ARTICLE IN PRESS

Theriogenology xxx (2016) 1–9

Contents lists available at ScienceDirect

Theriogenology

journal homepage: www.theriojournal.com

Review

Fertility management of bulls to improve beef cattle productivity

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Keywords:
Beef cattle
Reproduction
Bull
Semen
Fertility

ABSTRACT

Global demand for animal proteins is increasing, necessitating increased efficiency of global food production. Improving reproductive efficiency of beef cattle, especially bull fertility, is particularly critical, as one bull can breed thousands of females (by artificial insemination). Identifying the genetic basis of male reproductive traits that influence male and female fertility, and using this information for selection, would improve herd fertility. Early-life selection of elite bulls by genomic approaches and feeding them to optimize postpubertal reproductive potential are essential for maximizing profitability. Traditional bull breeding soundness evaluation, or systematic analysis of frozen semen, eliminates bulls or semen samples that are grossly abnormal. However, semen samples classified as satisfactory on the basis of traditional approaches differ in fertility. Advanced sperm function assays developed for assessing compensatory and noncompensatory (submicroscopic) sperm traits can predict such variations in bull fertility. New knowledge on epigenetic modulations of sperm DNA, messenger RNA, and proteins is fundamental to refine and expand sperm function assays. Sexed semen, plus advanced reproductive technologies (e.g., ovum pickup and *in vitro* production of embryos) can maximize the efficiency of beef cattle production. This review is focused on genetic considerations for bull selection, physiology of reproductive development, breeding soundness evaluation, recent advances in assessing frozen semen, and existing and emerging uses of sexed semen in beef cattle production.

1. Introduction

World population is estimated to reach 9×10^9 by 2050, making it critical to increase efficiency of food production [1]. With $\sim$35 $\times$ 10^6 beef cows in American beef herds, a modest 3% increase in reproductive rate would yield 1×10^6 more beef calves annually [2]. Ironically, poor reproductive performance is the most common cause for culling beef cows [3]. Birth of a calf is essential to generate breeding stock and animals to produce meat; consequently, fertility is five-fold more important than production traits. Bull fertility is particularly critical, as bulls classified as satisfactory based on a traditional bull breeding soundness evaluation (BBSE) are typically used for natural breeding 20+ females per annum, or their frozen semen can be used for many thousands. Fertility varies $\sim$20% among bulls classified as satisfactory (traditional BBSE), due to submicroscopic differences in sperm. Accurate selection of superior bulls, optimizing their reproductive potential (good management), accurately assessing fertility, and marketing semen are critical.

2. Use of genetics and genomics for bull selection

Genetic selection reduces generation interval, and increases prediction accuracy and selection intensity [4,5]. Genome-based selection requires quantification of effects of genome-wide single nucleotide polymorphism (SNP) markers on adjusted phenotype (deregressed estimated breeding value) from a reference population large enough

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0093-691X/$ – see front matter
http://dx.doi.org/10.1016/j.theriogenology.2016.04.054

to make accurate measurements [6,7]. These data can be used to estimate direct genomic breeding values (DGV), enhance selection of specific genotypes [8,9], and hasten genetic progress [4]. Genome-based selection is much more advanced in dairy than that in beef; challenges include development of genome-based strategies useful across breeds, lack of data, and quantitative trait loci (QTL) validation [10]. For example, Nelore cattle have a critical role in beef production in tropical countries. Therefore, genetic improvement of production and fertility of this breed will substantially improve tropical beef cattle production. Accuracies of genomic predictions in Nelore cattle were influenced by genetic relatedness between reference and tested populations [10], and the estimated breeding value of bulls were determined with a high-density SNP panel to identify loci affecting scrotal circumference (SC) [11].

3. Reproductive development of bulls

3.1. Regulation of puberty in the bull

Puberty in bulls is defined as an ejaculate with greater than or equal to 50×10^6 sperm with greater than 10% motility [12]. In addition, bulls must have adequate libido and penile development to copulate and ejaculate [13]. Puberty is regulated through the hypothalamo-hypophyseal-testis axis. Pulsatile release of GnRH from the hypothalamus induces pulses of LH and FSH from gonadotrophs in the adenohypophysis, with LH causing a pulsatile release in testosterone (from Leydig cells), which is subsequently converted to dihydrotestosterone and estradiol in Sertoli cells. High testosterone concentrations in the seminiferous tubule are essential for normal spermatogenesis. Sertoli cell function is regulated by FSH [6] and testosterone (nonclassical steroid signaling) [14,15]. Testosterone and estradiol downregulate GnRH release, particularly in prepubertal bulls. However, as puberty nears, sensitivity of GnRH-secreting neurons to testosterone and estrogen decreases, with a concomitant increase in concentrations of GnRH, LH, FSH, and testosterone, culminating in puberty [2]. Neurons producing GnRH communicate with other neurons that convey nutritional status (metabolic sensors) through nutrients and concentrations of leptin, Insulin-like Growth Factor-I (IGF-I), insulin, and growth hormone [2]. It is expected that this enables GnRH neurons to overcome negative steroid feedback and increase frequency and amplitude of GnRH pulses.

3.2. Endocrine and testicular changes during reproductive development of the bull

Bull reproductive development has three periods: infantile, prepubertal, and pubertal. The infantile period (0–8 weeks) is characterized by low secretions of gonadotropins and testosterone. However, there is a transient increase in gonadotropin secretion (early gonadotropin rise) and concomitant rise in testosterone in the prepubertal period (8–20 weeks). Concentrations of LH and FSH increase from 4 to 5 weeks, peak at 12 to 16 weeks, and then decline, reaching a nadir at 25 weeks. This increased LH affects sexual development and is inversely related to age at puberty [16,17]. The decline in gonadotropins by 25 weeks is attributed to rising testosterone [18]. In the postpubertal bull, every GnRH pulse is followed by a pulsatile secretion of gonadotropins and testosterone (4–8 pulses daily; [2]). The early gonadotropin rise is critical for reproductive development [19,20]. Testes are comprised of prespermatogonia, spermatogonia, adult Leydig cells, and undifferentiated Sertoli cells before 25 weeks. Thereafter, rapid testicular development occurs through puberty [20], with marked increases in diameter and length of seminiferous tubules, proliferation and differentiation of germ cells, and development of adult Leydig cells (30 weeks), Sertoli cells (30–40 weeks), and mature sperm (32–40 weeks).

3.3. Nutrition and reproductive development of bulls

Early-life nutrition of bulls profoundly affects reproductive potential. Beef bull calves fed ~130% of maintenance requirements of energy and protein from 10 to 30 weeks had increased testicular weight and sperm production by 74 weeks compared with bull calves fed 100% of maintenance [20,21]. Beneficial effects of early-life nutrition on postpubertal bulls are attributed to increased LH secretion during the early rise. Furthermore, because detrimental effects of restricted feeding during early-life are not overcome by nutritional supplementation during the pubertal period, early-life nutrition predetermines age at puberty, testis size at sexual maturity, and sperm production potential. Because the early rise in gonadotropins is associated with a concurrent increase in IGF-I, that hormone may be involved in regulating the early rise. We recently conducted a similar study in dairy bull calves; bulls fed a high-nutrition diet had an earlier and more substantial early rise in LH and IGF-I [22]. In addition, bulls on early-life high-nutrition consistently had larger testes and were younger at puberty (~45 days, based on semen) than those fed a low-nutrition diet. It has been demonstrated that morphologic improvements of the testis (i.e., increased testicular size) hastened sexual maturity and improved daily sperm production [21]. Therefore, early-life supplemental nutrition substantially improves future reproductive potential of bulls. There is a growing tendency to select beef cattle for improved nutritional efficiency, based on residual feed intake, the difference between actual and expected feed consumption (based on body weight and rate of gain [23]). Since reproduction is a low priority, it is very likely that bulls with a genetic background for negative residual feed intake (improved feed efficiency) may have compromised reproductive development. Consistent with this hypothesis, Awda et al. [24] reported that young beef bulls with greater feed efficiency have decreased sperm quality and SC. This undesirable effect needs to be addressed through multiple trait selection.

3.4. Early-life predictors of bull fertility and potential use of bull fertility traits to advance herd fertility

Various reproductive traits of bulls and its relationship to other measures were reviewed [25]; these could be used as early-life predictors of bull fertility. Furthermore, some traits have implications for enhancing herd fertility by