



Fertility of non-puberal estrus, pregnancy rates and progesterone concentrations of beef heifers bred at puberal or third estrus
by Darryl Jay Byerley

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:

The objectives of this study were to determine: 1) if pregnancy rates of beef heifers bred at puberal estrus differed from pregnancy rates of heifers bred at their third estrus; 2) if the pattern of progesterone concentrations differed between heifers bred during the puberal or third estrous and relate these changes to pregnancy rates associated with breeding at these times; and 3) if heifers bred at a non-puberal estrus have the ability to become pregnant.

Crossbred beef heifers were obtained from Manhattan, MT (L1, N = 102) and Miles City, MT (L2, N = 54), and the experiment was conducted at Miles City. Heifers were assigned randomly within location to one of two treatments: 1) to be bred by a fertile bull on their puberal estrus (E1, N = 89) and 2) to be bred by a fertile bull on their third estrus (E3, N = 67). Heifers were fed to gain .56 kg • head-1 • d-1 and were observed for estrus twice daily. After exhibiting first estrus (puberty) and breeding, each heifer in E1 was palpated rectally on d 6, 9 and 12 ± 1d (Estrus = d 0) for the presence of a corpus luteum, and a venous blood sample was collected for assay of progesterone (P4) by radioimmunoassay. Heifers in E3 were palpated and bled on the same schedule as heifers in E1 after first estrus and after being bred to a fertile bull on their third estrus. Pregnancy rates were determined by rectal palpation at a minimum of 38 d post-breeding. Location did not affect ($P > .10$) weight at puberty or breeding, however, heifers from L1 were younger ($P < .05$) than heifers from L2 at puberty and breeding. Pregnancy rates were 57 and 78% for heifers in E1 and E3, respectively ($P < .05$). The probability of a heifer in E1 becoming pregnant increased ($P < .05$) with increasing age, while age was not a factor ($P > .10$) for heifers in E3. Progesterone concentrations were higher ($P < .05$) for heifers in E1 compared to heifers in E3 on d 6, 9 and 12. Progesterone concentrations on d 6, 9 and 12 did not differ ($P > .10$) between pregnant heifers in E1 and E3. Non-pregnant heifers in E1 had higher ($P < .05$) concentrations of P4 compared to non-pregnant heifers in E3 on each day. Concentrations of P4 did not differ ($P > .10$) between non-pregnant heifers in E1 and heifers in E3 during their puberal cycle. Pregnant heifers in E1 and E3 had higher ($P < .05$) concentrations of P4 on each day compared to non-pregnant heifers in their respective treatments. No difference ($P > .10$) was observed in concentrations of P4 during the puberal cycle of heifers in E3 which were determined to be pregnant or non-pregnant after breeding on their third estrus. There were no interactions ($P > .10$) between treatment, pregnancy status and day-of-cycle for concentrations of P4. Of the heifers in E1 (n = 27) that exhibited non-puberal estrus, none became pregnant after breeding by fertile bulls. In conclusion, puberal estrus in beef heifers had a lower fertility compared to breeding at third estrus. Differences in P4 concentrations in pregnant and non-pregnant heifers of E1 and E3 indicated the possibility that P4 concentrations may play a role in determining fertility of beef heifers bred at puberty. In addition, the potential to become pregnant is apparently absent in heifers which are bred at a non-puberal estrus.

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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, bibliography, and consistency, and is ready for submission to the College of Graduate Studies.

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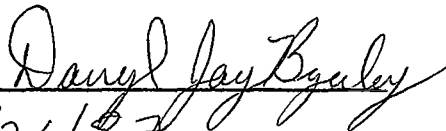
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ABSTRACT

The objectives of this study were to determine: 1) if pregnancy rates of beef heifers bred at puberal estrus differed from pregnancy rates of heifers bred at their third estrus; 2) if the pattern of progesterone concentrations differed between heifers bred during the puberal or third estrous and relate these changes to pregnancy rates associated with breeding at these times; and 3) if heifers bred at a non-puberal estrus have the ability to become pregnant.

Crossbred beef heifers were obtained from Manhattan, MT (L1, N = 102) and Miles City, MT (L2, N = 54), and the experiment was conducted at Miles City. Heifers were assigned randomly within location to one of two treatments: 1) to be bred by a fertile bull on their puberal estrus (E1, N = 89) and 2) to be bred by a fertile bull on their third estrus (E3, N = 67). Heifers were fed to gain .56 kg · head⁻¹ · d⁻¹ and were observed for estrus twice daily. After exhibiting first estrus (puberty) and breeding, each heifer in E1 was palpated rectally on d 6, 9 and 12 + 1d (Estrus = d 0) for the presence of a corpus luteum, and a venous blood sample was collected for assay of progesterone (P4) by radioimmunoassay. Heifers in E3 were palpated and bled on the same schedule as heifers in E1 after first estrus and after being bred to a fertile bull on their third estrus. Pregnancy rates were determined by rectal palpation at a minimum of 38 d post-breeding. Location did not affect ($P > .10$) weight at puberty or breeding, however, heifers from L1 were younger ($P < .05$) than heifers from L2 at puberty and breeding. Pregnancy rates were 57 and 78% for heifers in E1 and E3, respectively ($P < .05$). The probability of a heifer in E1 becoming pregnant increased ($P < .05$) with increasing age, while age was not a factor ($P > .10$) for heifers in E3. Progesterone concentrations were higher ($P < .05$) for heifers in E1 compared to heifers in E3 on d 6, 9 and 12. Progesterone concentrations on d 6, 9 and 12 did not differ ($P > .10$) between pregnant heifers in E1 and E3. Non-pregnant heifers in E1 had higher ($P < .05$) concentrations of P4 compared to non-pregnant heifers in E3 on each day. Concentrations of P4 did not differ ($P > .10$) between non-pregnant heifers in E1 and heifers in E3 during their puberal cycle. Pregnant heifers in E1 and E3 had higher ($P < .05$) concentrations of P4 on each day compared to non-pregnant heifers in their respective treatments. No difference ($P > .10$) was observed in concentrations of P4 during the puberal cycle of heifers in E3 which were determined to be pregnant or non-pregnant after breeding on their third estrus. There were no interactions ($P > .10$) between treatment, pregnancy status and day-of-cycle for concentrations of P4. Of the heifers in E1 (n = 27) that exhibited non-puberal estrus, none became pregnant after breeding by fertile bulls. In conclusion, puberal estrus in beef heifers had a lower fertility compared to breeding at third estrus. Differences in P4 concentrations in pregnant and non-pregnant heifers of E1 and E3 indicated the possibility that P4 concentrations may play a role in determining fertility of beef heifers bred at puberty. In addition, the potential to become pregnant is apparently absent in heifers which are bred at a non-puberal estrus.

INTRODUCTION

Attainment of puberty is an important physiological and economical event in domestic animals. Physiologically, puberty represents the first time in an individuals' life when reproduction becomes possible.

Decisions concerning reproductive management of beef heifers have been based on the following studies. Beef heifers which calve at two years of age produce more calves in their lifetime than heifers which calve first at three years of age or older (Donaldson, 1968). In addition, heifers that conceive early in their first breeding season calve earlier and wean heavier calves than those which conceive late in their first breeding season (Short and Bellow, 1971; Lesmeister et al., 1973). Furthermore, Lesmeister et al. (1973) indicated that heifers which conceived early in their first breeding season maintained this production advantage throughout their lifetime. Thus the current recommendation is to breed heifers as early in their first breeding season. However, this may result in heifers being bred on their puberal estrus.

The effect of breeding beef heifers at puberty on pregnancy rate is unknown. This study was undertaken to address questions concerning the physiological aspects of puberty as they relate to fertility in beef heifers.

The following section of this thesis a review of literature summarizing the physiological processes of puberty and fertility in the female bovine and other species where data for the bovine are absent or unsupported.

REVIEW OF LITERATURE

The ability to reproduce for the first time in an animals' life is typically referred to as puberty. Joubert (1963) defined this time in the domestic female ruminant as the occurrence of first estrus accompanied by ovulation and the potential to reproduce. Many genetic, environmental and physiological factors are known to influence the occurrence of puberty in female mammals.

Characterization of Puberty in Domestic Female Cattle

First observed estrus has been used by many investigators to characterize the occurrence of puberty in female cattle (Kaltenback and Wiltbank, 1962; Laster et al., 1972; 1976; 1979; Gregory et al., 1979). Nelsen (1985) and Rutter and Randel (1986) have described a phenomenon termed non-puberal estrus in which estrus behavior is not accompanied by subsequent corpus luteum (CL) development or normal progesterone (P4) concentrations. If this is a common phenomenon associated with prepuberal development in beef heifers then many studies that used estrus as the only criteria for puberty may be inaccurate. Other investigators have used periodic rectal palpation for the presence of a CL in conjunction with first estrus to define puberty, (Arije and Wiltbank, 1971) but this may not be sufficient due to objective and subjective deficiencies in the technique of rectal palpation for "visualizing" ovarian morphology.

If future data regarding puberty is to be accurate, more specific criteria in determining puberty are needed. Studies by Gonzalez-

Padilla et al. (1975a) and Berardinelli (1976) characterized puberty in beef heifers using three specific criteria 1) occurrence of behavioral estrus associated with, 2) the presence of a palpable CL, and 3) a rise in serum P4 above 1 ng/ml during the luteal phase of the puberal estrous cycle. Utilization of these criteria should increase the confidence in determining when puberty has been reached and should remove inaccuracy caused by non-puberal estrus. Currently, there are no studies that have used these criteria in association with fertility of the puberal cycle to confirm the definition given by Joubert (1963).

Factors Influencing the Onset of Puberty

The following section discusses genetic and environmental factors which are known or have been implicated in influencing the attainment of puberty in heifers.

Genetic Influences

Joubert (1963) summarized data that indicated differences in age at puberty between breeds of beef heifers. Since then, differences in age and weight at puberty in beef and dairy breeds have been reported by numerous investigators. For extensive summaries see Berardinelli (1976), Steffan (1983) and Roberson (1985). In general, large variability in these traits has been observed among and between breeds. Heifers of Bos taurus breeds tend to be younger and lighter at puberty than heifers of Bos indicus breeds (Reynolds et al., 1963; Plasse et al., 1968). Cundiff (1981) stated that differential selection applied to Bos taurus and Bos indicus breeds for age at puberty may have given rise to these differences. Within Bos taurus, heifers of beef breeds

reach puberty at slightly older ages than heifers of dairy breeds (Laster et al., 1972).

Breed of sire can influence age and weight at puberty: probably the most striking example is that observed between heifers sired by Bos taurus or Bos indicus bulls. Heifers sired by Bos taurus bulls tend to be lighter and younger at puberty than heifers sired by Bos indicus bulls (Young et al., 1978; Gregory et al., 1979; Steward et al., 1980). In addition, heifers sired by bulls of "late-maturing breeds" tend to be older at puberty than those sired by bulls of "early-maturing" breeds (Laster et al., 1976; Laster et al., 1979).

Breed of dam has been reported to affect age and weight at puberty among breeds of Bos taurus. However, the effect of breed of dam is consistent with ranking for age and weight at puberty associated with their respective sire breeds (Laster et al., 1972, 1976, 1979; Swierstra et al., 1977; Gregory et al., 1978). Within a breed, age at puberty may be influenced by maternal effects such as age of dam (Gregory et al., 1978; Laster et al., 1979). These investigators found a negative relationship between age at puberty and age of dam for dams with ages ranging from 2 to 8 years.

Crossbreeding decreases age at puberty in beef heifers (Kaltenback and Wiltbank, 1962; Wiltbank et al., 1966; Short and Bellows, 1971; Laster et al., 1972, 1976; Gregory et al., 1978; Burfening et al., 1979; Nelsen et al., 1982). Burfening et al. (1979) reported inbreeding depression reduced reproductive fitness in beef heifers. Wiltbank et al. (1966) concluded that heterosis for age at puberty was independent of heterosis for growth rate. This is an indication that

the effects of crossbreeding or inbreeding were due to changes in alleles for reproductive fitness.

Age at puberty in beef heifers appears to be heritable, estimates have ranged from $.20 \pm .16$ (Arije and Wiltbank, 1971) to $.67 \pm .26$ (Smith et al., 1976). These estimates indicate that age at puberty could be decreased by selection. Progress in decreasing age at puberty in heifers by selection is slow. However, scrotal circumference of bulls has a high negative genetic correlation to age at puberty in female half-sibs (Brinks et al., 1978; King et al., 1983). King et al. (1983) and Lunstra (1982) reported heritability estimates for scrotal circumference as being .26 and .52, respectively. These estimates indicate that selection for larger scrotal circumference in bulls may allow for more rapid reduction in age at puberty in their female progeny.

Environmental Influences on Puberty

Environment represents a complex set of interactive factors. Because of this it is difficult to define the affects of these factors on puberty. The following section addresses the known environmental factors and there relationship to the attainment of puberty.

Nutrition. Age and weight at puberty can be influenced by level of nutrition in beef heifers (Wilkbank et al., 1966, 1969; Arije and Wilkbank, 1971; Short and Bellows, 1971). High levels of nutrition either pre- or post-weaning reflected in average daily weight gain (ADWG) during these periods resulted in decreasing age at puberty. Pre-weaning nutrition can be a function of milk production of the dam,

since increased milk production of dams is related to ADWG in their progeny (Plasse, 1968; Laster et al., 1976; Gregory et al., 1979). Ferrell (1982) showed that restrictive diets (protein or energy) post-weaning can delay the attainment of puberty. Short and Bellows (1971) reported that age at puberty was inversely related to the amount of energy in the diet. However, the mechanism by which nutrition effects puberty in beef heifers remains unclear (Grass et al., 1982).

Temperature, Photoperiod and Season of Birth. Lack of data precludes any valid conclusion concerning the effect of temperature on the attainment of puberty in beef heifers. However, Dale et al. (1959) reported that among small groups of Brahman, Santa Gertrudis and Shorthorn heifers raised at either 50°, 80° F or outdoor conditions that Brahman heifers reached puberty at 463 d at 80° F, but did not reach puberty within the test period at 50° F or outdoor conditions. Means for age at puberty among Shorthorn heifers did not differ between treatments. Thus, temperature may influence attainment of puberty but its' influence may be breed dependent.

Roy et al. (1980) reported that Holstein heifers born during periods of increasing photoperiod reached puberty at a younger age compared to those born during periods of decreasing photoperiod. On the other hand, Greer (1984) reported that there was no relationship between length of photoperiod at birth and age at puberty in beef heifers. Spring-born heifers reach puberty at younger ages than those born during other seasons (Hawk et al., 1954; Arije and Wiltbank, 1971; Grass et al., 1982). However, this effect may be mediated through increased pre-weaning growth rate due to increased forage supply during

this time of the year. The effect of season of birth on age at puberty may be the result of interactions among photoperiod, temperature and forage availability and(or) quality.

Social Factors. The presence of bulls, for short or long periods of time, does not affect age or weight at puberty in beef heifers (Berardinelli et al., 1978; MacMillian et al., 1979; Roberson, 1985). However, Izard and Vandenberg (1982) reported that oronasal application of bull urine to beef heifers reduced age at puberty. Nelsen et al. (1985) showed that the presence of mature cows decreased age at puberty in one crossbreed type, but did not in others. Because of the lack of data and inconsistency of reports, no valid conclusions can as yet be drawn for the influence of social factors on the attainment of puberty in beef heifers.

Physiological Factors in Puberty

Understanding the physiological factors involved in the puberal process requires knowledge of the hypothalamic-pituitary-ovarian axis and changes in its' interactions during the prepuberal and puberal periods. The following sections summarize changes in the relationships and functions of the components of this axis related to puberty in beef heifers.

Endocrine Patterns During the Prepuberal Period

Desjardin and Hafs (1968) characterized pituitary gonadotropin content of luteinizing hormone (LH) and follicle stimulating hormone (FSH) in prepuberal heifers. They reported LH concentrations in the

pituitary increased from birth to 3 months of age, fluctuated from 3 to 7 months of age and then decreased until 12 months of age. Concentrations of FSH exhibited fluctuations from birth to 2 months of age and then remained constant from 3 to 12 months of age. They concluded that the attainment of puberty was associated with decreased content of pituitary LH prior to puberty and an increase content of LH near the following estrus.

Gonzalez-Padilla et al. (1975a) measured concentrations of gonadotropin releasing hormone (GnRH), FSH, LH, prolactin (PRL), P4 and estrogen (E2) during the peri-puberal period in beef heifers. There were no significant changes in FSH, GnRH or PRL concentrations as puberty approached or during the first estrous cycle. Concentrations of E2 were high before d -40, (d 0 = preovulatory peak of LH) then decreased for 3 to 4 d to a level which remained constant until puberty. There was no rise in E2 concentrations associated with preovulatory-like LH peaks. The prepuberal period was characterized by concentrations of LH which fluctuated to concentrations higher than those measured after d 0. In addition to a puberal peak of LH (d 0), another peak of LH (priming) of similar magnitude and duration was detected between d -11 and -9. Progesterone concentrations were low in the prepuberal period, except for two distinct elevations prior to d 0. The first elevation was always followed by the priming peak of LH, while the second preceded the prepuberal LH peak. They suggested that the profile of the two major LH peaks and the second P4 elevation mark the transition between pre- and post-puberal LH release patterns.

They suggested that P4 plays a key role in the development of phasic LH release which is characteristic of a cycling female bovine.

Berardinelli (1979) determined that the prepuberal elevations of P4 in female cattle and sheep, which were thought to be of adrenal origin, were actually due to luteal tissue embedded within the stroma of the ovary. In neither species was this development of luteal tissue preceded by estrus or ovulation. It is unknown what events lead to the development of this luteal tissue.

Regulation of Puberty

A unifying concept regarding the endocrine mechanisms which control initiation of puberty in females remains obscure at present (Day et al., 1984). It has been reported that all neuroendocrine and endocrine organs are functional and could respond to stimulus to initiate estrous cycling activity in prepuberal females (Seidel et al., 1971; William et al., 1975; Barnes et al., 1980; Schillo et al., 1982; Day et al., 1984; Foster et al., 1972a,b, 1975; Trounson et al., 1977). One reason that they do not become fully functional sooner may be that the components of the entire system are not yet integrated temporally. The key to this integration appears dependent upon maturational changes in the hypothalamus.

Ramirez and McCann (1963) hypothesized that a decrease in sensitivity of the hypothalamic-pituitary centers which control gonadotropin secretion, to estradiol negative feedback is required for the attainment of puberty. This theory ("Gonadostat Theory") is based on the idea that decreased sensitivity of steroid negative feedback on

regulation of pituitary function allows an increase in gonadotropin release which result in ovarian follicular maturation and ovulation.

This theory has been tested in ewe lambs (Foster and Ryan, 1979), heifers (Day et al., 1984), gilts (Berardinelli et al., 1984) and female rats (Andrews et al., 1981). Andrews et al. (1981) reported that in rats no change in the sensitivity of the hypothalamus occurred prior to the preovulatory LH peak. However, in heifers (Day et al., 1984), gilts (Berardinelli et al., 1984) and ewe lambs (Foster and Ryan, 1979) it was observed that the puberty was at least in part, due to a hypothalamic decrease in sensitivity to E2 negative feedback on LH secretion. Differing results among these species leads one to conclude that certain concepts of the gonadostat theory may not be applicable to all species. Further work is needed to determine if the change in hypothalamic sensitivity is actually due to steroid environment or is simply a result of maturational change in the hypothalamus.

Among species in which the gonadostat theory appears applicable other factors may limit the attainment of puberty. It has been reported that a prepuberal heifer's ovary may respond in a proper endocrinological manner as early as 3 to 4 months of age. The pituitary of prepuberal females has also been show to be responsive to GnRH in a manner similar to puberal females far in advance of the normal time of puberty (Swanson, 1974; Williams et al., 1975). Adams et al. (1984) reported changes in quantitative and qualitative character of secretory forms of LH: biologically active LH increased near the time of puberty in ewe lambs.

To those who view puberty as first estrus followed by ovulation, puberty is a discrete event. However, given the chronological changes which must take place, puberty may more properly be viewed as a process. The phenomena of non-puberal estrus (Nelsen et al., 1985; Rutter and Randel, 1986) and silent estrus prior to puberty indicate that puberty may require the maturation of more than one system. In addition, many other biologically important systems and substances have been implicated in the control of the attainment of puberty. A few of these are neurotransmitters (McCann, 1977), opioids (Brooks et al., 1986ab) and non-steroidal ovarian factors (Schwartz and Channing, 1977). Thus, it appears that any component of the hypothalamus-pituitary-ovarian axis is quite functionally independent of each other during the prepuberal period. However, it appears that each component of the system works to limit full functionality of the others until puberty. The mechanism whereby the entire system becomes integrated remains unclear at present.

Fertility Associated With Breeding at Puberty

Fertility in the female is defined as the degree to which she is able to produce young. However, little work has been done to relate fertility of the puberal estrous to later estrous cycles.

Rutledge et al. (1974) reported that litters of early-mated female rats produced smaller litters than late-mated females (about 1 pup difference). They concluded that early breeding procedures would satisfactorily shorten generation interval without serious impact on reproductive performance. However, low overall mean litter size

(8.2 and 9.2 pups for early- and late-bred females, respectively) in this study indicate other reproductive problems may have been present. Evans (1986) reported that in rats, early-bred Sprague-Dawley females had 3 to 4 fewer young than females bred at an older age. They concluded that caution should be employed when early breeding females due to possible decreases in reproductive performance.

Stewart (1945) reported that gilts farrowing at 14 months of age produced larger litters than gilts farrowing at one year of age or less. Squiers et al. (1950) indicated that litter size increased 0.5 pigs per litter for each 10 d increase in age at breeding in gilts. Warnick et al. (1951) and Robertson et al. (1951) reported increased conception rates from the puberal estrus to the third estrus of gilts. They concluded this difference was primarily due to a change in ovulation rate. It is unknown if this change in ovulation rate is due to ovarian and(or) pituitary maturation or the consequence of changes in uterine factors affecting ovulation.

Hare and Bryant (1985) indicated that fertility (pregnancy rate) of ewe lambs increased approximately 20% when mating occurred at the second estrous rather than the puberal estrous. However there was no difference in ovulation rate between treatments. It appeared that differences in pre-implantation ovum loss resulted in lowering fertility. Bichard et al. (1974) reported similar results in which a trend was observed towards progressive improvement in fertility from first to third estrus. Edey et al. (1978) and Williams et al. (1978) reported there was no difference in fertility between the puberal

estrous and the third estrous. However in both studies small numbers of ewes were used.

It is unknown if changes in fertility from puberty to later cycles seen in other species is a phenomena common to beef cattle.

Physiological Factors in Fertility

Since the establishment and maintenance of pregnancy consists of a series of complex endocrinological, physiological and immunological events, progress towards identifying the relative importance of individual factors which contribute to embryo loss has been slow (Heap et al., 1986).

Studies in domestic ruminants involving changes in the relationship of ova viability and fertility between immature and adult females are few in number. Katska and Smorag (1984) reported no difference in numbers of ovum classified as morphologically normal between heifers (age 18-24 months), young cows (age 3-6 yrs) and old cows (age 9-17 yrs). Quirke and Hanrahan (1977) showed that fertilization rates were similar for ova collected from either ewe lambs and adult ewes. However, McMillian and McDonald (1985) reported that the ability of 8-16 cell Romney ewe-lamb ova to develop to term in mature ewes was less (25%) than that of ova from adult ewes (52%). Differences in the measurements used to determine viability in these studies may account for differing results. Changes in ova viability may be due to the lack of exposure of oocyte from ewe lambs to the cyclic changes of the estrous cycle.

Analysis of chromosome anomalies in early pregnancy (d 2-16) in sheep (Long and Williams, 1980), cattle (McFeely and Rajakosk, 1968;

Gayerie de Abreu et al., 1984) and pigs (McFeely, 1967) were reported to be 14.6%, 7.5% and 10%, respectively. However no study compared the frequency of anomalies between the peri-puberal period and later periods in any farm species.

Normal embryonic development depends on a sequence of changes in oviductal and uterine environment (Wilmot and Sales, 1982; Wilmot et al., 1985) and these changes are dependent on particular patterns of ovarian steroids (Roberts et al., 1975; Miller and Moore, 1976; Wilmot et al., 1985; Lee and Ax, 1984). Jacoby et al. (1984) reported P4 may play a role in the suppression of immunological rejection of embryos. However, Kaplan (1961) reported that hypophysectomized women, in which P4 levels were very low, gave birth to healthy babies. The possible role of P4 in immunological regulation is not known in farm species. Effects of P4 concentrations during the estrous cycle preceding breeding have been contradictory. An inverse relationship between P4 concentrations for the two-day period prior to the estrus of breeding and fertility was reported by Hendricks et al. (1971) and Shotton et al. (1978). However, a positive relationship between P4 concentrations and fertility during the two day period prior to the estrus of breeding was reported by Folman et al. (1973), Corah et al. (1974) and Rosenberg et al. (1977). The relationship between P4 concentrations after breeding and subsequent fertility is not clear. A positive relationship has been reported for beef cattle between P4 concentrations on d 3 (Maurer and Ecternkamp, 1982), d 6 (Erb et al., 1976) and d 7 (Randel et al., 1971) and pregnancy rates. However, other investigators have not observed this relationship until about d

d 16 (Shemesh et al., 1968; Folman et al., 1973; Hasler et al., 1980). It is unknown if differences in P4 concentrations prior to d 16 is a cause or an effect of infertility and(or) embryo survival. The differences observed in P4 concentrations between pregnant and non-pregnant heifers at d 16 is due to luteolysis in heifers which failed to become pregnant (Wilmut et al., 1985).

The role of E2 in maintenance of pregnancy in cattle is not well known. In swine, E2 is considered to be the signal for maternal recognition of pregnancy (Perry et al., 1973; Heap et al., 1979). In addition, E2 has been shown to increase blood flow to the uterus (Ford and Christenson, 1979; Ford et al., 1982a,b) and stimulates blastocyst formation (Niemann and Elsaesser, 1986). Ford and Christenson (1979) reported that in pregnant cows, blood flow increased to the uterus at d 14. This corresponds with the time when intrauterine E2 concentrations are highest. Randel et al. (1971) reported changes in the ratio of E2 to P4 between the puberal and second estrous cycle in heifers. Progesterone concentrations were higher and E2 concentrations were lower during the puberal cycle than the second estrous cycle. The implication of this observation to fertility is unknown. No studies could be found that relate changes in sensitivity of the oviductal or uterine environments to ovarian steroids, or P4 to E2 ratios and their effect on fertility between puberal and later estrous cycles.

STATEMENT OF PROBLEM

As stated in the review of the literature, breeding on the puberal estrus in some species has resulted in pregnancy rates and (or) litter sizes which were lower than if breeding occurred at a later estrus. Some data have indicated that hormone concentrations during the puberal cycle are different than later estrous cycles. It may be that hormone levels during the puberal estrus cycle may be a reflection or cause of lower pregnancy rates. In addition, a newly described phenomena of non-puberal estrus (NPE) in beef heifers may result in decrease reproductive efficiency if heifers which exhibit NPE do not have the potential to become pregnant.

Current management practices for beef heifers require heifers to become puberal and pregnant by 15 months of age. This often results in breeding occurring at the puberal estrus. If the puberal cycle has a lower potential for fertilization, conception and(or) maintenance of pregnancy it may limit overall reproductive efficiency.

Therefore, the objectives of this study were to determine:

- 1) if pregnancy rates of heifers bred at puberal estrus differed from heifers bred at their third estrus; 2) if the pattern of P4 concentrations differed between beef heifers bred at puberty or third estrus and relate P4 concentrations to fertility; and 3) if heifers bred at a non-puberal estrus have the potential to become pregnant.

MATERIALS AND METHODS

The study was conducted at the Fort Keogh Livestock and Range Research Laboratory, Miles City, MT. Beef heifers were obtained at weaning from Manhattan (L1; n = 102) and Miles City, MT (L2; n = 54). Crossbred heifers from L1 were 50% Angus, 12.5 to 25% Brown Swiss and Hereford. Heifers from L2 were crossbred types derived by using Angus, Brahman, Charolais, Shorthorn and Jersey sires on composite Hereford, Angus and Simmental crossbred dams. At the beginning of the experiment, heifers from L1 were older and heavier ($P < .05$) than heifers from L2. Age and weight for L1 heifers averaged 253 ± 3 d ($X \pm SEM$) and 264 ± 3 kg, respectively, while heifers from L2 averaged 222 ± 2 d and 230 ± 5 kg, respectively. During the experiment, heifers were fed to gain approximately $.56 \text{ kg} \cdot \text{head}^{-1} \cdot \text{d}^{-1}$ and body weights were obtained every 28 d for recalculation of rations to meet this rate of gain. The ration was formulated to meet the requirements of growing beef heifers (NRC, 1984), and consisted of corn silage, chopped hay, rolled barley, soybean meal and trace minerals. Water was available supplied free choice. Weights at first estrus and breeding were obtained by linear interpolation when first estrus and(or) breeding occurred between two consecutive weighing periods.

Heifers from L2 were stratified by breed then heifers from both locations were assigned by randomly within location and breed to one of two treatments; 1) bred by a fertile bull on their first (puberal) estrus (E1; n = 89) or 2) bred by a fertile bull on third estrus (E3; n = 67). Animals were housed in two sets of four adjacent pens of similar size. Four pens contained intact mature bulls (1 bull per pen)

that had been fertility tested (Simons, 1976). The other four pens contained vasectomized bulls (1 bull per pen) that were azoospermic. Each bull was fitted with a marking harness to aid in detecting estrus. All bulls had previous breeding experience.

Heifers in E1 were equally distributed among the four pens containing the fertile bulls with approximately one bull per 20 heifers. When a heifer was detected in estrus (first estrus) and mating had occurred, she was moved into one of the four pens containing a vasectomized bull. The heifer remained in this pen for observation of estrus and was pregnancy tested by rectal palpation at a minimum of 38 d after breeding. Heifers were removed from the experiment after being pregnancy tested.

Heifers in E3 were equally distributed among the pens containing vasectomized bulls at the same male to female ratio as that for E1 heifers. When a heifers' first estrus was detected, she was moved into an adjacent pen containing a vasectomized bull until after her second estrus was detected. Then, she was moved into a pen containing a fertile bull until breeding at third estrus and subsequently moved back into a pen containing a vasectomized bull until she was either detected in estrus or pregnancy tested and removed from the experiment. A heifer was randomly assigned to a pen each time a move occurred and bulls were either added or removed to maintain the male to female ratios of the pens.

Heifers were observed for estrus from November 19, 1984 to August 1, 1985. Ovaries of each heifer were examined rectally for the presence of a corpus luteum and a 10 ml blood sample for assay of P4

was collected by venipuncture of a tail or jugular vein on d 6₊₁, 9₊₁ and 12₊₁ post-estrus (Estrus = d 0) and breeding. An additional blood sample was collected from each heifer at the time of pregnancy diagnosis for assay of P4.

Blood samples were allowed to clot at 22 C for 4 h, centrifuged at 1000 x g at 4 C for 30 min. Serum was decanted and stored at -25 C until assayed for P4. Serum (.2 ml) samples were extracted with 5 ml of methylene chloride and assayed by a double antibody procedure developed and validated by Staigmiller et al. (1979). Sensitivity of this assay was 16 pg and intra- and inter-assay coefficients of variation were 9.7 and 12.8%, respectively, for a sample with a mean concentration of 4.46 ng/ml.

The following criteria were used to characterize normal cycling activity: 1) display of behavioral estrus, 2) presence of a palpable CL on d 6₊₁, 9₊₁ and 12₊₁ post-estrus and 3) an increase in P4 concentration to greater than 1 ng/ml on d 9 and 12. Only heifers that met all three criteria were considered in the statistical analyses.

Statistical Analyses

Average daily weight gain (ADG), weight and age at puberty, weight and age at breeding and estrous cycle lengths of heifers post-breeding (return cycle lengths) were dependent variables. Treatment, location and the treatment by location interaction were the independent variables. These data were analyzed by the General Linear Model (GLM) procedure of SAS (SAS, 1985). Pre-breeding estrous cycle lengths of

heifers in E3, i.e. first and second cycles, were compared by using a paired t-test. Return cycle lengths for E1 and E3 heifers were compared to pre-breeding estrous cycle lengths for heifers in E3 using a grouped t-test (Steel and Torrie, 1980). Pregnancy rates were analyzed using the Categorical Data Modeling (CATMOD) procedure of SAS (SAS, 1985). This procedure allowed the derivation and testing of a model for pregnancy rates that included continuous variables as covariates. Initially, the model included effects of treatment, location and the treatment by location interaction. Since, the two-factor interaction was not significant, it was removed from the model and the data were reanalyzed using models which contained the following covariates: weight at puberty, age at puberty, weight at breeding and age at breeding.

Concentrations of progesterone were analyzed initially by least-squares analysis of variance for a completely randomized split-plot design with repeated measures (Gill and Hafs, 1971) using the GLM procedure. The main plot was treatment and sub-plot factors were day-of-cycle and the treatment by day-of-cycle interaction. Heifer within treatment was used as the error term to test treatment. An additional analysis was performed on P4 concentrations after classification of heifers into pregnant and non-pregnant groups. The model included treatment, pregnancy status, heifer within treatment, day-of-cycle and the two-way interactions. Heifer within treatment was used as the error term for treatment and pregnancy status. Analysis of P4 concentrations for the puberal estrous cycle of heifers in E3 employed a model that included pregnancy status by day-of-cycle interaction.

Heifer within pregnancy status was used as the error term for pregnancy status. Least-squares means for P4 concentrations for all comparisons were tested by the Least Significant Difference test (SAS, 1985).

RESULTS

Four heifers were removed from the data set because they had not reached their assigned estrus by the end of the experiment and seven other heifers were removed because of sickness or injury. Additionally, thirty-seven heifers exhibited low P4 concentrations and lack of a palpable corpus luteum following estrus. These animals were classified as having exhibited non-puberal estrus (Nelsen et al., 1985).

Age and Weight at Puberty

Average daily weight gain and age and weight at puberty did not differ ($P > .10$) between heifers in E1 and E3 (Table 1). However, heifers in E3 were older ($P < .05$) and heavier ($P < .05$) at breeding than heifers in E1 (Table 1). Location did not affect ($P > .10$) ADG or weight at puberty and breeding (Table 1). However, heifers from L1 were younger ($P < .05$) at puberty and breeding than heifers from L2 (Table 1). There was no interaction ($P > .10$) between location and treatment for ADG, age and weight at puberty or age and weight at breeding.

Pregnancy Rates

Overall pregnancy rate for heifers bred during this experiment was 66% (Table 2). A greater percentage of heifers in E3 became pregnant compared to heifers in E1 (78 and 57%, respectively, $P < .05$; Table 2). Likewise, a greater percentage of heifers from L2 became pregnant compared to heifers from L1 (73 and 61%, respectively, $P < .05$; Table 2). There was no interaction ($P > .10$) between location and treatment for

Table 1. Least-squares means for average daily gain (ADG), age and weight at puberty and age and weight at breeding for heifers bred at puberal (E1) or third estrus (E3) from Manhattan (L1) or Miles City (L2)^a

Classes	n	ADG kg·head ⁻¹ ·d ⁻¹	Age at puberty d	Weight at breeding kg	Age at breeding d	Weight at breeding kg
Treatment						
E1	63	.56	322	295	322*	295*
E3	45	.49	339	306	375	326
Location						
L1	64	.51	316*	298	330*	305
L2	44	.55	349	301	363	309

^aStandard deviation for : ADG = .17; age at puberty = 49.4; weight at puberty = 35.0; age at breeding = 47.5; and weight at breeding = 35.6.

*Effect of treatment or location, $P < .05$.

pregnancy rates. Additional statistical analyses were employed to examine the possible nature of the treatment effect. Neither weight at breeding nor age and weight at puberty influenced pregnancy rates when used as within treatment covariates. However, age at breeding affected ($P < .05$) pregnancy rates for heifers in E1, but not for heifers in E3 ($P > .10$; Table 3). Age at breeding within treatment regression coefficient for heifers in E1 indicated that as age of breeding increased the probability of a heifer becoming pregnant increased (Table 3).

Proportions of heifers that returned to estrus after being bred to a fertile bull were 27 of 63 (43%) and 10 of 45 (22%) for heifers in E1 and E3, respectively ($P < .05$).

Table 2. Pregnancy rates for heifers bred at puberal (E1) or third estrus (E3) from Manhattan (L1) or Miles City (L2)

Classes	Pregnancy Rate (%)		χ^2
Treatment			
E1	36/63	(57)	8.80*
E3	35/45	(78)	
Location			
L1	39/64	(61)	4.62*
L2	32/44	(73)	
Overall	71/108	(66)	

* $P < .05$.

Table 3. CATMOD^a analysis of individual parameters for their effect on pregnancy rates in beef heifers bred on their puberal (E1) or third estrus (E3)

Effect	Estimates of Regression ^b	Standard Error	χ^2	P
Intercept	-1.64318	1.56049	1.11	.2923
Treatment				
E1	-4.62977	1.56049	8.80	.0030
E3	4.62977	1.56049	8.80	.0030
Age bred (Treatment)				
E1	.020633	.0061878	11.12	.0009
E3	-.0048213	.0062011	0.60	.4369

^aCATMOD; Categorical Data Modeling procedure (SAS, 1985).

^bUse of Estimates: $\text{logit} = \ln(p/1-p) = \text{intercept} + \text{treatment effect} + (b \cdot \text{age bred})$ and logit is converted to percentage by the formula, $100 / 1 + e^{-\text{logit}}$.

Estrous cycle lengths for heifers in E3 that were bred to infertile bulls were 24.5 ± 1.5 and 20.7 ± 1.0 d for their first and second cycles, respectively ($P > .10$; Table 4). Return estrous cycle lengths did not differ ($P > .10$; Table 4) between heifers in E1 and E3 and were similar ($P > .10$) to estrous cycle lengths for heifers bred to sterile bulls (21 ± 1.0 and 22.6 ± 1.1 d, respectively).

Table 4. Estrous cycle lengths for heifers bred at puberal estrus (E3) and return cycle lengths for heifers bred at either their puberal (E1) or third estrus (E3)

Item	Treatment	
	E1	E3
Estrous cycle length (d)		
1st cycle	--	24.5+1.5 (n=45) ^{a,b}
2nd cycle	--	20.7+1.0 (n=45)
Return estrous cycle lengths (d)	22.8+1.2	19.3+3.1 ^{a,c}

^aMean+SEM.

^bP>.10; 1st vs 2nd estrous cycle lengths.

^cP>.10; E1 vs E3.

Progesterone Concentrations

Concentrations of P4 increased ($P<.05$) from day 6 to 12 in E1 and E3 heifers after breeding to fertile bulls. However, concentrations of P4 were higher ($P<.05$) in E1 compared to E3 heifers on d 6, 9 and 12 (Figure 1). There was no interaction ($P>.10$) between treatment and day-of-cycle.

Within a treatment, pregnant heifers had higher ($P<.05$) P4 concentrations than non-pregnant heifers on each day (Figure 2). Progesterone concentrations did not differ ($P>.10$) between pregnant heifers in E1 and E3 (Figure 2). However, P4 concentrations were higher ($P<.05$) on d 6, 9 and 12 in non-pregnant heifers in E1 compared to non-pregnant heifers in E3 (Figure 2). There was no interaction ($P>.10$) between pregnancy status and day-of-cycle.

After being bred to a non-fertile bull at puberal estrus, E3 heifers had similar ($P > .10$; Figure 3) P4 concentrations on d 6, 9 and 12 as non-pregnant E1 heifers. There was no interaction ($P > .10$) between treatment and day-of-cycle.

Progesterone concentrations did not differ ($P > .10$) during the puberal cycle between E3 heifers which were pregnant or non-pregnant after breeding on their third cycle. There was no interaction ($P > .10$) between pregnancy status and day-of-cycle.

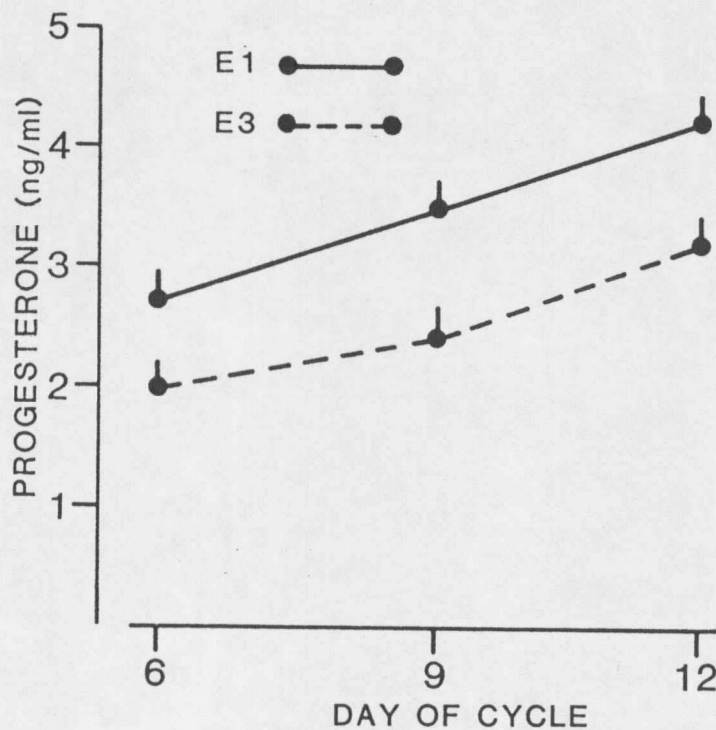


Figure 1. Least-squares Means \pm SEM (vertical lines) for P4 concentrations of heifers bred to fertile bulls at puberty (E1; N = 63) and third estrus (E3; N = 45).

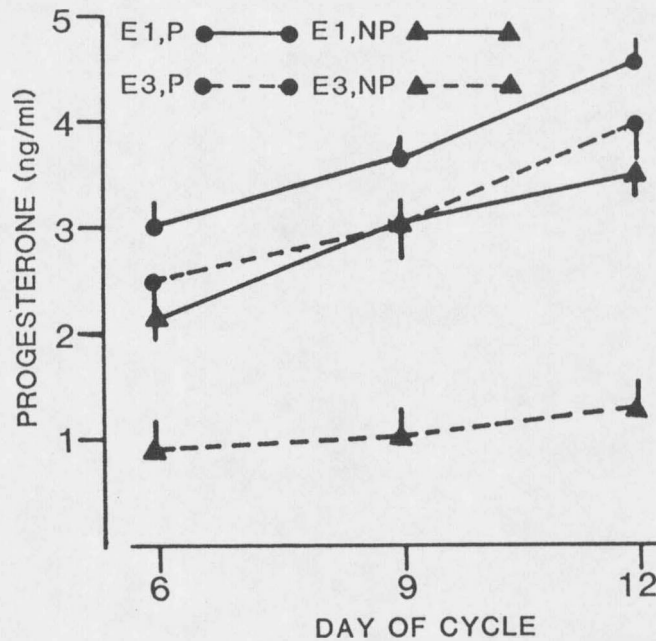


Figure 2. Least-squares Means \pm SEM (vertical lines) for P4 concentrations in pregnant (P) and non-pregnant (NP) heifers bred to fertile bulls at either puberty (E1; P and NP, N = 36 and 26, respectively) or third estrus (E3; P and NP, N = 30 and 11, respectively).

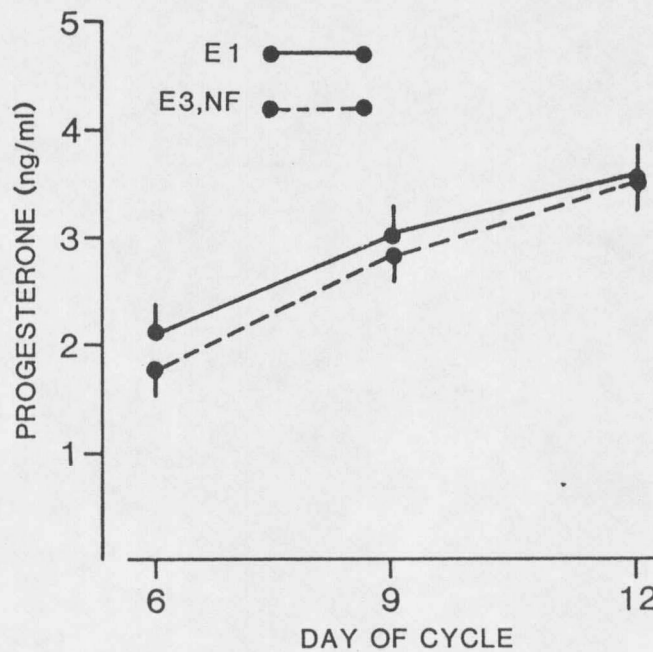


Figure 3. Least-squares Means \pm SEM (vertical lines) for P4 concentrations in non-pregnant heifers bred to fertile bulls at puberty (E1; N = 26) and heifers bred to non-fertile (NF) bulls at puberty (E3 NF; N = 50).

Non-Puberal Estrus

Heifers classified as having exhibited non-puberal estrus averaged 295.7 \pm 11.0 d and 275.3 \pm 11.6 kg for age and weight when they exhibited non-puberal estrus. These were not different ($P > .10$) from age and weight at puberty in normal heifers. None of 27 (0%) heifers in E1, classified as having exhibited non-puberal estrus, became pregnant after breeding by fertile bulls.

DISCUSSION

Age and weight at puberty are determined by environmental and genetic factors in beef heifers. Environment, management and nutrition reflected by ADG were similar for heifers in this experiment, and any difference in age and weight at puberty should primarily be a result of the genetic composition of heifers. Heifers from L1 were younger at puberty than heifers from L2, but weights at puberty were similar. This was not unexpected, since heifers from L1 were 12.5 to 25% Brown Swiss. It is known that dairy heifers typically attain puberty at younger ages, but not necessarily lighter weights than beef heifers (for review, see Berardinelli, 1979). Results from crossbreeding studies by Laster et al. (1972; 1979), in which dairy and beef crossbred heifers were compared to crossbred beef heifers, indicated that heifers from dairy crosses attained puberty at younger ages relative to their body weight than heifers from beef crosses.

Heifers in E3 were older and heavier at breeding than heifers in E1. Heifers in E3, by design, were two cycle lengths older and consequently 24 kg heavier at breeding than E1 heifers since age and weight at puberty were similar between treatments. The difference in age at breeding between heifers from L1 and L2 was directly related to the difference in age at puberty.

The difference in pregnancy rates between heifers from L1 and L2 may have been due to breed type. Gregory et al. (1979) reported differences in pregnancy rates between groups of different crossbreeds of heifers. Season may have been a factor for pregnancy rates between heifers from L1 and L2 since heifers from L1 were bred approximately

one month earlier than heifers from L2 . Pregnancy rates in cattle can vary with season. In areas outside the tropics, where seasonal changes in temperature and photoperiod are greatest, fertility is lowest in winter and early spring (Salisbury et al., 1978; de Kruif and Brand, 1978; Montgomery, 1985).

Pregnancy rates were higher for heifers in E3 compared to heifers in E1. Weight at puberty, weight at breeding or ADG did not affect pregnancy rates in these heifers. However, age at breeding was found to play a role in determining pregnancy rates for heifers. Adjusting pregnancy rates for the effect of age at puberty failed to remove the treatment effect, but the analysis indicated a treatment by age at breeding interaction. Examination of the regression coefficients for age at breeding within treatment indicated that the probability of a heifer in E1 becoming pregnant increased with advancing age at breeding (puberty), while age at breeding had no effect on pregnancy rates for heifers in E3. The difference observed in overall pregnancy rates between treatments indicates that fertility of beef heifers bred at puberty is sub-optimal. This effect is similar to those observed in gilts (Robertson et al., 1951), rats (Evans, 1985) and ewe lambs (Hare and Bryant, 1985). In gilts, lower pregnancy rates for breeding at first estrus appeared to be a direct result of low ovulation rate, which increases from the first to the third estrous cycle (Andersson and Einarsson, 1980). This may be true for rats since it is a polytocous species like the gilt, however, there are no data to support this idea. The ovine is a ruminant with reproductive characteristics similar to those observed in the bovine, except for their seasonality

in breeding patterns. Hare and Bryant (1985) reported that breeding ewe lambs at puberty resulted in a 20% lower pregnancy rate compared to that of ewe lambs bred at their second estrus. Gonzales-Padilla et al. (1975b) reported that heifers of a control group experienced low fertility when bred at their first estrus. Sub-optimal fertility associated with breeding at first estrus may be a general phenomenon in female mammals.

The physiological basis of sub-optimal fertility at puberal estrus in beef heifers or other species is not clear. Ovulation rate may have been different between heifers in E1 and E3 and has been implicated as a cause of lower litter size in gilts and rats bred on their first estrus. Although we do not have direct evidence that there was a difference in ovulation rate, the evidence for normal cycling activity, i.e. increasing concentrations of P4 from d 6 through 12 and associated palpable CL on these days, leads us to conclude that ovulation rate was not a factor in accounting for the difference in pregnancy rates between treatments.

The possibility exists that lower pregnancy rate of heifers in E1 was due to either early (d 1 or 15) or late (d 15 to 19) embryonic mortality. If late embryonic mortality occurred in either treatment, then one would expect an extension in return cycle lengths since Northey and French (1980) reported that removal of embryonic tissues between d 15 through 19 post-breeding resulted in extending the inter-estrus interval. However, return estrous cycle lengths did not differ between heifers bred to either fertile or sterile bulls. Nevertheless, early embryonic mortality could have occurred differentially in E1 and

E3 heifers. It was not possible to assess the possibility in the present study, however, McMillan and McDonald (1985) reported that embryos collected after breeding at first estrus in ewe lambs had lower survivability scores compared to embryos from adult ewes after the embryos were transferred to adult ewes.

Progesterone and estrogen concentrations have been implicated in other species in the immunologic regulation of fetal-maternal balance (Jacoby et al., 1984), blastocyst formation (Niemann and Elsaesser, 1983) and implantation (Levasseur, 1984).

Several studies failed to establish a relationship between P4 concentrations and pregnancy status in pregnant, non-pregnant or non-bred cycling cows until approximately d 16 (Shemesh et al., 1968; Folman et al., 1973; Hasler et al., 1980). However, other studies have shown a higher P4 concentration during the early luteal phase (d 3 (Maurer and Echterkamp, 1982), d 6 (Erb et al., 1976), d 7 (Randel et al., 1971), the first 15 days of the cycle (Hendricks et al., 1971)) in pregnant compared to non-pregnant females. In the present study, P4 concentrations were higher in pregnant heifers in E1 and E3 on d 6, 9 and 12 post-breeding than non-pregnant heifers in these treatments.

Randel et al. (1971) found that P4 concentrations were higher and estrogen concentrations were lower during the puberal estrous cycle than the second estrous cycle. Steroidal asynchrony may be a problem associated with the puberal estrus cycle which could contributed to the difference observed in pregnancy rates between E1 and E3.

Shotton et al. (1978) reported that age at first estrus was inversely related to prepuberal P4 concentrations and heifers which

exhibited higher prepuberal concentrations of P4 exhibited lower pregnancy rates. Wilmut et al. (1986) reported that the uterus is able to respond to higher levels of P4 during the luteal phase only if exposed to low levels of P4 from the time of estrous. One could theorize that higher prepuberal P4 concentrations, which do not allow for proper synchrony of the uterine and(or) ovarian environments, could result in decreased fertility at puberty.

Sreenan and Diskin, (1983) hypothesized that the reason for lower pregnancy rates in heifers compared to cows, was inadequate levels of P4 during mid-cycle. This does not appear to be the case in E1 heifers where P4 concentrations were highest. However, pregnant heifers in E1 had higher P4 concentrations than non-pregnant heifers in E1. This raises the possibility that P4 requirements may be greater for the establishment and(or) maintenance of pregnancy in the puberal cycle. On the other hand luteal insufficiency may have been a factor in non-pregnant E3 heifers which showed the lowest progesterone concentrations overall.

Other physiological factors that could account for the difference in pregnancy rates between treatments include maturational changes in oviductal and(or) uterine environment, sensitivity to estrogen and P4 or cervical, uterine and oviductal factors associated with sperm transport and fertilization. The roles of these factors are not known. In addition, Murray et al. (1983) found that exposure to dead semen prior to breeding in gilts resulted in larger litter size, but did not appear to affect farrowing percentages. It may be that use of the

vasectomized bulls for heifers in E3 induced some analogous response causing increased pregnancy rate.

Pregnancy rate was a positive logistic function of age at breeding (puberty) for heifers in E1, but age at breeding for heifers in E3 was not a factor in determining pregnancy rate. The reasons for this finding are not clear. It may be that any maturational changes associated with age at breeding for heifers in E3 had been overcome by physiological changes that occurred as a result of recurrent estrous cycles. An explanation of how age at puberty, independent of weight, determines pregnancy rates in heifers is elusive. It is possible that just because a heifer reaches puberty at a given age does not necessarily mean that physiological processes related to fertility have matured to a degree acceptable for conception. The effect of season cannot be excluded as a factor for the effect of age at puberty on pregnancy rates in E1 heifers. Heifers in E1 that were younger at puberty were bred earlier in the year than heifers that attained puberty at older ages. It has been reported that fertility in the bovine increases from winter and early spring to late spring and early summer (Salisbury et al., 1978; de Kruif and Brand, 1978; Montgomery, 1985), thus heifers attaining puberty at an early age during late winter and early spring were less likely to become pregnant when bred at puberty than those reaching puberty at older ages in late spring and early summer.

Nelsen et al. (1985) and Rutter and Randel (1986) described the phenomenon of non-puberal estrus (NPE) in beef heifers. It is characterized by expression of estrus without luteal function.

Its occurrence may be due to environmental and genetic factors (Nelsen et al., 1985) but the physiological processes involved in NPE are unknown. Rate of occurrence of NPE in the present study was 25% (37/145) which is lower than that reported by Rutter and Randel (1986) but similar to rates (12 to 24%) observed by Nelsen et al. (1985). Environmental and management conditions and breed-types were similar between our study and the study of Nelsen et al. (1985).

Of particular interest to this study was that none of 27 heifers in E1 classified as having exhibited NPE became pregnant after breeding to fertile bulls. Thus, the potential for conception is absent in heifers which show NPE and should be considered a characteristic in the description of NPE. This observation plus those of Nelsen et al. (1985) and Rutter and Randel (1986) supports the notion that investigators emphasize and employ specific, well-defined criteria when studying puberty in beef heifers.

In conclusion, pregnancy rate of heifers can be adversely affected by breeding at puberal estrus. Increased age at breeding may improve pregnancy rates associated with puberty, but not above rates associated with breeding on third estrus. Progesterone concentrations were higher in heifers bred on their puberal estrous compared to heifers bred on their puberal estrus. The relationship between pregnancy rate and P4 concentrations for these two cycles is not clear. Based on previous literature and the results of this study, there appears to be two separate mechanisms for explaining pregnancy rates in heifers bred at their puberal or third estrus. The first concerns those heifers bred at their puberal estrus and involves prepuberal changes in steroids or

asynchronony of estrogen and P4 concentrations during the prepuberal cycle. This may result in ovarian and (or) uterine conditions that would have adverse effects on fertilization, conception and(or) maintenance of pregnancy. The second concerns heifers in E3 which failed to become pregnant. In this case luteal insufficiency appeared to be the cause since these heifers exhibited the lowest concentrations of P4 on d 6, 9 and 12. Further research is necessary to elucidate the physiological basis of sub-optimal fertility in beef heifers bred at puberty, changes in P4 concentrations between the puberal estrus and third estrus, and the maturational relationships between age at puberty and increasing fertility. Finally, another characteristic associated with NPE is the inability to become pregnant. Recommendations concerning breeding of beef heifers should include being bred as soon as possible in the breeding season and that heifers exhibit at least one or possibly two estrous cycles before the start of breeding.

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