HAY QUALITY, BREED, AND OVARIAN DEVELOPMENT EFFECTS ON ONSET OF PUBERTY AND REPRODUCTIVE PERFORMANCE OF BEEF HEIFERS

by

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DEDICATION

This thesis is dedicated to the three most important people in my life, my wife, Susan Henderson-Perry and my parents, Ed and Charlotte Perry. My parents are included in this dedication because they are mainly responsible for what I am today, and what I have accomplished to this point in my life. They have provided me with more than my share of opportunities and experiences. They have always provided guidance and support, but at the same time permitted the freedom that has allowed me to grow and to learn about life.

I am very fortunate to have Susan as my wife and best friend. She has changed my life in many positive ways, and I look forward to our life together. Without her, I would probably never have left California nor continued my education. This document is dedicated to her because of the part she plays in my life and also because of all the help, support, and encouragement that she gives me everyday we are together.

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Introduction

Age at puberty influences the lifetime production of a beef female. Heifers reaching puberty at younger ages calve earlier in the calving season (Laster et al., 1979), and have higher pregnancy rates (Ferrell, 1982). Heifers calving early in the first calving season tend to calve earlier throughout the remainder of their productive years (Burris and Priode, 1958; Short and Bellows, 1971), and produce more kg of calf in their productive lifetime than heifers calving later initially (Lesmeister et al., 1973). Likewise, heifers calving first as 2 yr-olds weaned 1.1 more calf per cow during their productive lives than heifers calving first as 3 yr-olds (Zimmerman et al., 1957). And in agreement, lines of cattle that reach puberty at younger ages conceive earlier, wean heavier calves, and have higher most probable producing ability indexes through four lactations (Werre and Brinks, 1986). For heifers to calve at 2 yr of age, puberty must be attained by 15 mo of age. Preferably heifers should reach puberty before the start of the breeding season, as heifers bred on puberal estrus had lower pregnancy rates than heifers bred on third estrus (Byerley et al., 1987).

The goals of this review are threefold 1) to review the factors influencing puberty, 2) to characterize ovarian and follicular growth in heifers, and 3) to discuss the effects of forage maturity on animal performance, daily intake, and dry matter digestibility. The possible application of this information would involve the importance of forage quality in the growth, onset of puberty, and subsequent reproductive performance of heifers; and secondly, the use of ovarian development at a given age as an indicator of age at puberty in heifers.

Mechanisms Associated with Puberty

Onset of Puberty. Puberty, or the period when an organism becomes sexually mature, is characterized, according to Hammond and Marshall (1922), by the changes whereby the two sexes become fully differentiated. However, Crew (1931) stated that puberty and sexual maturity are not the same. In agreement, puberty was defined as the time when reproduction first becomes possible, and sexual maturity as the time when an animal reaches its full reproductive power (Asdell, 1946). Puberty is now defined as the period during which the secondary sex characteristics begin to develop, and the capacity of sexual reproduction is attained. It is characterized by the events leading to the first estrus that is combined with ovulation. It appears that the mechanisms involved in the expression of puberty are progressive rather than abrupt events (Pelletier et al., 1981).

The most widely accepted theory regarding endocrine control of puberty is the "gonadostat" hypothesis proposed by Ramirez and McCain (1963). This hypothesis suggests that increased negative feedback of small amounts of estradiol from the ovary on luteinizing hormone (LH) secretion is responsible for prepuberal anestrous. As the female matures, the hypothalamo-pituitary axis becomes less sensitive to the negative feedback of estradiol, which results in follicular growth and development, and ultimately ovulation. This hypothesis can be applied to humans (Weitzman et al., 1975), rats (Ojeda et al., 1980), pigs (Lutz et al., 1984), lambs (Foster and Ryan, 1979; Ryan and Foster, 1980), and heifers (Day et al., 1982).

A considerable amount of literature supports this hypothesis. First, the frequency of LH pulses increases towards the onset of puberty (Schams et al., 1981; Day et al., 1984). Secondly, the sensitivity of the hypothalamo-pituitary axis to positive feedback control of estradiol increases during the prepuberal period in heifers (Swanson and McCarthy, 1978; Staigmiller et al., 1979), ewe lambs (Squires et al., 1972; Foster and Karsch, 1975), and gilts (Elsaesser and Foxcroft, 1978; Elsaesser and Parvizi, 1979). And thirdly, the sensitivity toward the negative feedback control exerted by estradiol remains relatively constant and only decreases just before the onset of puberty (Kiser et al., 1981; Schillo et al., 1982b; Day et al., 1984; Mosely et al., 1984).

Unlike most mammals, the prepuberal bovine female responds to the administration of ovarian and gonadotropic hormones virtually from birth (Casida et al., 1943; Rowsen, 1951; Marden, 1953). The ovaries are capable of responding to injections of gonadotropins with follicular development and ovulation in young prepuberal heifers (Foote and Onuma, 1970; Seidel et al., 1971), and ewes (Foster, 1984). The responsiveness of the pituitary gland to gonadotrophin releasing hormone is maximal before cycling is initiated (Barnes et al., 1980). Considering all these findings, it would appear that the limiting factor in the endocrine system of the maturing female is the hypothalamus.

It has recently been reported that an interaction between stage of sexual maturation, estradiol, and the opioid neuropeptides regulates LH secretion in the maturing bovine female (Wolfe et al., 1988). No other literature could be found to either support or refute this hypothesis.

Progesterone and LH concentrations in serum are characterized by distinct patterns of secretion just prior to puberty. Two peaks of LH are associated with puberty. The first is a priming peak, 9 to 11 d before the second, which occurs at puberty (Gonzalez-Padilla et al., 1975a). Progesterone concentrations increase prior to puberty, and are also characterized by two elevations during this period (Gonzalez-Padilla et al., 1975a), the first elevation preceding the priming peak of LH, and the second preceding the puberal LH peak. It was first suggested that the first increase in progesterone may be of adrenal origin, and the second from luteinized ovarian follicles (Gonzalez-Padilla et al., 1975a). However, it has since been suggested that luteinized follicles embedded in the ovary are the source of both increases in progesterone prior to puberty (Berardinelli et al., 1979). The exact significance of the progesterone increase is unknown, however, Schams et al. (1981) suggested this rise probably plays a key role in the establishment of a pulsatile pattern of gonadotrophin secretion appropriate for the development of an ovulatory surge.

Desjardins and Hafs (1969) suggested that secretions from the large population of follicles present on the ovaries of heifers at 4 mo of age may be associated with the onset of estrous cycles. Whether follicles present at 4 mo of age secrete steroid hormones is not known, but even the fetal bovine ovary is capable of some steroid transformations (Roberts and Warren, 1964). It has been suggested that the ovary containing the largest follicle is required to mediate the stimulus which leads to the LH surge before puberty, and the opposite ovary plays no important role in this mechanism (Tortonese et al., 1988).

Nonpuberal Estrus. Nonpuberal estrus, which is characterized by expression of estrus without luteal function, appears to be a fairly common occurrence in heifers at first estrus. More heifers exhibited a nonpuberal estrus than had normal luteal development after their first behavioral estrus (Rutter and Randel, 1986); and nonpuberal estrus was more common in younger heifers, and more common earlier in the season or year (Nelson et al., 1985; Rutter and Randel, 1986). More heifers that had a puberal first estrus, also had an elevation in serum progesterone before the first estrus, and the elevation was greater in these heifers than in heifers that had a nonpuberal estrus (Rutter and Randel, 1986).

The interval between the first nonpuberal estrus and puberty has been reported to be as long as 89 d (Nelson et al., 1985).

It appears that the reproductive system of heifers continues to mature after puberty is obtained. The occurrence of silent estrus decreased from 74% at first ovulation to 43% at second ovulation to 21% at third ovulation (Morrow, 1969). The occurrence of anovulation was greater at first estrus than during subsequent estrous periods (Morrow, 1969), and incidence of standing heat increased from 65 % at first estrus to 91 % at seventh estrus (Swanson et al., 1972). In addition, heifers have been reported to have higher progesterone concentrations during their second estrous cycle compared to first (Rutter and Randel, 1982). This maturation may also affect fertility, as heifers bred on third estrus had higher pregnancy rates than heifers bred on puberal estrus (78% vs 57%; Byerley et al., 1987). Similar findings have been reported in other species, as pregnancy rates associated with breeding ewe lambs at puberal estrus were lower than pregnancy rates of ewe lambs bred at a subsequent estrus (Hare and Bryant, 1985); and litter size has been reported to be lower when breeding occurred at puberty compared with breeding during subsequent estrous periods in gilts (Robertson et al., 1951), and rats (Evans, 1985).

Induction or Synchronization of Puberty. Reports indicate that it is possible to induce and synchronize a fertile estrus in prepuberal heifers of normal age and weight. Synchrony of estradiol and LH peaks, which lead to normal cyclic estrous patterns, can be induced as early as 9 to 10 mo of age by use of progestin implants (Short et al., 1976). Gonzalez-Padilla et al. (1975b) showed progesterone treatment followed by estrogen stimulated LH release in prepuberal heifers, and they concluded that progesterone was necessary for estrogen to immediately induce puberty. The most successful treatments for inducing puberty combined a pretreatment of progesterone followed by an injection of estrogen 24 h after the end of progesterone treatment (Short et al., 1976). In four trials, treating prepuberal heifers with 5 mg of estradiol valerate and 3 mg norgestomet, in conjunction with a 6 mg norgestomet implant for 9 d, resulted in inducing estrus in 94, 93, 79, and 89% of heifers within 4 d (Gonzalez-Padilla et al., 1975c), however, pregnancy rates associated with the induced estrus in 3 of the trials were 50, 56, and 43%. More current work indicates it is possible to induce an LH surge and ovulation with repeated injections of LH in prepuberal heifers (Tortonese et al., 1988).

Nutritional Influences on Puberty

Plane of Nutrition. Numerous researchers have documented that increasing nutritional levels during the growing period decrease age at puberty (Joubert, 1954; Wiltbank et al. 1957; Crichton et al., 1959; Sorenson et al., 1959; Reid, 1960; Bellows et al., 1965; Wiltbank et al., 1966; Wiltbank et al., 1969; Short and Bellows, 1971; Grass et al., 1982; Greer et al., 1983). Joubert (1954) found 64 percent of heifers receiving a high plane of nutrition reached puberty during the winter, whereas 86 percent of heifers receiving a low plane of nutrition did not reach puberty until the subsequent summer, resulting in a difference of 9.6 mo in the avg age at puberty. Similarly, 93 percent of heifers on a high protein, high energy diet reached puberty by 15 mo of age compared to only 36 percent of heifers receiving other diets (Clanton et al., 1964). Arije and Wiltbank (1971) noted that puberty was delayed until sufficient forage was available in the spring for heifers to start making rapid gains, then all heifers reached puberty rather rapidly. Recent information indicates that somatotropin and dietary energy influence average daily gain, skeletal growth, and body composition of beef heifers, but only dietary energy influences age at puberty (McShane et al., 1988).

Nutritional influences on weight at puberty are not as clear. Several studies indicate that increasing nutritional levels during the development period increase weight at puberty (Short and Bellows, 1971; Stewart et al., 1980; Greer et al., 1983). While, others show that even though higher nutritional levels decrease age at puberty, they have little or no effect on weight at puberty (Sorenson et al., 1954; Crichton et al., 1959; Dedeckova-Saliva, 1975). Plane of nutrition affected age at puberty, but not weight at puberty; however, within each treatment group, the fastest growing heifers reached puberty at the same age but a heavier weight than the slowest growing heifers (Little et al., 1981). Crichton et al. (1960) reported heifers reach puberty at the same percentage of their mature size, regardless of plane of nutrition. Likewise, weight at puberty only differed by 9.2% between heifers on a low or high plane of nutrition compared to a 62.9% difference in age at puberty (Hansel, 1959).

Target Weight Concept. Developing heifers to a desired target weight before the breeding season can influence puberty and subsequent performance. A higher percentage of light weight heifers that were separated at weaning, and fed a rate to achieve a desired target weight reached puberty by the start of the breeding season, and became pregnant in the fall when compared to light weight heifers fed together with heavier heifers (Varner et al., 1977). Wiltbank et al. (1985) reported that by increasing the target weight of heifers prior to the first breeding season, more heifers showed estrus and became pregnant in the first 20 d of the breeding season, and more were pregnant at the end of the breeding season. These heifers weaned 43.4 kg more calf/cow the first year, and continued to maintain advantages in reproductive performance during their second year of production.

Other factors such as season and prior nutrition can influence the optimum target weight. The optimum target weight of Sahiwal x Shorthorn heifers was less than 318 kg in late summer and autumn, but greater than 318 kg in winter and spring (Baker, 1967). Sparke and Lamond (1968) and Wiltbank et al. (1969) indicated that the target weight should be higher in heifers which have experienced prolonged undernutrition.

Feeding Strategies. Different feeding strategies have been studied to determine their influence on puberty. Park et al. (1987) designed a growing program in which dairy heifers were fed 15% below maintenance requirements for five mo, followed by 40% above maintenance for two mo, and then the same amounts for the same time periods were repeated. They were attempting to take advantage of compensatory growth. Heifers exposed to this growing scheme gained more weight, consumed less dry matter, were more efficient, and exhibited higher milk yields during their first lactation than controls. If the growing period is split into two periods, increased feeding during the second period results in similar ages at puberty when compared to increased feed levels during both periods (Dufour, 1975). Heifers on a high followed by low plane of nutrition were later in reaching puberty compared to heifers on a low level during both periods; because heifers on a higher level early had increased growth, and thus higher maintenance requirements during the second period (Crichton et al., 1959). Clanton et al. (1983) noted it is not important when gains occur, as long as heifers reach a set weight before the breeding season. It is probably more economical to obtain these gains later because of smaller maintenance requirements for a longer period of time (Clanton et al., 1983). Herman and Ragsdale (1946) concluded the ideal nutritional program for developing dairy heifers is attained by feeding milk for the first few months, followed by grain and hay, and after eight to nine months, heavy roughage with minimum grain.

Average Daily Gain. Average daily gain also influences onset of puberty. Age and weight at puberty are highly associated with postweaning rate of gain (Reynolds et al., 1963; Wiltbank et al., 1966; Arije and Wiltbank, 1971; Arije and Wiltbank, 1974; Little et al., 1981). Age at puberty decreased from 411 to 380 d when rate of gain increased from .45 to .68 kg/(hd•d) (Short and Bellows, 1971). In addition, Angus and Hereford heifers reached puberty at 374 and 387 d of age and 305 and 294 kg, respectively, when postweaning rate of gain was .77 and .68 kg/(hd•d), respectively (Wiltbank et al., 1969). In dairy heifers, the occurrence of scours caused up to a 136 d delay in onset of puberty (Menge et al., 1960). This effect was almost totally due to the negative effect of scours on heifer weight at 3 and 6 mo of age (Hawk et al., 1960).

Nutritional level and average daily gain interact in affecting puberty. As average daily gain affected age at puberty in heifers on a low plane of nutrition; however, average daily gain had little or no effect on puberal age in heifers on a high plane of nutrition (Wiltbank et al., 1966; Wiltbank et al., 1969).

Implants. It is well documented that implants increase average daily gain in heifers (Sharp and Dyer, 1968; Perry et al., 1970; Sharp and Dyer, 1971). Implanting prepuberal heifers also affects their age at puberty. Trenbolone acetate when implanted at 16 wk had no apparent effect on age at puberty, but when implanted at 31 wk of age improved growth rate and feed conversion, and delayed onset of puberty (Kay et al., 1977). In agreement, heifers implanted with trenbolone acetate at 16 wk and again at 31 wk of age were later in reaching puberty, and had increased incidence of dystocia, with virilization of the clitoris and vulva being observed (Heitzman et al., 1979). Staigmiller et al. (1978) reported that zearalonone implants, administered in November and again 84 d later, increased both rate of gain and pelvic area, had no effect on hastening onset of puberty, and tended to adversely affect fall pregnancy rate.

Feed Additives. The administration of certain feed additives appears to positively affect puberty, while others negatively influence puberty. The addition of monensin to the diet hastened onset of puberty without increasing average daily gain (Mosely et al., 1977; McCartor et al., 1979; Mosely et al., 1982). Harrison and Randel (1986) stated that dietary monensin seems to be able to "override" seasonal influences on puberty, and the more mature, well developed endocrine system is less sensitive to the monensin-induced physiological changes. However, heifers fed protein-protected lipids showed similar weight gains and conception rates, but were later in reaching puberty compared to controls (Rhodes et al., 1978).

Tissue Growth. The literature indicates that nutrition affects the growth of some body tissues more than others. Late maturing characters such as weight and heart girth were most affected by restricted feeding, while earlier maturing characters such as height and length were least affected (Crichton et al., 1959). The relative difference induced by feed level seemed to be greater for condition score and progressively less for body weight and pelvic area, thus feed level had a greater effect on soft tissue development than on skeletal growth (Short and Bellows, 1971).

Subsequent Reproductive Performance. Nutritional levels during the development period also affect subsequent reproductive performance. Numerous reports indicate that restricted feed intake or lower nutritional levels prior to and during the breeding period result in decreased pregnancy rates (Schilling and England, 1968; Hill et al., 1970; Spitzer et al., 1978). Lemenager et al. (1980) suggested that winter gains were more important than gains made during the breeding period in affecting pregnancy rate in heifers. The literature is not consistent in identifying causes of the decreased reproductive performance when nutrition is restricted in heifers. Heifers wintered at lower levels conceived later because they were bred later and not because of increased number of services per conception (Joubert, 1954). Similarly, plane of nutrition had no effect on first service conception rate or services per conception (Little et al., 1981). In contrast, reduced pregnancy rate in cattle on restricted energy is the result of embryonic loss after d 4 of pregnancy (Spitzer et al., 1978). However, Hill et al. (1970) suggested fertilization failure and not embryonic death causes reduction in fertility in undernourished heifers.

The effects of nutrition on reproductive performance may vary with breed. Patterson (1988), studying the effects of postweaning energy in Brahman x Hereford and Angus x Hereford heifers, found energy level influenced conception rate in Brahman x Hereford heifers, and incidence of dystocia at first calving in Angus x Hereford heifers.

Overfeeding. While increasing nutrition positively influences heifer development, overfeeding to the extent that results in obesity can have a detrimental effect on reproductive performance. Fat heifers have decreased fertility (Little et al., 1981; Ferrell, 1982), increased incidence of dystocia, and higher calf mortality (Bond and Wiltbank, 1970). Dairy heifers grown at rapid rates tend to have inferior productive performance compared to heifers grown at moderate or slow rates (Reid et al., 1963), and a similar relationship appears to exist in beef heifers (Pope, 1967).

Nutritional Effects on Hormonal Concentrations. The mechanism in which undernutrition affects the reproductive system is probably complex. The findings describing hormonal changes associated with undernutrition are conflicting. Undernourished heifers have been shown to have both similar (Apgar et al., 1975; Spitzer et al., 1978), and decreased (Beal et al., 1978; Imakawa et al., 1983) progesterone concentrations compared to heifers fed maintenance diets. Additionally, undernutrition initially increased progesterone concentrations, but prolonged undernutrition decreased progesterone concentrations (Donaldson et al., 1970; Gombe and Hansel, 1973). It appears that the effects of undernourishment on growth and maintenance of the corpus luteum, and secretion of progesterone depends on the length of restricted feeding (Hill et al., 1970).

The literature describing the effects of undernutrition on serum concentrations of luteinizing hormone (LH) is also inconsistent. Undernutrition reduces the secretion of gonadotropin from the pituitary gland in most species (Leathem, 1966). LH concentrations were decreased in cows (Apgar et al., 1975), and heifers (Imakawa et al., 1983) on a restricted energy diet. The reduced secretion of LH seen in prepuberal heifers on a restricted energy diet resulted from a delay in the prepuberal decline of the negative feedback of estradiol (Schillo et al., 1982a). Additionally, Imakawa et al. (1987) determined that dietary energy restriction in beef heifers has a direct action on the hypothalamo-pituitary axis to lower the number of LH pulses in the absence of ovarian steroids.

In contrast to these findings, Beal et al. (1978) found heifers fed low energy diets had higher peak LH concentrations, and greater total LH release following an initial gonadotropin releasing hormone injection. Likewise, Gombe and Hansel (1973) concluded that since energy restriction decreased progesterone concentrations after a short period of time, and since progesterone secreted by the corpus luteum exerts a negative feedback on LH, restricted energy increased LH concentrations. They suggested that the decrease in ovarian function seen on restricted energy is not due to a decrease in LH, but rather in the way the ovary responds to LH.

Other Environmental Influences on Puberty

Season. Season affects reproduction in farm animals, with considerable variation noted among species in the degree of influence. Results addressing seasonal influences on age at puberty in heifers have been conflicting. Heifers born in the spring were younger at puberty than those born in other seasons (Hawk et al., 1960; Roy et al., 1980; Little et al., 1981). In contrast, heifers born in September had higher average daily gains, and attained puberty at slightly younger ages than heifers born in March (Schillo et al., 1982b). Grass et al. (1982) concluded that winter environments tend to delay puberty in heifers that have not reached puberty before November; and Hansen (1985) suggested that winter environments during the first six mo. of life hasten onset of puberty, while the same conditions after six mo delay puberal onset.

Temperature, Photoperiod, and Phase of Moon. Other environmental factors such as temperature, photoperiod, and phase of the moon influence puberty. Heifers reared at 10 C reached puberty earlier, and at lighter weights than heifers reared at 27 C (Dale et al., 1959). Chronic exposure to elevated temperature (35 C, 35% relative humidity) did not affect food intake or average daily gain in gilts, however onset of puberty was delayed by 9 d, and the incidence of cystic follicles was increased from 0 to 50% (Flowers et al., 1986). Increasing the amount of light to 18 h/d had no effect on growth rate, or LH concentrations in serum, but it increased ovarian growth and decreased age at first estrus (Hansen et al., 1983). Sixteen h light/d decreased age and weight at puberty (Ringuet et al., 1988), and tended to hasten onset of puberty from November to March, but had no effect on age at puberty from April to August (Peters and Tucker, 1978). Schillo et al. (1983) reported 6 mo old heifers exposed to temperature and photoperiod conditions representative of spring to fall conditions reached puberty at earlier ages than heifers exposed to conditions representative of fall to spring. Roy et al. (1980) determined phase of the moon affected young heifers by positioning the cycles of initial estrous activity with the occurrence of the full moon.

Housing Conditions. Other environmental conditions such as housing affect puberty in gilts. Gilts reared under confinement conditions exhibit a delay in onset of puberty compared to gilts reared under nonconfinement conditions (Christenson and Young, 1978; Ford and Teague, 1978; Christenson and Ford, 1979a,b; Rampacek et al., 1981; Hawkins et al., 1986; Zimmerman and Kopf, 1986; Zimmerman et al., 1988)

Social Environment. The effects of social environment on age at puberty have been confounding. Izard and Vandenbergh (1982) showed treating heifers with bull urine hastened onset of puberty, and increased the percentage of heifers calving early in the calving season. Similarly, boar exposure decreases age at puberty of gilts (Zimmerman et al., 1974; Hawkins et al., 1986; Zimmerman and Kopf, 1986). Additionally, Nelson et al. (1984) reported that exposing heifers to mature cows affected age at puberty, but in contrast to these results, neither the presence of mature bulls (Roberson et al., 1987), or estrous females (Roberson et al., 1983) influenced age or weight at puberty. Similarly, presence of a bull for 3 wk had no effect on age at puberty and electrical stimulation did not influence onset of puberty or size of the largest follicle (Berardinelli et al., 1978).

Genetic Influences on Puberty

Breed. Numerous reports document breed differences in age and weight at puberty (Kaltenbach and Wiltbank, 1962; Wiltbank et al., 1966; Short and Bellows, 1971; Laster et al., 1972; Arije and Wiltbank, 1974; Laster et al., 1976; Smith et al., 1976a; Gregory et al., 1978; Gregory et al., 1979; Laster et al., 1979; Stewart et al., 1980; Grass et al., 1982; Greer et al., 1983). The majority of these results are summarized in Table 1. Females from Angus dams were similar to females from Hereford dams in weight at puberty , but were 22 d younger at puberty (Gregory et al., 1979), and heifers from Angus dams were 26 d younger and 9 kg lighter at puberty than those from Hereford dams (Laster et al., 1976). Likewise, a higher percentage of heifers from Angus dams reached puberty by 15 mo than those from Hereford dams, 95 and 71%, respectively (Laster et al., 1972). Some researchers suggest that breeds selected for high levels of milk production reach puberty at younger ages and lighter weights, relative to their mature weight when compared to breeds selected solely for beef production (Laster et al., 1972; Laster et al., 1979; Ferrell, 1982).

Bos indicus. Bos indicus and *Bos indicus* cross heifers have been shown to be late maturing. Brahman heifers were older and heavier at puberty than British breeds (Warnick et al., 1956; Gregory et al., 1979; Stewart et al., 1980). Five percent of Brangus heifers and 7 percent of Brahman heifers were not puberal by 30 mo of age (Reynolds et al., 1963); and a lower percentage of Brahman x Hereford heifers reached puberty by the start of the breeding season compared to Angus x Hereford heifers (Patterson , 1988). Angus heifers were lighter and younger at puberty with Brahman x British heifers intermediate, and Brahman heifers considerably older and heavier at puberty (Reynolds, 1972; Franke and England, 1965). The reported ages at puberty of purebred Brahman heifers are 816 d

(Reynolds, 1972), 582 to 639 d (Plasse et al., 1968), and 382 to 479 d (Stewart et al., 1980). Randel et al. (1984) showed that 62.5% of Brahman x Hereford heifers had not reached complete maturation at their first standing estrus.

A limited amount of information exists describing possible causes of the slower reproductive development in *Bos indicus* heifers. The genital tract and ovaries at the mature luteal phase were generally smaller in *Bos indicus* than in *Bos taurus* heifers, and peak progesterone levels were higher in *Bos taurus* than *Bos indicus* heifers (Adeyemo and Heath, 1980). Corpora lutea were smaller in Brahman heifers than in Hereford and Brahman x Hereford heifers (Irvin et al., 1978), however, luteal progesterone concentrations were similar between the breed groups, as corpora lutea of Brahman heifers had higher 3-ß hydroxysteroid dehydrogenase activity, which is responsible for the conversion of pregnenolone to progesterone (Irvin et al., 1978). Plasse et al. (1968) reported a decrease in ovarian activity during the winter months in Brahman and Brahman cross heifers, as the number of corpora lutea decreased when temperatures dropped below 16 C.

Heterosis. Heterosis reduces age at puberty independent of its effects on average daily gain (Wiltbank et al., 1966; Wiltbank et al., 1969; Burfening et al., 1979). Smith et al. (1976a) noted the primary effect of heterosis is to speed up the maturing process. Crossbreds were 58 d younger and 12.3 kg lighter (Kaltenbach and Wiltbank, 1962), and 41 d younger and 2.6 kg lighter (Wiltbank et al., 1966) at puberty than purebreds. Similarly, inbreeding increased age at puberty, and its effect was almost totally due to decreased weight at 3 and 6 mo of age (Hawk et al., 1960). However, partially confounding these results, crossbreds were younger and heavier at puberty than purebreds (Gregory et al., 1978; Nelson et al., 1982), and heterosis in Hereford-Angus reciprocal crosses for age at puberty was -19.5 d with no effect on weight at puberty (Laster et al., 1976). Additionally, heterosis had no effect on puberal age of heifers on a high plane of nutrition (Wiltbank et al., 1969; Stewart et al., 1980).

Heritability. Researchers have estimated the heritability of age at puberty, and have correlated it with other factors. Reported heritability estimates for age at puberty include .64 (Smith et al., 1976b), .41 (Laster et al., 1979), and .20 (Arije and Wiltbank, 1971). The correlation between 6 mo weight and age at puberty was -.42 (Hawk et al., 1960), and the correlation between weaning weight and age at puberty was -.23 (Wiltbank et al., 1959). Laster et al. (1979) determined the genetic correlations between puberty age and the following traits: birth weight, .66; puberty weight, .90; percentage pregnant, -.42; milk production as 3 and 4 yr-olds, -.88; and percentage fat trim of steer contemporaries at a constant age, -.70.

Dam age. The influences of dam age on puberal attainment of female offspring have been contradictory. Age at puberty was 13 d younger in heifers from cows 5 yr and older compared to those from 4 yr-old dams (Laster et al., 1979). Additionally, fewer heifers from 2 yr old dams reached puberty by 390 d of age compared to heifers from older dams (Laster et al., 1976). Contrary to these results, age of dam was reported to affect weight at various ages, but did not affect age at first estrus (Anderson et al., 1973), and age of dam had no effect on puberty (Burfening et al., 1979).

Factors Determining Puberty

Researchers have tried to predict what factor or factors actually determine pubertal age. Mosley et al. (1982) suggested age limits the occurrence of puberty in heavy weight heifers, and weight in light weight heifers. Dufour (1975) concluded that once a minimum age is achieved, weight is a major factor in determining pubertal onset. Crichton et al. (1960) predicted that heifers reach puberty at a similar percentage of their mature size. A similar relationship appears to exist in humans, as puberty occurs at a common weight (Frisch and Reville, 1970). Others such as Greer et al. (1983) determined that wt/d of age may be the best estimate of the genetic physiological determinant of age at first estrus. Smith et al. (1976b) indicated that heifers heavier at any age tended to be younger at puberty, and heifers larger at one yr of age are younger and taller at puberty (Baker et al., 1988). Conversely, Little et al. (1981) reported onset of puberty was related to body weight but not to age.

Ovarian and Follicular Development

Ovarian Growth. The embryonic ovary increases in weight and volume, showing an approximate straight line relationship with the growth of the embryo in swine and cattle (Sakai, 1955). Ovarian weight increased nearly four times more rapidly than bodyweight from birth to 5 mo, plateaued from 5 to 8 mo, and resumed growth comparable to that of the body after estrous cycles were initiated during the 7 mo of age (Desjardins and Hafs, 1969). This growth rate continued until approximately 12 mo of age. It was determined that this growth pattern could be explained by changes in follicular growth, as numbers of small and large follicles increased to a maximum at 4 mo, decreased from 4 to 8 mo, and remained relatively constant thereafter (Desjardins and Hafs, 1969). Supporting the finding that increases in ovarian size are accompanied by increases in follicular development, Hansen et al. (1981) reported increases in ovarian volume in prepuberal heifers were accompanied by increases in the number of large follicles.

If the pattern of ovarian growth described by Desjardins and Hafs (1969) does exist, then the finding that no correlation existed between age and total ovarian weight in heifers under 6 mo of age (Howe et al., 1964) would appear logical. Casida et al. (1935) noted the morphological state and physiological activity of the ovary, which are attendant upon puberty, are the product of gradual development, and are not affected briefly before reproductive maturity is attained.

Ovarian Size and Puberty. In the one study found that described the relationship between ovarian size in heifers and puberal onset, heifers with greater ovarian volume at 7 mo of age reached puberty earlier (Schillo et al., 1983). However, a considerable amount of literature exists addressing the relationship between gonadal size and pubertal age in bulls. Lunstra (1982) suggested scrotal circumference is the best single indicator of puberty in bulls, and numerous studies (Brinks et al., 1978; Lunstra et al., 1978; King et al., 1983) have indicated a negative genetic correlation exists between scrotal circumference and age at puberty in young bulls. Favorable relationships also exist between scrotal circumference in bulls and age at puberty (Brinks et al., 1978; Lunstra, 1982; King et al., 1983), and age at first breeding (Toelle and Robison, 1985) in closely related females.

Follicular Growth. The primary follicle appears in the ovaries of bovine, porcine, and equine embryos when the crown-rump length of the embryo is 9.7 cm, 15 cm, and 20 cm, respectively (Sakai, 1955). No follicles were visible macroscopically on the ovaries of heifers at birth (1 to 3 d of age, Desjardins and Hafs, 1969), but follicular development is present in calves from a few d of age to puberty (Casida et al., 1935; Erickson, 1966; Henricson and Rajakoski, 1959; Howe et al., 1962; Howe et al., 1964; Morrow, 1969; Forrest et al., 1984; Goff et al., 1984). The number of vesicular follicles, growing follicles, and primordial oocytes from birth through 20 yr of age are shown in Figure 1 (Erickson, 1966).

Preantral and antral follicles increase coincidently in number from birth to approximately 70 d of age (Goff et al., 1984). However, between 3 and 9 mo of age, the number of antral follicles remains relatively constant (Howe et al., 1964; Forrest et al., 1984), until the onset of puberty (Swanson et al., 1972). Follicular activity increased approximately 20 d, and in some heifers 40 d, before first ovulation (Morrow, 1969).

The literature documents that large follicles are present on the ovaries of young heifers; 13 mm follicles were present in heifers between 1 and 14 wk of age (Casida et al., 1935), and 12 to 14 mm follicles were present in heifer calves ranging in age from 30 to 180 d (Howe et al., 1962). In general, the number and size of large follicles increase with age (Casida et al., 1935; Henricson and Rajakoski, 1959), and the degree of development of larger follicles is correlated with both body weight and uterine horn diameter (Casida et al., 1935).

In ewes, a total of 6 mo is required for complete development of an ovulatory follicle (Cahill and Mauleon, 1980; Turnbull et al., 1977), indicating that follicles must be present in ewe lambs for a sufficient amount of time prior to puberty.

Follicles go through continual growth and regression in young bovine females. Many atretic follicles are found in the ovaries of prepuberal heifers (Sorenson et al., 1959), and continuous follicular degeneration occurs during early postnatal life (Casida et al., 1935). Howe et al. (1962) reported follicular growth followed by atresia occurs in young calves as early as 1 mo of age. In their study, follicles developed to 7 to 12 mm before regressing.

Age does not appear to be the controlling factor in ovarian activity, since follicular development varies largely in individual heifers of the same age (Howe et al., 1962; Howe et al., 1964). However, the high variation in number of follicles observed among gilts of similar ages, within breeds, decreased markedly when gilts were grouped based on the morphology of their ovaries (Dufour et al., 1985). These researchers determined three morphological types of ovaries could be distinguished based on size and number of antral follicles. Bolamba et al. (1988) reported that follicular development in gilts is in a dynamic state prior to puberty, and that the three ovarian types mentioned above could be a result of a cyclic phenomenon taking place during this period of life.

Heifers with greater follicular development responded better to inducing puberty, and had higher pregnancy rates (Gonzalez-Padilla et al., 1975c), indicating that follicular development is related to reproductive maturation.

Nutritional Influences on Ovarian Characteristics

Ovarian Development. Limited information exists describing nutritional effects on ovarian development in heifers. A submaintenance diet reduced ovarian weight in ewes (Allen and Lamming, 1961), and restricting energy to 1/3 the recommended level had no effect on fertilization rate, follicle numbers and volume, or luteal volume; however, the ovulatory ovary was 57% larger in heifers on recommended feeding levels (Spitzer et al., 1978).

Follicular development. The exact mechanism by which nutrition controls ovarian activity is not fully understood. Nutrition influences follicular development in both heifers and postpartum anestrous cows. Lowering postpartum energy intake increased the interval from parturition to both the development of a follicle greater than 10 mm, and first ovulation (Oxenreider and Wagner, 1971). Additionally, ovarian development was greater in cows receiving 150% of maintenance, as these cows had larger follicles and greater ovarian volume (Wiltbank et al., 1964).

Undernutrition reduced the follicular population in heifers, and a transitory decline in follicle number and size occurred after 12 d of undernutrition (Hill et al., 1970). Additionally, submaintenance feeding resulted in a reduction of follicle numbers (Allen and Lamming, 1961), and size (Allen and Lamming, 1961; Lamond, 1970). Likewise, ewes on a lower plane of nutrition had decreased follicular development (Allison, 1977), and ewes receiving a grain supplement showed an increase in total follicular fluid weight (Bellows et al., 1963). However, contrary to these results, level of feeding had little effect on ovarian function once puberty was reached (Sorenson et al., 1959).

In gilts, the effect of nutrition on follicular development may differ depending on breed. In Hampshires, a late-maturing breed, changing the feeding regimen for different periods failed to affect follicular development. However, in Yorkshires, an early-maturing breed, follicular development decreased in slower growing gilts (Dufour et al., 1985).

Feeding increased energy during the time of follicular development, also known as "flushing," influences ovulation rate. Demonstrated by findings that ovulation rate is stimulated by increasing the nutrient intake for only a short interval of time before ovulation in gilts (Self et al., 1955; Zimmerman et al., 1960), heifers (Dufour et al., 1981; Lamond, 1970), and ewes (Clark, 1934; Allen and Lamming, 1961; Allison, 1968; Allison, 1977). The mechanism by which "flushing" increases ovulation rate is not known. In heifers, high energy increased the number of follicles < 1.58 mm, and increased atresia of follicles measuring 1.58 to 3.67 mm (Maurasse et al., 1985). The number of follicles measuring 3.68 to 8.56 mm was decreased, and thus high energy may accelerate both the growth and turnover of follicles.

Nutrition also affects development of corpora lutea. Energy restriction reduced corpora lutea weights (Apgar et al., 1975; Harrison et al., 1982), as weights of corpora lutea formed in undernourished heifers were approximately 70% of controls (Hill et al., 1970).

Other Influences on Ovarian Characteristics

Body condition. Body condition also affects follicular development. Body condition at mating affected ovulation rate in ewes (Clark, 1934; Gunn et al., 1972). Exogenous insulin increased ovulation rate in energy deprived heifers (Harrison et al., 1982), indicating that the body's perception of well being may influence follicular development. Nutrition and body condition appear to interact in influencing follicular development. The level of food intake before and at mating had no effect on ovulation rate of moderately fat ewes, but increasing intake had a positive effect on ovulation rate in thin ewes (Gunn et al., 1972). Likewise, fasting for 72 h decreased the number of ovulations in heifers on a high plane of nutrition, and had no effect in heifers on a low plane of nutrition (Lamond, 1970).

Season. Season influences ovarian growth (Hansen et al., 1981). Plasse et al. (1968) reported ovarian activity decreased during the winter period, with a decrease in the number of corpora lutea when temperatures dropped below 16 C. Also, higher doses of progesterone were required to suppress ovarian activity during winter and early spring compared to other times of the year (Lamond, 1965).

Photoperiod. Photoperiod may also influence ovarian development, as heifers exposed to 18 h light/d showed increased ovarian size compared to heifers in natural conditions (Hansen et al., 1983).

Breed. Breed appears to influence follicular development in gilts. The number of secondary follicles measured at 42 d of age was greater in Yorkshire gilts, which have a higher ovulation rate than that of Poland China gilts (Bhalla at al., 1969), and follicular development was greater in Hampshire than Yorkshire gilts at 140 and 175 d of age (Dufour et al., 1985).

Forage Quality and Digestibility

Maturity Effects on Forage Quality, Quanity, and Digestibility. As plants mature, the percentage of total plant dry matter represented by stem material increases, and stems have been shown to contain more cell wall and lignin than do leaves (Griffin and Jung, 1983; Wilman and Altimimi, 1984). Both leaves and stems show increases in lignified sclerenchyma cells during maturation (Wilkens, 1972), and cells with higher concentrations of lignin are generally less digestible (Akin and Burdick, 1975; Akin et al., 1983). Several studies have documented the negative correlations between forage lignin concentration and dry matter and fiber digestibility (Van Soest, 1964; Ingalls et al., 1965; Mowat et al., 1969; Allinson and Osbourn, 1970; Minson, 1971; Van Soest et al., 1978), and this relationship may be curvilinear in nature (Meyer et al., 1960; Jung and Vogel, 1986).

As forage matures, the percentage of dry matter represented by fibrous components increases. The content of cellulose, and hemicellulose are positively correlated to increasing maturity (Meyer et al., 1960; Van Soest et al., 1978) with more mature forages having increased content of neutral detergent fiber, acid detergent fiber, and acid detergent lignin (Bertilsson and Burstedt, 1983; Collins, 1983; Erickson et al., 1986; Funk et al., 1986; Rihawi et al., 1987; Brown, 1988).

The protein content of forages decreases with increasing maturity (Mellin et al., 1962). This relationship has been found to exist in cereal silages and hays (Haile, 1984; Azimi et al., 1988), bromegrass (Erickson et al., 1986), timothy hay (Mellin et al., 1960), grass hay (Brown, 1988; Hunt et al., 1988), and alfalfa hay (Meyer et al., 1960; Collins, 1983). The crude protein content of legume-cereal mixtures decreased from 14.3% for hay harvested at 10% flowering to 11.7% for hay harvested at 100% flowering (Rihawi et al., 1987).

The only positive effect of forage maturation is that dry matter yields/ha are increased. This has been reported in cereal silages and hays (Haile, 1984; Azimi et al., 1988), bromegrass (Knutti and Hidiroglou, 1967; Erickson et al., 1986), timothy (Knutti and Hidiroglou, 1967), mixed hays (Spahr et al., 1960; Rihawi et al., 1987), and alfalfa (Jones et al., 1953).

When considering the conflicting effects of maturity on quality and yield of forage, one must select the optimum date of harvest that results in the highest possible yield of adequate quality forage. With alfalfa, the optimum time to harvest has been predicted to be when 10% of the stems have one or more flowers in bloom (Weir et al., 1960; Meyer et al., 1960).

Numerous reports indicate the negative effects of increasing forage maturity on digestibility (Kamstra et al., 1958; Reid et al., 1959; Weir et al., 1960; Mellin et al., 1962; Mowat et al., 1965; Calder, 1977; Bertilsson and Burstedt, 1983; Llano and DePeters, 1985; Cleale and Bull, 1986; Erickson et al., 1986; Jung and Vogel, 1986; Ye et al., 1986; Rihawi et al., 1987; Roth and Klopfenstein, 1987; Anderson et al., 1988; Brown, 1988; Hunt et al., 1988). The dry matter and protein digestibility of timothy hay decreased from 81.6 and

84.9% to 51.9 and 51.6%, respectively, for hay cut on May 27 compared with July 22 (Mellin et al., 1960). Likewise, in vitro dry matter digestibility decreased from 52.2% for grass hay cut on June 12 to 37.5% for hay cut on July 26 (Flipot et al., 1984). Additionally, the digestibility of alfalfa decreased from 67.6% for hay harvested at bud stage to 60.1% when harvested at late bloom stage (Collins, 1983). It has been suggested that the digestibility of grasses decrease at a rate of approximately 0.5 percentage units/d (Pritchard et al., 1963; Calder and Macleod, 1968; Gervais and St-Pierre, 1979).

Other Influences on Digestibility. Breeds of cattle may differ in their digestive capabilities. British steers exhibited lower dry matter and apparent nitrogen digestibility than Zebu and Zebu-cross steers on low quality diets (Ashton, 1962). Brahman heifers were slightly more efficient than British heifers in digesting all nutritional components except ether extract (Howes et al., 1963). However, others have shown that Zebu and European cattle were relatively similar in their digestive capabilities (French, 1940; Duckworth, 1946; Phillips et al., 1960). The differences in breeds may be affected by quality of diet, as digestible dry matter values were higher for Hereford bulls than Brahman bulls when fed a high energy ration, however, when fed a low energy ration, digestible dry matter values were higher for Brahmans than Herefords (Moore et al., 1975).

Bos indicus cattle have been shown to possess a shorter rumen retention time (Phillips et al., 1960; Howes et al., 1963; Hunter and Siebert, 1985b), a higher fermentation rate (Hungate et al., 1960; Howes et al., 1963), and a faster rate of digestion (Hunter and Siebert, 1985a) than *Bos taurus* cattle. In relation to these findings, Brahmans were shown to possess a larger rumen mucosal weight per unit of empty body weight (Alexander, 1961).

In dairy cattle, as proportion of high energy concentrates increase in the ration, fiber digestibilities decrease (Nelson et al., 1968; Mertens and Loften, 1980; Colucci et al., 1982; MacLeod et al., 1984; Stokes et al., 1985).

Processing of roughage may also affect digestibility. The reported effects of grinding hay on the digestibility of a ration have been conflicting. One study (Bechdel and Williams, 1928) showed grinding hay in a ration caused an increase in digestibility, while other reports indicate the digestibility of a ration is decreased by grinding hay (Forbes et al., 1925; Bechdel et al., 1927; Bechdel et al., 1929; Heller et al., 1941; Balch, 1950; Blaxter and Graham, 1956; Rodrique and Allen, 1960; Alwash and Thomas, 1974; Shaver et al., 1986). Yet, others (Morrow and La Master, 1929; Olson, 1930; Meyer et al., 1959) have found no differences in digestibility between ground and/or pelleted and unground hay. However, all agree, when dry matter digestibility was decreased, it was mainly due to a decrease in the digestibility of the cell wall constituents (Bechdel et al., 1927; Bechdel et al., 1929; Heller et al., 1941; Balch, 1950; Blaxter and Graham, 1956; Rodrique and Allen, 1960). The effects of grinding may also differ with different forages, as grinding had no effect on the digestibility of lucerne hay, but reduced that of wheat hay (Hogan and Weston, 1967).

Level of intake may also affect digestibility, as organic matter and neutral detergent fiber digestibility were decreased at higher intakes (Shaver et al., 1986).

Mechanisms Controlling Feed Intake. Blaxter et al. (1956) and Blaxter et al. (1961) suggested the mechanism controlling feed intake in ruminants is purely one of digestive tract distension which is a function of both the digestibility of the feedstuff, and its rate of passage through the gut. In agreement, Milchunas et al. (1978) indicated that voluntary intake is a function of the turnover time of consumed forage, and the quantity of dry matter fill possible within the alimentary tract. Thus, slower digestion and passage of undigested residues from the rumen results in decreased intake (Campling et al., 1961). When dry matter digestibility increased from 52% to 67% by earlier harvest, dry matter intake of forages was improved by 40%, and 82% for digestible dry matter (Reid, 1962). Conrad et al. (1964) suggested that when animals are consuming forages ranging in digestibility from 52% to 66%, voluntary intake is positively related to digestibility. However, when digestibility exceeds 66.7%, intake is regulated by energy requirements, and thus intake decreases with increasing digestibility (Conrad et al., 1964). In contrast, other results demonstrate that feed intake increases with increasing digestibility, even when dry matter digestibility exceeds 67% (Bertilsson and Burstedt, 1983). Other researchers have indicated that feed intake is more highly related to cell wall content than to digestibility (Van Soest, 1965; Osbourn, 1967; Minson, 1977; Bertilsson and Burstedt, 1983).

Forage Quality Effects on Intake. Lignin and fiber content of forages has been shown to be negatively (Stallcup et al., 1956; Hawkins et al., 1964) correlated with dry matter intake. Animals consuming forages harvested at later maturities have shown decreased dry matter intakes (Bohman, 1955; Spahr et al., 1960; Blaxter et al., 1961; Spahr et al., 1961; McCarrick, 1966; Troelsen and Campbell, 1969; Kawas, 1983; Flipot et al., 1984; Johnson et al., 1984). Possible explanations for these findings include decreased passage rate (Blaxter et al., 1961; Cleale and Bull, 1986; Hunt et al., 1988), and fluid dilution rate (Funk et al., 1986) with more mature forage, and shorter mean retention time shorter for early vs late cut hay (Hunt et al., 1988). Dairy cows consuming hay harvested June 12 consumed 2.19% of their body weight compared to 2.0% for hay harvested on June 22 (Bertilsson and Burstedt, 1983).

Other Influences on Intake. Voluntary intake of animals is correlated with liveweight (Frisch and Vercoe, 1969), and breed differences in intake have been shown to exist. *Bos indicus* breeds appear to consume less than *Bos taurus* breeds on similar diets (Rogerson et al., 1968; Ledger et al., 1970; Frisch and Vercoe, 1977). At the same adjusted liveweight, Brahman steers consumed 21% less dry matter than Hereford x Shorthorn steers on a similar lucerne hay diet (Frisch and Vercoe, 1969). The voluntary intake of zebu crossbreds has been shown to be between the means of the parental breeds (Ledger et al., 1970; Warnick et al., 1973; Frisch and Vercoe, 1977), However, Shorthorn x Brahman crossbreds consumed more than either parental breed (Hardgrove et al., 1959). Frisch and Vercoe (1977) suggested that differences in voluntary intakes between *Bos indicus* and *Bos taurus* breeds are correlated with differences in fasting metabolic rate/kg liveweight. In contrast to these results, Brahmans and Herefords on similar diets exhibited similar intakes (Hunter and Siebert, 1985b).

If differences in voluntary intakes exist between *Bos taurus* and *Bos indicus* breeds, differences in daily gains should also be apparent. Research has shown that *Bos taurus* breeds exhibit higher daily gains than *Bos indicus* crossbreds in unstressful temperate areas (Deland et al., 1974; Morgan et al., 1976), and feedlots (Rogerson et al., 1968; Ledger et al., 1970; Baker et al., 1973). However, this relationship may not exist in all environments, as environmental stresses affect intake and d gain (Frisch, 1976). On protein deficient diets, Brahman steers consumed more dry matter than Hereford steers (Howes et al., 1963), and it has been suggested that this may partially explain their ability to thrive under adverse nutritional conditions. In addition, Brahman steers maintained higher rumen NH_3 concentrations than Herefords, when consuming grass hay diets that were deficient in nitrogen (Hunter and Siebert, 1985a), and they had a faster rate of digestion on these diets.

Processing of forages has been shown to affect intake. Grinding increased the consumption of both lucerne and wheaten hays (Hogan and Weston, 1967), and the intake of pelleted hay was greater than that of hay fed long stem or chopped (Blaxter et al., 1956; Rodrique and Allen, 1960). The positive effect of processing long hay increased with increasing forage fiber content (Heaney et al., 1963).

Forage Quality Effects on Animal Performance. Through its effects on both intake and digestibility, forage maturity influences animal growth and performance. Crampton et al. (1960) suggested that dry matter intake of a particular forage has a greater effect on animal performance than the concentration of digestible energy in the forage.

Animals fed more mature forages have shown decreased weight gains (Erwin et al., 1956; Spahr et al., 1961; McCarrick, 1966; Calder, 1977). When daily gains were adjusted for differences in feed consumption, lambs fed less mature alfalfa hay showed increased gains (Meyer et al., 1960), and animals fed strains of switchgrass selected for higher in vitro dry matter digestibility showed higher gains (Anderson et al., 1988). Hereford bulls fed grass hay cut on June 12 gained .62 kg/d with a feed efficiency of 9.2, whereas, bulls fed hay cut on July 26 exhibited a daily gain and feed efficiency of .41 kg/d and 13.0, respectively (Flipot et al., 1984). Additionally, animals fed early cut hay gained three times more rapidly during the winter period than those fed late cut hay (Bohman, 1955). In contrast, the effects of forage maturity on weight gain in heifers and sheep fed hay or silage were inconsistent (Thomas et al., 1969).

In dairy cattle, for each d of delayed harvest of grass silage, one percentage unit more concentrate was needed in the ration to meet the nutritional requirements of lactating cows (Cleale and Bull, 1986). The predicted net energy for lactation of forage decreased as acid detergent fiber content increased (Harlan et al., 1988). Likewise, milk production was improved by earlier harvest of forages (Spahr et al., 1961), and forage intake has been shown to be positively correlated with milk yield (Ekern and Macleod, 1978).

With alfalfa hay, of the two constituents, lignin and protein, lignin was more highly related to differences in lamb gains (Meyer et al., 1960), and thus they determined fiber fractions should be preferred to protein for indicating the quality of alfalfa hay for energy. In agreement, in dairy cattle, acid detergent fiber content of alfalfa hay was the main quality factor correlated with milk production (Mokhtar and Fonnesbeck, 1986).

Other Influences on Animal Performance. Grinding and pelleting of feedstuffs results in increased animal productivity (Meyer et al., 1960; Moore, 1964), and the positive response to processing increases with advancing forage maturity (Meyer et al., 1960; Smith et al., 1986). Lambs fed dehydrated alfalfa exhibited faster gains than those fed sun cured hay, and these differences were largely due to differences in feed consumption (Meyer et al., 1960).

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TABLE 1. BREED AVERAGES FOR AGE AND WEIGHT AT PUBERTY

Source	Breed	Age at puberty	Weight at puberty
Kaltenbach and Wiltbank (1962)	Angus	382	238
	Hereford	483	279
	Shorthorn	427	231
Franke and England (1965)	Angus	387	
	Brahman	537	
	Brangus	504	
	Hereford	471	
Laster et. al. (1972)[a]	Angus	372	275
	Brown Swiss	347	272
	Charolais	399	312
	Chianina	399	310
	Gelbvieh	341	277
	Hereford	372	275
	Jersey	323	228
	Limousin	399	301
	Maine Anjou	372	298
	Red Poll	352	256
	Simmental	373	295
	South Devon	365	283
Reynolds (1972)	Africander x Angus	543	283
	Angus	432	243
	Brahman	816	320
	Brahman x Angus, F_1	459	302
	Brangus	531	290
Gregory et. al. (1979)	Angus x Hereford	331	296
	Brahman x Angus	394	343
	Brahman x Hereford	402	332
	Hereford x Angus	321	296
	Pinzgauer x Angus	287	288
	Pinzgauer x Hereford	319	294
	Sahiwal x Angus	376	306
	Sahiwal x Hereford	390	304
	Tarentaise x Angus	301	292
	Tarentaise x Hereford	335	300
Stewart et. al. (1980)	Angus	303	230
	Brahman	382	275
	Hereford	300	197
	Holstein .	288	242
	Jersey	331	164

[a] Sire breed.

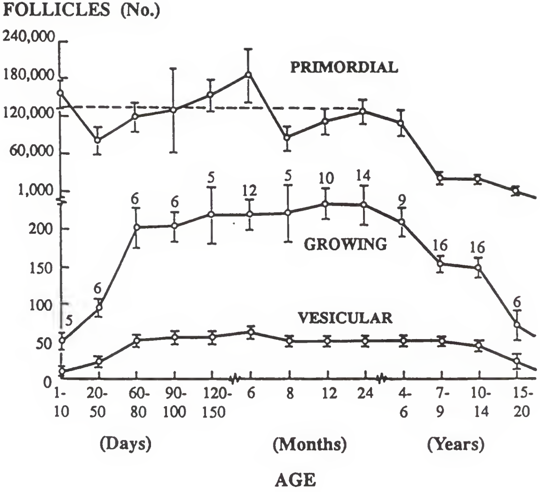

Figure 1. Number of vesicular follicles, growing follicles, and primordial oocytes from birth through 20 yr of age. Broken line represents avg of animals aged 0 to 24 mo. Vertical bars and numbers represent standard error and no. of ovarian pairs analyzed, respectively (Erickson, 1966).

HAY QUALITY, BREED, AND OVARIAN DEVELOPMENT EFFECTS ON ONSET OF PUBERTY AND REPRODUCTIVE PERFORMANCE OF BEEF HEIFERS[1]

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Abstract

Fifty one 3/4 Hereford x 1/4 Angus (HA) and 47 3/4 Hereford x 1/4 Brahman (HB) heifers were utilized in a split plot design to determine the influence of hay quality, breed, and ovarian development on the onset of puberty and reproductive performance. Heifers received either high quality [HQ; neutral detergent fiber (NDF) = 44.3%; crude protein (CP) = 19.5%] or low quality (LQ; NDF = 53.5%; CP = 18.3%) alfalfa hay, ad libitum, and 1.4 kg ground sorghum grain/(hd•d). Puberty was defined by three criteria 1) behavioral estrus, 2) presence of a palpable corpus luteum, and 3) serum progesterone above 1 ng/ml. Ultrasonography was used to determine bilateral ovarian dimensions and follicular populations when heifers were 11 mo old. Heifers were artificially inseminated (AI) for 49 d, and conception and pregnancy rates were determined by fetal aging via

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rectal palpation. More HB heifers were puberal by 14 and 15 mo of age ($P < .02$), while HA heifers reached puberty at lighter ($P < .03$) weights than HB heifers. A higher percentage of the heifers receiving HQ hay were puberal by 16 mo of age ($P = .08$), and more HB heifers and those heifers receiving HQ hay became pregnant during the AI breeding period ($P = .10$). Heifers bred on puberal estrus had lower ($P = .04$) first service conception rates than heifers bred on a later estrus (52 vs 90%). Ovarian size and diameter of the largest follicle were not related to onset of puberty in either breed type, but HB heifers with more follicles at 11 mo of age reached puberty at heavier weights and older ages ($P < .01$). These data indicate onset of puberty and reproductive performance of beef heifers are influenced by hay quality and breed. Additionally, onset of puberty appeared to be related to number of follicles at 11 mo of age in HB heifers.

(Key Words: Puberty, Ultrasonography, Ovarian Development, Forage Quality.)

Introduction

Beef heifers calving first at two yr of age produce more calves during their productive life than heifers calving first at older ages (Donaldson, 1968). If a female is to calve at 2 yr of age, she must reach puberty by 15 mo of age. However, it may also be economically beneficial if heifers reach puberty before the start of the breeding season, in that heifers bred on third estrus have higher pregnancy rates than heifers bred on puberal estrus (Byerley et al., 1987). Additionally, heifers that conceive earlier in their first breeding season calve earlier (Short and Bellows, 1971), and wean heavier calves (Lesmeister et al., 1973).

Puberty in beef heifers is influenced by age (Laster et al., 1972), breed (Gregory et al., 1979), plane of nutrition (Grass et al., 1982) and growth rate (Arije and Wiltbank, 1974). A negative relationship exists between age at puberty of heifers and scrotal circumference in closely related bulls (Brinks et al.,1978; King et al., 1983). Schillo et al. (1983) determined ovarian volume subjectively via rectal palpation and reported heifers with greater ovarian volume reached puberty at younger ages. However, this relationship has not been studied objectively. Our first objective was to use ultrasonography to objectively measure ovarian development and to determine the influence of ovarian size and follicular development on onset of puberty of beef heifers.

Forage maturity has been shown to affect animal performance (Flipot et al., 1984), daily intake (Bertilsson and Burstedt, 1983), and dry matter digestibility (Cleale and Bull, 1986). The effects of forage maturity on pubertal onset and reproductive performance have not been studied. Therefore, our second objective was to evaluate the influence of hay quality on growth, onset of puberty, and subsequent reproductive performance of beef heifers of two breed types.

Materials and Methods

Animals and Management. Fifty one 3/4 Hereford x 1/4 Angus (HA) and 47 3/4 Hereford x 1/4 Brahman (HB) prepuberal heifers (7 to 10 mo old) were utilized in a split plot design, in which hay quality was the whole plot factor and breed the sub plot factor. All heifers except 1 HA and 5 HB were sired by one sire. Heifers were stratified by age, weight, and body condition and were subsequently allotted at random to four groups within each breed type. Two randomly selected groups from each breed type received either high quality (HQ) or low quality (LQ) alfalfa hay, ad libitum. Heifers had access to trace mineral salt, and received an avg of 1.4 kg ground sorghum grain/(hd • d).

Alfalfa hay was purchased from several local sources based on crude protein (CP) content with HQ being higher in CP than LQ. Hay was sampled upon delivery by extracting two core samples from each large round bale and one sample from every 10th small square bale. Hay samples from each delivery were combined prior to grinding with a Cyclotec[4] sample mill to pass a 1 mm screen. Duplicate samples from each hay source were analyzed for dry matter, Kjeldahl nitrogen, calcium, and phosphorus by standard procedures (AOAC, 1984); and acid detergent fiber (ADF) and neutral detergent fiber (NDF) as described by Goering and Van Soest (1970). The avg nutritional characteristics of the two hay qualities are shown in Table 1. The ADF and NDF values suggested that LQ hay was, in fact, of greater maturity than HQ hay (Erickson et al., 1986; Brown, 1988). Because hay was fed in bunks, it was ground prior to feeding to minimize wastage.

The duration of the trial was from December 17, 1986 to June 19, 1987. Heifers were maintained in four adjacent drylots, with two groups, one from each breed type, in each lot. Groups were randomly assigned to lots at the start of trial and rotated at 28 d intervals. At the beginning and the first d of the breeding season (May 1, d 135), heifers were weighed, scored for body condition by two independent researchers on a scale from 1 to 9 (1 = emaciated, 9 = obese), and scanned for backfat between the 12th and 13th rib with ultrasonic equipment (Miller et al., 1986). Heifers were also weighed at 28 d intervals throughout the trial, and a final weight was recorded on the last day of the experiment.

Puberty. Heifers were observed for estrus twice daily for 1 h at 0700 and 1700 h from d 1 to 134 and three times daily for 1 h at 0600, 1300 and 2000 h from d 135 to the end of trial. Sterilized bulls equipped with chest harnesses filled with colored grease were

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[4] Tecator, Inc., P.O. Box 405, Herndon, VA 22070.

used to aid in estrous detection. Bulls were rotated biweekly among lots before d 135 and weekly after d 135. Three criteria were used to define puberty (Nelson et al., 1985): 1) seen in standing estrus or marked by bull; 2) presence of a palpable corpus luteum; 3) serum progesterone above 1 ng/ml. Between 6 to 12 d after the occurrence of a visible estrus or mark, heifers were weighed, palpated rectally for the presence of a corpus luteum, and a 7 ml jugular blood sample was taken. Heifers showing first visible signs of estrus after the start of the artificial insemination (AI) period (d 135) were not palpated rectally nor bled as mentioned above, and their attainment of puberty was determined by either their return to estrus or confirmed pregnancy. The 20 heifers used in the intake and digestibility study mentioned below were bled on last d of this study, and then again 10 d later to determine if any of these heifers had reached puberty while in individual feeding pens.

Blood Collection and Radioimmunoassay. Blood samples were refrigerated and allowed to clot for 16 h until centrifuged at 5 C for serum collection. Serum samples were stored at - 20 C until assayed for progesterone using a validated radioimmunoassay procedure described by Skaggs et al. (1986). The intra- and inter-assay coefficients of variation of 11 assays used to determine progesterone averaged 11.7% and 27.7%, respectively.

Artificial Insemination. Heifers were artificially inseminated (AI) approximately 12 h after standing estrus during a 49 d AI period. One technician performed all inseminations using semen from one sire. Conception and pregnancy rates were determined by fetal aging via rectal palpation.

Intake and Digestibility. Starting on d 33, 20 heifers (five from each treatment group) were used to determine daily dry matter intake and dry matter digestibility. Following a 7-d period to allow adaptation to the individual feeding pens, intake and digestibility were determined during a subsequent 7-d period. Heifers received 1.7 kg ground sorghum grain/(hd•d) and sufficient hay to insure ad libitum intake. Hay was offered at a rate of 120 % of the previous 5 d intake. Daily samples of feed and orts were collected for 7 d starting on d 7 and twice daily fecal grab samples were collected for 7 d starting on d 8. Feed, orts, and fecal samples were dried at 50 C in a forced-air oven for determination of partial dry matter and then were allowed to air equilibrate. All samples were ground with a Cyclotec sample mill to pass a 1 mm screen, and duplicate samples were analyzed for dry matter and ash by standard procedures (AOAC, 1984). Triplicate samples were analyzed for indigestible acid detergent fiber (Cochran et al., 1986), and in vivo dry matter digestibility was determined from the feed:feces ratio of indigestible acid detergent fiber (Schneider and Flatt, 1975).

Ovarian Determinations. Ultrasonography was used to determine bilateral ovarian dimensions and follicular populations when heifers were 338 ± 2 d of age. A real-time B-mode, diagnostic ultrasound scanner (Technicare 210DX) equipped with a linear-array, 5 MHz transducer was used for these examinations. After rectal insertion, the transducer was moved along the dorsal surface of the reproductive tract for orientation and then moved laterally to examine the ovaries (Pierson and Ginther, 1987). Both ovaries were measured at their widest points both vertically and horizontally with integral electronic calipers. Because only two dimensions of the ovary could be measured, ovarian diameter was used as a measure of ovarian size and not ovarian volume. Diameter of the largest follicle was measured, and number of follicles in the following categories were recorded: 2 to 3 mm, 4 to 6 mm, 7 to 10 mm, and > 10 mm.

Statistical Analyses. Differences in weight, average daily gain, body condition, backfat, and weight at puberty were analyzed using the General Linear Model procedure of SAS (1985). Sources of variation were hay, group within hay, breed, and hay x breed interaction. The group within hay term was used to test for the hay effect while the random error term was used to test all other effects. The same procedure was used to determine differences in intake and digestibility, and the sources of variation were the same with the exception of the deletion of the group within hay term. Cumulative percent of heifers reaching puberty by 13, 14, 15, and 16 mo of age, conception rate at first service, and pregnancy rate were analyzed using the Categorical Data Modeling (CATMOD) procedure of SAS (1985). Sources of variation were the same as previously mentioned. However, with conception rate at first service, the model also allowed the comparison between heifers inseminated on puberal vs later estrus. The General Linear Model procedure of SAS (1985) was also used to determine the relationship of ovarian development to age and weight at puberty. These relationships were determined within breed types, and sources of variation were hay, group within hay, ovarian diameter, diameter of the largest follicle, and total number of follicles. All possible interactions were tested and were non significant, therefore they were deleted from the final model. All data are least-squares means, and because the number of heifers among groups were unequal, approximated standard errors (Milliken and Johnson, 1984) were used for data presentation.

Results and Discussion

Performance. Hereford x Brahman (HB) heifers were heavier initially ($P < .03$) and maintained this weight advantage throughout the experiment (Table 2). HB heifers received higher body condition scores, and were carrying more backfat at the start of the trial ($P < .03$). Heifers receiving high quality (HQ) hay weighed more at the start of the breeding season and the end of the trial ($P < .03$), which agrees with earlier studies which indicated that less mature forages support higher wt gains compared with forages of greater maturity (Calder, 1977; Flipot et al., 1984). As a result of their increased wt gains, heifers receiving HQ hay were also carrying more body condition and backfat at the start of the breeding period ($P < .03$).

A hay x breed interaction influenced ($P < .06$) both the ADG prior to the breeding season, and during the entire experiment. Hereford x Angus (HA) and HB heifers gained at similar rates on HQ hay, however on low quality (LQ) hay, HA heifers showed greater ADG before the breeding season, and during the entire trial ($P < .02$). Observed differences in ADG are supported by the level of dry matter (DM) intake for HB heifers (Table 4), particularly on the LQ hay. With the exception of forages low in protein (Howes et al., 1963), Zebu-type cattle have been reported to consume less forage DM than British cattle (Rogerson et al., 1968; Ledger et al., 1970; Frisch and Vercoe, 1977). Our observations support these reported trends. However, the degree of response is somewhat surprising in that the HB heifers were only 1/4 Brahman and such intake effects have not been as pronounced in Zebu-cross cattle (Warnick et al., 1973; Frisch and Vercoe, 1977). It is possible that the influence of the LQ hay was moderated in our study by grinding. Smith et al. (1986) reported that positive response to processing increased as forage maturity advanced. In this study, both HA heifers ($P < .04$) and HB heifers ($P < .06$) gained at faster rates on HQ than on LQ hay. These findings agree with previous research (Calder, 1977; Flipot et al., 1984) which indicated that animals consuming forages harvested earlier exhibited faster gains than animals consuming forages harvested at later maturities.

Puberty. A higher percentage of HB heifers reached puberty by 14 ($P = .008$) and 15 ($P < .02$) mo of age (Table 3). These results disagree with earlier findings which have shown Brahman and Brahman cross heifers to be older at puberty than British heifers (Gregory et al., 1979; Stewart et al., 1980). However, our differences may have been due to HB heifers being heavier at the start of the experiment, as previous research has shown that heifers heavier at any age reach puberty at younger ages (Smith et al., 1976). The fact that HB heifers were only 1/4 Brahman may also account for some of the difference between our findings and the earlier studies.

In the current study, HA heifers were older at puberty than previously reported for this breed type. In two separate studies, Laster et al. (1972; 1976) indicated greater than 90 percent of Hereford x Angus heifers were puberal by 15 mo of age. Additionally, reported ages at puberty of Hereford x Angus heifers were 11.7 mo (Laster et al., 1972), 12.6 mo (Smith et al., 1976), and 12.0 mo (Gregory et al., 1978). The differences between our results and these studies for HA heifers cannot be explained as HB heifers in our study reached puberty at ages more similar to other research reports. Franke and England (1965) showed the avg age at puberty of British x Zebu heifers was 14.1 mo, and 3/4 British x 1/4 Zebu heifers averaged 13.5 mo at puberty.

More heifers receiving HQ hay were puberal by 16 mo of age ($P = .08$, Table 3). This difference would be expected as these heifers were heavier at this age, which indicates the importance of high quality forages for heifer development. These results agree with numerous reports (Short and Bellows, 1971; Grass et al., 1982; Greer et al., 1983) that suggest an increased plane of nutrition decreases age at puberty.

The fact that HA heifers were lighter ($P < .03$) at puberty when compared to HB heifers (Table 2) is in agreement with earlier studies (Reynolds, 1972; Gregory et al., 1979) which indicated that British heifers reached puberty at lighter weights than Brahman x British heifers. However, both breed types reached puberty a similar percentage of their mature wt, which agrees with Crichton et al. (1960) who reported that heifers reach puberty at a similar percentage of their mature size. HA heifers were considerably heavier at puberty than the previously reported weights for Hereford x Angus heifers of 278 kg (Laster et al., 1972), 284 kg (Gregory et al., 1978), and 296 kg (Gregory et al., 1979). Additionally, HB heifers were also heavier at puberty than 332 kg reported by Gregory et al. (1979) for Brahman x Hereford heifers, and 302 kg (Reynolds, 1972) for Brahman x Angus heifers. Our only explanations for these differences are that the majority of our heifers were sired by one sire, and it is possible that this sire may have produced offspring that were later maturing than breed average, and secondly, both HA and HB heifers were 3/4 Hereford, and some reports (Kaltenbach and Wiltbank, 1962; Franke and England, 1965) indicate Herefords reach puberty at older ages than other British breeds.

Conception Rate. Hay quality nor breed influenced conception rate at first service ($p > .82$; Table 3). This concurs with the report of Little et al. (1981) that plane of nutrition has little effect on conception rate (Little et al., 1981). Heifers inseminated on puberal estrus had lower conception rates than heifers inseminated on a later estrus ($P = .04$, Figure 1). This relationship has been previously reported in heifers (Byerley et al.,

1987) and ewes (Hare and Bryant, 1985). These results indicate the importance of proper heifer development so that heifers reach puberty before the breeding season and therefore are not serviced on their puberal estrus.

Pregnancy Rate. Pregnancy rates were extremely low (Table 3), however, they did not appear to be due to unsatisfactory conception rates, but rather delayed age at puberty. Many of the heifers did not reach puberty until late in the breeding period, and thus had only one opportunity to conceive. A similar relationship has been reported in heifers wintered on low nutritional levels; Joubert (1954) suggested that these heifers conceived later because they were bred later and not because of increased number of services per conception.

A higher percentage of HB heifers became pregnant during the AI breeding period ($P = .10$). This difference is mainly due to a higher percentage of HB heifers reaching puberty by 15 mo of age, thus more HB heifers were inseminated earlier in the breeding season, and less were inseminated on their puberal estrus. Similarly, Ferrell (1982) reported that heifers reaching puberty at younger ages have higher pregnancy rates. A higher percentage of heifers receiving the HQ hay became pregnant during the AI period ($P = .10$). More of these heifers were puberal by 16 mo of age, and thus more were inseminated and had the opportunity to conceive during the breeding period. Numerous studies document that higher nutritional levels during the developmental period result in increased pregnancy rates (Spitzer et al., 1978; Lemenager et al., 1980).

Intake and Digestibility. A hay x breed interaction influenced DM intake ($P =.06$; Table 4). No breed differences existed when heifers were fed HQ hay; however, when fed LQ hay, HA heifers consumed more hay than HB heifers ($P = .003$). These results agree with earlier findings which indicate *Bos indicus* breeds consume less than *Bos taurus* breeds on similar diets (Ledger et al., 1970; Frisch and Vercoe, 1977). However, Howes et al. (1963) reported that Brahman steers consumed more than Hereford steers when fed low quality, protein deficient diets. Our LQ diet was not deficient in protein, and therefore the comparison between our results and those of Howes et al. (1963) does not appear to be justified. HB heifers consumed more HQ than LQ hay ($P = .02$). This effect may be partially explained by the differences in digestibility between the two hay types, in that slower digestion of feedstuffs leads to decreased intake (Conrad et al., 1964). In agreement with these results, animals consuming less mature forages have increased DM intakes (Blaxter et al., 1961; Bertilsson and Burstedt, 1983). Why a similar effect was not observed in HA heifers is not readily apparent. .

No breed differences existed in digestibility ($P > .94$), however, both breed types exhibited higher DM digestibility coefficients on HQ hay ($P < .001$). Numerous reports substantiate the negative effects of increasing forage maturity on digestibility (Llano and DePeters, 1985; Cleale and Bull, 1986; Brown, 1988).

Ovarian Size and Follicular Development. Ovarian diameter at 11 mo of age was not related to either age or wt at puberty in either breed group ($P > .50$). In contrast, Schillo et al. (1983) showed that heifers with greater ovarian volume at 7 mo of age reached puberty earlier. However, differences in ovarian diameter, as measured in this study, may not truly reflect differences in ovarian volume. Diameter of the largest follicle was not related to either age or weight at puberty in either breed group ($P > .18$). But, HB heifers with greater total number of follicles present on their ovaries at 11 mo of age reached puberty at older ages ($P < .001$), and heavier weights ($P = .004$). In HB heifers, for each one follicle increase in total number of follicles, age at puberty was increased by 10.7 d (SE = 2.0), and wt at puberty was increased by 6.9 kg (SE = 2.1). In HA heifers, number of follicles was not related to either age or wt at puberty (P > .71). Ovarian characteristics of heifers at 11 mo of age are shown in Table 5.

In conclusion, hay quality, breed, and number of follicles at 11 mo of age in Hereford x Brahman heifers influenced onset of puberty and reproductive performance. Because heifers inseminated on puberal estrus had lower conception rates, these data indicate the importance of higher quality forages for heifer development. The increased plane of nutrition from such forages allow heifers to reach puberty before the start of the breeding season, and thus they are not serviced on their puberal estrus. Earlier puberty and the decrease in no of heifers serviced on their pubertal estrus should result in more heifers conceiving earlier, and higher pregnancy rates at the end of the breeding season.

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TABLE 1. CHEMICAL COMPOSITION OF ALFALFA HAY

Item, %[a]	Low quality	High quality
Crude protein	18.28	19.48
Acid detergent fiber	36.67	32.90
Neutral detergent fiber	53.51	44.25
Calcium	1.31	1.43
Phosphorus	.25	.27

[a] Dry matter basis.

TABLE 2. HAY QUALITY AND BREED EFFECTS ON LIVE WEIGHT, AVERAGE DAILY GAIN, BODY CONDITION,[a] BACKFAT,[b] AND WEIGHT AT PUBERTY

Item	Hay Quality Breed[c]	Low HA	 HB	High HA	 HB	SE
Number		26	23	25	22	
Initial wt, kg[f]		197	227	198	226	5
Prebreeding wt, kg[f,g]		300	316	308	332	6
Final wt, kg[f,g]		329	349	333	364	6
Prebreeding ADG, kg[d,h,i,j,k]		.76	.66	.82	.79	.02
184 d ADG, kg[e,h,i,j,k]		.73	.68	.75	.77	.02
Initial body condition[f]		5.0	5.3	4.9	5.3	.09
Prebreeding body condition[g]		5.2	5.3	5.5	5.7	.10
Initial backfat, cm[f]		.20	.24	.23	.25	.01
Prebreeding backfat, cm[g]		.38	.39	.50	.50	.02
Weight at puberty, kg[f]		325	345	339	358	6

[a] Scored on a scale from 1 to 9 (1 = emaciated, 9 = obese).

[b] Ultrasonic measurements between the 12th and 13th rib.

[c] HA = Hereford x Angus, HB = Hereford x Brahman.

[d] Prebreeding ADG = ADG from d 1 to the first d of the artificial insemination period.

[e] 184 d ADG = ADG during the entire experiment.

[f] Significant main effect (breed, $P < .03$).

[g] Significant main effect (hay, $P < .03$).

[h] Significant hay x breed interaction ($P < .06$).

[i] Significant single effect (breed within low quality hay, $P < .02$).

[j] Significant single effect (hay quality within Hereford x Angus heifers, $P < .04$).

[k] Significant single effect (hay quality within Hereford x Brahman heifers, $P < .06$).

TABLE 3. HAY QUALITY AND BREED EFFECTS ON CUMULATIVE PERCENT OF HEIFERS REACHING PUBERTY BY VARIOUS MONTHS OF AGE, CONCEPTION RATE, AND PREGNANCY RATE

Item	Hay Quality Breed[a]	Low HA	 HB	High HA	 HB	SE
% Puberal by[b]						
13 mo		3.8	4.4	7.6	14.6	5
14 mo[e]		11.5	30.6	11.3	42.6	8
15 mo[f]		34.6	57.1	39.3	69.7	10
16 mo[g]		50.0	61.4	67.6	78.2	10
Conception Rate[c]		64.1	76.8	77.0	66.4	10
Pregnancy Rate[d,h,i]		34.6	48.4	47.3	69.7	10

[a] HA = Hereford x Angus, HB = Hereford x Brahman.

[b] Cumulative no. of heifers reaching puberty by indicated mo of age/total no. of heifers.

[c] Conception rate = Conception rate at first service.

[d] Pregnancy rate=No. of heifers that became pregnant during AI period/total no. of heifers.

[e] Significant main effect (breed, $P = .008$).

[f] Significant main effect (breed, $P < .02$).

[g] Significant main effect (hay, $P = .08$).

[h] Significant main effect (breed, $P = .10$).

[i] Significant main effect (hay, $P = .10$).

TABLE 4. HAY QUALITY AND BREED EFFECTS ON DRY MATTER INTAKE AND DIGESTIBILITY

Item	Hay Quality Breed[a]	Low HA	 HB	High HA	 HB	SE
Dry matter intake[b,d,f,g]		3.2	2.6	3.0	2.9	.001
Dry matter digestibility[c,e]		51.0	51.9	58.3	57.5	1.0

[a] HA = Hereford x Angus, HB = Hereford x Brahman.

[b] Dry matter intake is expressed as a percent of body weight.

[c] Total tract dry matter digestibility.

[d] Significant hay x breed interaction (P = .06).

[e] Significant main effect (hay, P < .001).

[f] Significant single effect (breed within low quality hay, P = .003).

[g] Significant single effect (hay quality within HB heifers, P = .02).

TABLE 5. OVARIAN CHARACTERISTICS OF HEIFERS AT 11 MONTHS OF AGE

Item	Puberal Status[a] Breed[b]	Puberal HA	 HB	Nonpuberal HA	 HB	SE
Ovarian Diameter, (cm^2)		1.71	2.19	1.83	2.11	.09
Largest Follicle[c], mm		7.7	8.3	6.9	7.1	.45
Follicular number[d]		2.5	3.4	2.7	3.3	.37

[a] Puberal status is not at the time that measurements were taken. Puberal = heifers that reached puberty during the experiment, Nonpuberal = heifers that did not reach puberty by the end of the experiment.

[b] HA = Hereford x Angus, HB = Hereford x Brahman.

[c] Largest follicle = diameter of the largest follicle.

[d] Follicular number = total number of follicles > 2 mm.

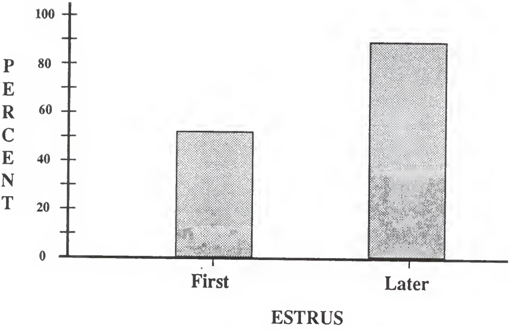

Figure 1. Conception rate at first service of heifers inseminated on first or later estrus. Heifers inseminated on a later estrus had higher (P = .04) conception rates than heifers inseminated on first (puberal) estrus (52 vs 90%; SE = 10).

APPENDIX

APPENDIX TABLE 1. INDIVIDUAL MEASUREMENTS OF DAILY DRY MATTER INTAKE AND DIGESTIBILITY

Tag	Breed[a]	Hay quality	Wt, kg	7d intake, kg[b]	7 d intake, % BW[c]	Digestibility[d]
6164	HA	High	198.6	6.04	3.04	57.88
6190	HA	High	236.4	6.98	2.95	58.52
6102	HA	High	219.5	7.19	3.27	58.58
6153	HA	High	249.1	5.60	2.25	57.89
650	HA	High	208.2	6.95	3.34	58.58
656	HB	High	273.6	7.53	2.75	55.51
6234	HB	High	265.5	7.79	2.93	56.57
6248	HB	High	225.0	6.77	3.01	61.24
6133	HB	High	253.6	7.06	2.78	56.13
6202	HB	High	233.2	7.00	3.00	58.08
6126	HA	Low	206.8	6.09	2.94	54.51
6146	HA	Low	197.3	6.52	3.31	51.32
604	HA	Low	229.5	7.00	3.05	48.10
6138	HA	Low	241.4	7.34	3.04	49.17
6120	HA	Low	217.7	7.49	3.44	51.84
6175	HB	Low	258.2	6.96	2.70	51.72
6147	HB	Low	240.9	5.96	2.47	53.90
6220	HB	Low	214.1	6.20	2.90	47.49
6188	HB	Low	232.7	5.89	2.53	53.05
6214	HB	Low	269.1	6.48	2.41	53.39

[a] HA = Hereford x Angus, HB = Hereford x Brahman.

[b] 7 d intake = Dry matter intake determined for a 7 d period.

[c] 7 d intake, % BW = Dry matter intake determined for a 7 d period and expressed as a % of body weight.

[d] Digestibility = Dry matter digestibility determined for a 7 d period.

HAY QUALITY, BREED, AND OVARIAN DEVELOPMENT EFFECTS ON ONSET OF PUBERTY AND REPRODUCTIVE PERFORMANCE OF BEEF HEIFERS

by

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Fifty one 3/4 Hereford x 1/4 Angus (HA) and 47 3/4 Hereford x 1/4 Brahman (HB) heifers were utilized in a split plot design to determine the influence of hay quality, breed, ovarian size, and follicular development on the onset of puberty and subsequent reproductive performance of beef heifers. Heifers were stratified by age, weight, and body condition, and were subsequently allotted at random to four groups within each breed type. Two randomly selected groups from each breed type received either high quality [HQ; neutral detergent fiber (NDF) = 44.3%; crude protein (CP) = 19.5%] or low quality (LQ; NDF = 53.5%; CP = 18.3%) alfalfa hay, ad libitum. Heifers had access to trace mineral salt, and received 1.4 kg ground sorghum grain/(hd•d). Puberty was defined by three criteria: 1) behavioral estrus; 2) presence of a palpable corpus luteum; 3) serum progesterone above 1 ng/ml. Ultrasonography was used to determine bilateral ovarian dimensions and follicular populations when heifers were 11 mo old. Heifers were artificially inseminated (AI) for 49 d by one technician using semen from one sire. Conception and pregnancy rates were determined by fetal aging via rectal palpation. Heifers receiving HQ hay weighed more at the start of the breeding season and the end of trial ($P < .03$). A hay x breed interaction influenced daily gain ($P < .06$). Both breeds gained at similar rates on HQ hay, however on LQ hay, HA heifers gained at a faster rate ($P < .02$) than HB heifers. More HB heifers were puberal by 14 and 15 mo of age ($P < .02$), while HA heifers reached puberty at lighter ($P < .03$) weights than HB heifers. A higher percentage of the heifers receiving HQ hay were puberal by 16 mo of age ($P = .08$), and more HB heifers and those heifers receiving HQ hay became pregnant during the AI breeding period ($P = .10$). Heifers bred on puberal estrus had lower ($P = .04$) conception rates at first service than heifers bred on a later estrus (52% vs 90%). Ovarian size and diameter of the largest follicle were not related to onset of puberty in either breed type, but HB heifers with more follicles at 11 mo of age reached puberty at heavier weights and older ages ($P < .01$). Twenty heifers (five from each treatment group) were used to determine daily dry matter (DM) intake and DM digestibility. A hay x breed interaction influenced ($P = .06$) DM intake; no differences existed on HQ hay, however on LQ hay, HA heifers consumed more than HB heifers ($P = .003$). Both breed types exhibited higher DM digestibility on HQ hay ($P < .001$). These data indicate onset of puberty and reproductive performance of beef heifers are influenced by hay quality, and breed. Additionally, onset of puberty appeared to be related to number of follicles at 11 mo of age in HB heifers.

(Key Words: Puberty, Ultrasonography, Ovarian Development, Forage Quality.)