. In the fall of 1998, he graduated from UT with a B.S. degree in Animal Science. Tim began graduate school in January 1999 at the University of Tennessee, Knoxville in the Animal Science department under the direction of Dr. F. Neal Schrick. In the summer of 2001, Tim graduated with a M.S. degree in Animal Science with a concentration in Reproductive Physiology.

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