Factors affecting bull sexual development

Leonardo Brito, STgenetics, Navasota, TX

Abstract

This review describes some of the physiological events associated with bull sexual development and factors that affect this development.

Keywords: Bull, puberty, testis, scrotal circumference, semen

Introduction

Sexual development is a major determinant of cattle production efficiency. The ability to breed animals at younger ages reduces generation intervals and increases genetic gains. However, reduced sperm production and poor semen quality due to immaturity are common causes of poor reproductive performance of young bulls, representing a serious loss of superior genetic stock. The ability to collect and freeze semen from younger bulls is also desired to reduce the time required for progeny testing and to hasten artificial insemination and sire selection. Therefore, an understanding of pubertal changes and factors that affect sexual development is required to promote successful use of young bulls for reproductive purposes.

The process of testicular development that leads to initiation of spermatogenesis in bulls involves complex maturation mechanisms of the hypothalamus-pituitary-testes axis. Sexual development can be divided into 3 periods according to changes in gonadotropins and testosterone concentrations, namely the infantile, prepubertal and pubertal periods. These changes are accompanied by changes in testicular cell proliferation and differentiation.

Infantile period is characterized by low gonadotropin and testosterone secretion and relatively few changes in testicular cellular composition. This period extends from birth to ~ 2 months of age in *Bos taurus* bulls. Gonadotropin secretion during the infantile period is low, due to reduced GnRH secretion; however, maturation of the hypothalamus increases GnRH pulse secretion and drives the transition out of the infantile period.[1-3] During this period, the testicular parenchyma is composed by seminiferous cords without a lumen lined by undifferentiated Sertoli cells and gonocytes. Mesenchymal-like cells are the majority of the cells in testicular interstitial tissue.[4-7]

Prepubertal period is characterized by a temporary increase in gonadotropins secretion, the "early gonadotropin rise."[1-3] This is a critical event in sexual development of bulls. It is not only associated with dramatic changes in testicular cellular composition, initial increases in testosterone secretion and timing of attainment of puberty, but also has long-lasting effects on testicular growth and sperm production. This period extends from ~ 2 - 6 months of age in *Bos taurus* bulls. The early gonadotropin rise is driven by increased gonsadotropin releasing hormone (GnRH) pulse secretion, as demonstrated by a dramatic increase in luteinizing hormone (LH) pulse frequency (Figure 1). The LH secretion pattern during the prepubertal period is also associated with age at puberty in bulls raised in contemporary groups, suggesting that this is the physiological mechanism by which genetics affect sexual development.[8-9] During the prepubertal period, there is a progressive increase in proportion of the testicular parenchyma occupied by seminiferous tubules, with increasing tubule diameter. Adult-type Sertoli cells develop, creating extended junctional complexes above newly formed spermatogonia. Furthermore, there is differentiation of testicular interstitial mesenchymal-like cells into Leydig cells and onset of testosterone secretion.[4-7]

Pubertal period is characterized by reduced gonadotropin secretion, increased testosterone secretion, initiation of spermatogenesis and eventual appearance of sperm in the ejaculate.[1-3] This period also coincides with the start of rapid testicular growth and extends from ~ 6 to 12 months of age in B*os taurus* bulls. Testicular growth is associated with increasing seminiferous tubule diameter and length. Most Sertoli cells complete their morphological differentiation and attain adult structure, forming a functional blood-testis barrier. Germ cell proliferation is maximal between 4 and 8 months of age, representing expansion of the spermatogonial stem cells, with mature sperm appearing in seminiferous tubules at ~ 8 - 10 months of age.[4-7]

Puberty

After spermatogenesis is established, there is a gradual increase in number of testicular germ cells supported by each Sertoli cell and an increase in efficiency of the spermatogenesis that results in the production of a number of sperm sufficient for those to appear in the ejaculate. In general, puberty is defined as the process of changes by which a bull becomes capable of reproducing. This process involves development of gonads and secondary sexual organs and acquiring the ability to breed. For research purposes, however, puberty in bulls is usually defined as an event instead of a process. Most researchers define attainment of puberty by production of an ejaculate containing ≥ 50 million sperm with ≥ 10% motile sperm.[10]

Age at puberty determined experimentally can be affected by the age that semen collection attempts are performed, interval between attempted collections, method of semen collection (artificial vagina or electroejaculator), response of the bull to the specific semen collection method and experience of the collectors. Moreover, age at puberty is affected by genetics, management and nutrition. Although data from large trials comparing bulls of various breeds raised as contemporary groups are scarce, some liberties could be taken to make some generalizations. Dairy bulls usually mature faster and attain puberty earlier than beef bulls. Bulls from continental beef breeds (with the exception of Charolais) usually attain puberty later than bulls from British beef breeds, especially Angus bulls. Bulls from double-muscled breeds are notorious for being late maturing. Puberty is delayed in bulls from tropically adapted *Bos taurus* breeds and in unadapted bulls raised in the tropics. In general, *Bos indicus* bulls attain puberty at considerably older ages than *Bos taurus* bulls.

There is large variation in age and body weight at puberty across and within breeds. Although on average *Bos taurus* bulls attain puberty with SC between 28 and 30 cm, regardless of the breed,[11] that there is still considerable variation in SC at puberty is sometimes overlooked. Interesting observations have been reported in studies evaluating differences between early- and late-maturing bulls.[8,9,12] Bulls that attain puberty earlier were generally heavier and had greater SC than bulls that attained puberty later; however, both weight and SC were smaller at puberty in early-maturing bulls. These observations not only indicate that precocious bulls develop faster, but also suggest that sexual precocity is not simply related to earlier attainment of a threshold of body or testicular development. In fact, these thresholds seem to be lower in early-maturing bulls, whereas late-maturing bulls must reach a more advanced stage of body and testicular development before puberty is attained.

Scrotal circumference is a moderately heritable trait in cattle; therefore, direct selection can have a very significant impact on SC. Studies have also demonstrated moderate to high phenotypical correlations between SC and growth traits and estimates of genetic correlations with growth traits are generally positive.[13-14] Either the combination of direct selection for SC and/or indirect selection for growth traits is likely responsible for the general trend of increasing SC over the years in certain breeds. Increased SC is expected to be associated with decreased age at puberty.

Effects of nutrition on sexual development

Very few studies have evaluated the effect of nutrition from birth to maturity on sexual development and reproductive function in bulls. A series of experiments have shown that the most pronounced effects of nutrition occur during the prepubertal period. These studies demonstrated that adverse effects of low nutrition during the prepubertal period cannot be compensated by improved nutrition during the pubertal period and that the beneficial effects of high nutrition during the prepubertal period are sustained, even if maintenance diets are fed thereafter. Low nutrition during the peripubertal period in beef bulls reduced gonadotropin secretion, delayed increases in circulating testosterone concentrations, delayed puberty and decreased testicular size at 16 months of age, whereas high nutrition produced opposite results.

In 1 study in which bulls received different nutrition from 2 to 16 months of age, reduced LH pulse frequency during the prepubertal period resulted in delayed puberty in bulls receiving low nutrition, whereas a more sustained increase in LH pulse frequency in bulls receiving high nutrition was associated with hastened testosterone production and larger testes at 16 months of age compared to bulls receiving low or medium (control) nutrition.[15] These observations were corroborated by additional studies designed to investigate effects of nutrition specifically during the prepubertal period. Bulls that received high nutrition only from 2 - 7 months of age also had a more sustained increase in LH pulse frequency, greater testosterone secretion, were 2 weeks younger at puberty and had greater testes weight at 16.5 months of age compared to bulls receiving control nutrition.[16] Conversely, reduced LH secretion resulting from low nutrition from 2 - 7 months of age was associated with increased age at puberty and smaller testes at 16 months of age, even when these bulls received control or high nutrition after 7 months of age and LH and testosterone secretion were not different after the change in nutrition.[17]

Differences in yearling SC due to age of the dam in beef bulls could also be interpreted as an indication that nutrition during the pre-weaning period affects sexual development, although possible in utero effects cannot be completely excluded. Scrotal circumference in *Bos taurus* beef bulls increases as age of the dam increases until 5 - 9 years of age and subsequently decreases as dams get older. Inclusion of weight as a covariate in the models describing SC resulted in decreased effects of age of the dam, indicating that effect of age of the dam on testicular growth seem to be primarily due to age of dam effects on bull's body weight, likely related to differences in milk production.[14,18,19] This theory is also supported by reports that, similar to that in bulls receiving low nutrition, LH secretion after GnRH challenge was greater from 3.5 - 6 months of age in bulls raised by multiparous versus primiparous females.[20]

Several studies described effects of nutrition only during the pubertal period, i.e. after initial hormonal changes that regulate sexual development have occurred. In general, these studies indicate that low nutrition has adverse effects on growth and sexual development. In 1 study, bulls receiving one-third of the amount supplied to their twin controls had lower body and vesicular gland weights, vesicular gland fructose and citric acid contents and circulating and testicular testosterone concentrations, whereas circulating androstenedione concentrations were increased.[21] In another series of experiments, beef bulls 8 -12 months old receiving diets with low levels of crude protein (8, 5 and 1.5%) for 3 - 6 months had markedly reduced testes, epididymis and seminal glands weights when compared to control bulls fed diets containing 14% crude protein.[22]

Although low nutrition during the pubertal period has adverse effects on reproductive function, potential beneficial effects of high nutrition after weaning are questionable at best. Under field conditions, postweaning high energy diets are frequently associated with impaired reproductive function in bulls, likely related to altered testicular thermoregulation due to excessive fat deposition above and around the testes. In 1 report, sperm motility decreased and proportion of sperm defects increased with age in Hereford bulls fed to gain > 1.75 kg/day, which was significantly different from bulls fed to gain ~ 1 kg/day (control). Even after the high-nutrition diet was changed to a control diet, bulls previously fed high nutrition continued to have lower semen quality. There was greater deposition of fat around the testicular vascular cone in the scrotal neck in bulls in the high-nutrition group and the difference between body and testes temperature was reduced in this group compared to bulls in the control group. This difference was still present after the high-energy diet was changed and bulls had lost considerable weight, indicating that fat in the scrotum is more difficult to lose than other body fat.[23]

In another series of experiments, Angus, Hereford, and Simmental bulls were fed high nutrition (80% grain and 20% forage) or medium nutrition (forage only) from ~ 6.5 to 12 - 24 months of age. In general, bulls receiving high nutrition had greater body weight and backfat, but paired testes weight was not affected by diet. Moreover, bulls receiving high nutrition had lower daily sperm production and epididymal sperm reserves and greater proportion of sperm abnormalities. The authors indicated that increased dietary energy may adversely affect sperm production and semen quality due to fat deposition in the scrotum, which reduced the amount of heat that can be radiated from the scrotal skin, thereby increasing scrotal and testicular temperatures.[24-27] Observations from another study indicated that bulls fed high-nutrition diets had greater SC and scrotal weight than bulls fed medium-nutrition diets, but paired testes weight was not different between the 2 groups, indicating that greater SC was likely associated with accumulation of scrotal fat.[28]

Conclusion

Studies have supported the intuitive assumption that low nutrition has adverse effects on sexual development and reproductive function, regardless of the bull's age. However, most research seems to indicate that high nutrition is only beneficial during the first 6 months of life, which presents a challenge to bull producers. Beef bull calves are usually nursing until 6 - 8 months of age and very little attention is paid to their nutrition, whereas nutrition offered to young dairy bull calves is often suboptimal. Efforts to obtain maximum weight gain during the first months after birth by offering high-nutrition diets and adopting management practices like creep feeding will be compensated by reduced age at puberty and greater sperm production capacity in adult bulls. It is also clear that, although high-nutrition diets after 6 months of age may be associated with greater SC, this effect is likely the result of fat accumulation in the scrotum and not actually greater testicular size. Moreover, sperm production, semen quality and serving capacity are all compromised in bulls receiving excessive nutrition after this age. Adjusting diets accordingly to maximize growth, but prevent over conditioning after the peripubertal period, is advisable.

Conflict of interest

There are no conflicts of interest to declare.

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