NUTRITIONAL MANAGEMENT OF DEVELOPING BULLS

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Overview

Bull development is a necessary and vital entity of beef production, as bulls account for a substantial portion of the genetic influence in a cow herd, and are the primary means through which the majority of producers affect genetic progress. The utilization of rapid development programs allows for the use of bulls at a younger age, reduces overall production costs, and decreases the down-time prior to implementing genetics within the herd. Breeding bulls are commonly fed high-energy diets in order to meet or exceed the rate of physiological development required to achieve sexual maturity prior to their first breeding season, while simultaneously evaluating genetic merit for growth and other economically-relevant traits. It is commonly thought that post-weaning nutrition has the greatest environmental influence on sexual development in bulls, yet there is compelling evidence to suggest that pre-weaning nutritional management influences these outcomes to a substantial, and possibly even a greater degree. This review will focus on the impact of both pre- and post-weaning plane of nutrition on sire development. While not addressed herein, readers are heavily cautioned to avoid overlooking the importance of mineral nutrition, as mineral deficiencies or toxicities should be expected to influence bull fertility.

Pre-weaning nutritional management

There is a pre-conceived notion that bull calves will generally receive the nutrients required to sustain growth at the level necessary to initiate the onset of puberty from their dams. While this may be the case in nutrient-rich environments that mitigate cow body condition loss, this should not be expected in nutrient-limited environments. Similarly, bull calves raised by multiparous dams have been observed to have larger testicles at weaning when compared to bulls raised by first-calf heifers (Lunstra et al., 1988). It is not uncommon for seedstock producers to creep feed or creep graze bull calves while nursing dams to maintain adequate growth. Bratton et al. (1956) found that nutrient restriction of Holstein bull calves from 1 to 80 weeks of age dramatically increased age and decreased weight at puberty, which was accompanied by a substantial decrease in the number of sperm per semen collection. This project serves as an example of some of the early work that was conducted that illustrates the role that early nutritional management plays in bull development and subsequent indicators of fertility.

Hormonal signaling drives the attainment of puberty. As suggested by Barth (2008), postnatal bull development occurs in three distinct phases: infantile, pre-pubertal, and pubertal, with each stage dependent on gonadotropin levels. Gonadotropins that are necessary for reproduction in bulls include luteinizing hormone (LH) and follicle-stimulating hormone (FSH), and their secretion is dependent upon gonadotropin-releasing hormone (GnRH). Low gonadotropin levels are commonly observed during the infantile stage, with levels generally remaining low until approximately 8 weeks of age. The pre-pubertal phase is then characterized by increases in gonadotropins and a subsequent increase in testosterone secretion between 8 and 20 weeks of age. Finally, as the pubertal period is reached, gonadotropin levels decrease, while testosterone levels remain elevated.

Luteinizing hormone is thought to be lower during the pre-weaning phase of development in bulls that are destined to have smaller testes and mature at an older age (Aravindakshan et al., 2000). In concert, supplementation of exogenous LH between 4 and 6 weeks of age has been shown to hasten the onset of puberty and increase testosterone levels in Hereford bulls when measured at 24 weeks of age (Chandolia et al., 1997). Furthermore, FSH and LH are thought to be the master regulators of Sertoli cell proliferation, seminiferous tubule size, and testes size (Bagu et al., 2004; Barth, 2008). Sertoli cell proliferation ceases at 25 weeks of age, therefore one should expect lean testicular mass to be pre-determined by this age, and bulls with greater calf-hood secretion of FSH are expected to have larger testes (Barth, 2008). On this basis, pre-weaning development is instrumental in determining the size of seminiferous tubules, the number of Sertoli cells, and overall testicular size, which can be expected to influence spermatogenesis.

Metabolic hormones that generally influence these reproductive hormones include leptin, insulin, and insulin-like growth factor-I [(IGF-I) Evans et al., 1995; Brito et al., 2007; Barth, 2008; Dance et al., 2015]. Nutrient restriction has been shown to decrease leptin levels and LH secretion in beef heifers (Amstalden et al., 2002), which would be expected to result in similar consequences in the bull. Insulin-like growth factor-I receptors reside on leydig and Sertoli cells, among other places, and are partially responsible for the production of testosterone and support of spermatogenesis, respectively (Borland et al., 1984; Barth, 2008). Proliferation of leydig cells occurs in response to exposure to IGF-I and LH, which is proceeded by an insulin-dependent increase in the production of testosterone (Bernier et al., 1986; Rouiller-Fabre et al., 1998). In support of these mechanisms, Brito et al. (2007) found that nutrient restriction resulted in lower concentrations of IGF-I and decreased LH secretion in peri-pubertal bulls, which led to decreases in overall testosterone production. In that same experiment, IGF-I concentrations accounted for a significant portion of the variation in scrotal circumference ($R^2 = 0.72$) and paired-testis volume ($R^2 = 0.67$) at any age, verifying the influence of nutrition on reproductive development in bulls (Brito et al., 2007).

In an experiment conducted by Dance et al. (2015), bulls were fed low [62.9 % total digestible nutrients (TDN) and 12.2 % crude protein (CP)], medium (66.0 % TDN and 17.0 % CP), and high (67.9 % TDN and 20.0 % CP) energy and protein diets from 2 to 31 weeks of age before all bulls were subjected to a medium-energy diet from 31 to 72 weeks of age. Bulls fed high levels of energy and protein achieved puberty quicker, had larger testes, and experienced greater levels of IGF-I secretion at a younger age when compared to medium- and low- energy and protein treatments.

In research conducted by Byrne et al. (2018), combinations of high- and low-energy diets were fed to Holstein bull calves during the pre-weaning phase (0 to 24 weeks of age) and post-weaning phase (24 weeks to puberty) of development. Following attainment of puberty, bulls were assigned to a moderate plane of nutrition until 60 weeks of age, followed by *ad libitum* access to concentrate prior to slaughter at 72 weeks of age. High-energy diets fed in the early development, pre-weaning phase hastened puberty by around 25 days compared to low-energy diets, and this subsequent onset of puberty was not affected by feeding lower energy diets following weaning. Moreover, bulls fed low-energy diets during the pre-weaning phase were restricted in the attainment of puberty, which was not reversed by feeding high-energy diets during the post-weaning phase. Bulls fed high-energy diets throughout their entire development period sustained an increase in scrotal circumference at the time of puberty and a numerical increase in the number of spermatozoa recovered per semen collection at 68 weeks of age when compared to all other treatment groups, with no differences in total semen volume observed across dietary treatments. Thus, pre-pubertal energy restriction may have long-term impacts on semen quality as it slows sexual maturation, and such energy restriction is not compensated for post weaning (Byrne et al., 2018).

Barth (2008) conducted a series of experiments in which Angus x Charolais bull calves were fed low-, medium-, and high-energy diets through distinct phases of development. Diets were distinguished based on concentrate level which were 0 %, 6.6 %, and 37 % concentrate for low-, medium-, and high-energy diets, respectively. Bull calves were weaned at 8 weeks of age and transitioned onto their respective diets. Bulls fed high-energy diets from 10 to 70 weeks of age attained puberty at a younger age (292 d of age) compared to medium- (305 d of age) or low-energy (327 d of age) diets. In this experiment, puberty was defined as the first time a semen collection contained at least 50×10^6 spermatozoa that were over 10% progressively motile. Paired testis weights in the high-energy group were 131 g heavier than bulls receiving the low-energy diet and 103 g heavier than bulls receiving the medium-energy diet. Nonetheless, these authors observed no effect of diet on spermatozoa morphology throughout the trial. Bulls that received the high-energy diet experienced an earlier rise in gonadotropin concentrations, characterized by increases in LH and FSH, which were likely mediated by elevated IGF-I concentrations observed between 10-22 weeks of age (Barth, 2008). In a separate experiment Barth (2008) developed Angus x Charolais bulls on a medium-nutrition diet fed *ad libitum* from 8 to 26 weeks of age, followed by either low-, medium-, or high-energy diets, containing 0%, 6.6%, and 37% concentrate, respectively. Bulls fed high-energy diets following 26-weeks of age attained puberty at 299 d of age compared to 328 d of age for medium-energy and 302 d of age for low-energy diets. Interestingly, bulls fed low-energy diets after 26 weeks of age had the greatest paired testis weight (619 g), followed by high-energy (611 g), and medium-energy (574 g). However, there was no impact of dietary energy composition on spermatozoa morphology.

Collectively, interpretation of the results obtained from these experiments suggests that the influence of diet on the attainment of puberty and testicular mass may be more critical prior to 26 weeks of age, as early nutrient restriction appears to have a greater influence on physical and sexual development of bulls. These results also suggest that calf-hood nutrient restriction may have long-term consequences on sexual development and measurements that commonly serve as objective indicators of sire fertility, regardless of post-weaning nutritional management. Furthermore, these findings support the notion that pre-weaning nutrition is a critical, albeit often overlooked component of bull development.

Post-weaning nutritional management

Post-weaning development is generally dependent on high-energy diets as they provide the greatest potential for evaluation of genetic merit for growth and other economically-relevant traits. While calf-hood (pre-weaning) nutritional management plays an inherent role in fertility outcomes, post-weaning nutritional management also has the ability to elicit changes in development and subsequent indicators of fertility. A great amount of concern exists across the beef cattle industry pertaining to the negative consequences of over-nutrition during the post-weaning development phase. These concerns have in large been driven by reductions in spermatozoa motility and increases in the prevalence of morphologically-abnormal spermatozoa that have coincided with the post-weaning development of bulls using aggressive nutritional management strategies that result in high levels of growth performance.

In a two-year study conducted by Coulter et al. (1987), 143 Angus and Hereford bulls were fed either a high- or medium-energy diet from the time of weaning through slaughter at 15 months of age. High-energy diets consisted of 80 % grain and 20 % forage whereas medium-energy diets consisted of 100 % forage. Bulls developed on the high-energy diet had a greater scrotal circumference at 12 months of age, but not 15 months of age, suggesting delayed but compensatory scrotal growth for bulls fed medium-energy diets. The total number of spermatozoa produced per day was 9 % greater in year one and 30 % greater in year two for bulls fed the medium-energy diet. Caput-corpus epididymal sperm reserves were 76 % greater in year one and 89 % greater in year two for bulls fed the medium-energy diet when compared to bulls fed the high-energy diet. Additionally, these researchers observed that cauda epididymal spermatozoa reserves were 52 % greater for bulls fed medium-energy and epididymal transit time from corpus to cauda epididymis was 0.5 days faster than bulls fed-high energy diets. Collectively, these data suggest that high-energy diets may increase testicular growth rate, but may also elicit negative effects on spermatozoa production and result in the maintenance of fewer epididymal spermatozoa.

In a two-year feedlot development study conducted by Mwansa and Makarechian (1991), 112 weaned bulls were developed over two 77-day performance-test intervals on one of four sequential combinations of diets that contained either high or low levels of energy. In this experiment, bulls were fed either high- or low-energy diets during the first 77-day test-phase, and two of the four groups were adjusted over a proceeding 14-day adaptation to the other ration for the remaining 77 days. High energy diets contained 1.54 Mcal of digestible energy (DE) per lb of DM and low-energy diets consisted of 1.06 Mcal of DE per lb of DM. This resulted in four dietary energy treatments: high-high, high-low, low-high, low-low. Bulls maintained on high-energy diets throughout the development period (high-high) had the greatest scrotal size (38.3 vs. 36.4, 36.4, and 35.5 cm for high-low, low-high, and low-low, respectively). However, bulls in the high-high treatment group had 24.2% head-defected spermatozoa compared to 15.2% for high-low, 17.1% for low-high, and 16.4% for low-low (Mwansa and Makarechian, 1991). Nonetheless, it should be noted that the percentage of normal spermatozoa would allow passage of a breeding soundness examination in all groups when compared to current standards (Koziol and Armstrong, 2018).

In a two year study conducted by Coulter et al. (1997), 72 Angus, Angus x Simmental, or Hereford x Simmental bulls were developed over the course of a 168-day feeding period in which bulls were fed either high-energy (80 % grain and 20 % forage) or moderate-energy (100 % forage) diets. Following the trial, duplicate semen collections were evaluated to determine semen quality. Bulls fed the high-energy diets yielded less motile (53.4 vs 44.5%) and morphologically-normal spermatozoa (68.8 vs 62.5%) but a higher scrotal surface temperature (3.9 vs 3.4°C) when compared to bulls fed the moderate-energy diet. Additionally, Pruitt and Corah (1985) fed varying amounts of the same diet to achieve high, medium, and low levels of energy intake in Simmental and Hereford bulls. Over a 200-day feeding period, 29 Simmental bulls were fed 14.6, 19.2, and 23.8 Mcal of metabolizable energy (ME) and 27 Hereford bulls were fed 13.4, 17.5, and 22.2 Mcal of ME per bull per day for low-, medium-, and high-energy treatments, respectively. Simmental bulls fed the highest amount of energy had a greater scrotal circumference, yet there were no differences in scrotal size in Herefords, and neither breed nor energy level affected attainment of puberty or semen quality (Pruitt and Corah, 1985).

Elevated dietary energy has been shown to increase scrotal fat deposits, which may in turn impact semen quality (Mwansa and Makarechian, 1991; Barth, 2008). Bull testes must be 4-6°C cooler than core body temperature to produce fertile spermatozoa (Kastelic and Thundathil, 2008). As scrotal fat increases, a subsequent rise in temperature is expected to follow, as the accumulation of adipose tissue around the vascular cone limits the ability of the pampiniform plexus to act as a countercurrent heat exchanger. Restriction of this mechanism from elevated dietary energy and scrotal adiposity offers one explanation to the effects of high-energy diets on semen quality. Although high-energy post-weaning diets generally maximize growth rate, they also seem to negatively affect spermatogenesis and may impact attainment of puberty and libido.

While bulls fed high-energy (80 % grain and 20 % forage) or moderate-energy (100 % forage) diets attained puberty at an earlier age in the experiment of Coulter et al. (1997), bulls fed high-energy diets by Pruitt and Corah (1985) did not differ in age at attainment of puberty. However, based on data reviewed herein, it is important to keep in mind that pre-weaning nutritional management likely impacts the attainment of puberty to a much greater degree, whereas post-weaning management may only play a minor role, pending energy contents are suitable to meet dietary requirements (Barth, 2008). It is also important to note that objective evaluations of the effects of nutritional management on scrotal adiposity are lacking in the published literature, and warrant further evaluation.

Another potential factor that may influence semen quality of developing bulls is rumen conditions. High-energy diets, when paired with aggressive feeding strategies, and/or nutritional mismanagement, increase the risk of bulls developing ruminal acidosis. Therefore, ruminal acidosis is of current interest, as this condition may result in physiological consequences that may ultimately influence semen quality or indicators of fertility in developing bulls. Although research on the effects of acidosis on the bull is limited, initial discoveries suggest that subacute ruminal acidosis (SARA) may negatively impact semen quality in developing bulls. In a study by Callaghan et al. (2016), bulls challenged with oligofructose (OFF) to induce SARA had a lower average rumen pH (6.27 vs. 7.19), higher rectal temperature (39.2 vs 38.6°C), and lower percentage morphologically-normal spermatozoa when compared to contemporaries that received a sham-dose of water administered via oral lavage. More specifically, sustained increases in morphological abnormalities of OFF-treated bulls were dominated by distal mid-piece reflections, proximal droplets, and vacuole and teratoid defects. Bulls induced that were experimentally-induced into SARA via OFF had lower serum testosterone and tended to have elevated cortisol concentrations. Cortisol concentrations peaked 5 days following OFF treatment. Although, it should be noted that elevations in cortisol concentrations may be a result of stress induced by several bouts of oral lavage in order to administer OFF. While the reduction in semen quality observed in this experiment may be the function of SARA, there is also the possibility that it was induced by stress, and independent of SARA.

As documented by Callaghan et al. (2016), blood FSH concentrations were also decreased on days 7, 23, and 32 in OFF-treated bulls. Increases in cortisol and depression of FSH were thought to account for the increase in distal mid-piece reflections at these times. Similarly, vacuole and other head defects did not occur until days 67, 74, and 88, which was more than 30 days following the rise in cortisol and drop in FSH. This signifies that stress that can be attributed to the SARA-inducting process may have interrupted the spermatogenic cycle and affected spermatozoa stored in the epididymis. Regarding gonadotropins, Thibier and Rolland

(1976) showed that dexamethasone decreases LH and testosterone in post-pubertal bulls; likely a result of stress. Similarly, Barth and Bowman (1994) showed that infusion of dexamethasone upregulated cortisol and decreased testosterone concentrations, leading to increases in the prevalence of morphologically-abnormal spermatozoa. It has long been established that cortisol has a strong negative feedback on LH and FSH secretion, and therefore an influence on testosterone concentrations and reproduction (Welsh and Johnson, 1981; Stoebel and Moberg, 1982). Testosterone is a critical component to the attainment of puberty and spermatogenesis, and factors that raise cortisol concentrations are of interest in bulls. It has been previously established that SARA may influence cortisol, yet it has been shown that secretion of histamine in response to an influx of glucose into the rumen may also increase cortisol concentrations (Majzoub, 2006). Histamine plays a complex role in SARA, as it has been shown to flourish in the rumen, induce laminitis, and has the potential to serve a role in the suppression of testosterone and indicators of fertility in bulls through increases in cortisol concentrations (Bergsten, 2003). Research in this field warrants further investigation to distinguish between the influence of both physiological stress and SARA on semen quality of developing bulls, and to determine if these results are repeatable in a real-world production scenario. Nonetheless, feeding and management conditions that are likely to result in SARA or stress should be avoided for a number of reasons; their potential influence on bull fertility being only one.

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