Genetic parameter estimation for beef bull fertility: A review

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Abstract

Reproductive efficiency is the major driver of profitability and genetic performance among all livestock species; advancements in husbandry practices and genetic selection tools to increase reproductive output have been well documented for cow fertility, but largely ignored for beef bull fertility in research and published literature. Estimation of beef sire fertility is economically relevant to not only the U.S. beef herd, but to the world, as the economic losses from sub fertile bulls and late pregnancies can have major implications on profitability while slowing genetic progress. Published studies that have assessed the genetic parameters of beef bull fertility traits are sparse in number, but indicate low to moderate heritability estimates for semen quality traits. Correlations amongst semen quality traits are also low to moderate, but favorable, indicating that indirect selection could provide opportunity for genetic advancement of particular traits. Genomic selection continues to make strides forward within the beef industry among other performance traits but has been underdeveloped in terms of fertility selection. Quantitative trait loci (QTL) for bull fertility discovered in dairy cattle have provided a basis for further research and examples of sire selection methods, however separations in management practices and slower adoption of AI forces the beef industry to look for other opportunities for data collection of phenotypic fertility traits. Ultimately, improvements in beef bull fertility have the potential to significantly impact the profitability of the global beef system by reducing cost, increasing selection intensity, and rapidly increasing genetic gain. Research regarding estimation of the genetic parameters of beef bull semen quality traits, development of genomic selection tools for fertility, and utilization of breeding soundness examination (BSE) records to provide valuable fertility phenotypes is gravely needed to make advancements in bull fertility a reality.

The objective of this report is to discuss the various literature surrounding male fertility genetic parameters within both the beef and dairy industries.

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Review of the Literature

Introduction

Improvements in reproductive performance increase the efficiency of beef cattle production. In both the beef and dairy industries, significant advancements in female fertility have been made through genetic selection and the use of reproductive technologies (Berry et. al., 2010; Taylor et al., 2018). Unfortunately, male fertility has not received the same level of focus or investment and therefore studies of fertility in beef cattle have not thoroughly addressed male fertility challenges (Berry et al., 2014; Taylor et al., 2018). Conception -and parturition- are the result of both female and male fertility (Senger, 2012). Therefore, use of sub-fertile bulls can limit achieving reproductive efficiency and production goals (Kalstelic and Thundathil, 2008). Though selection for growth traits is important, perhaps the most important trait to select for is fertility, due to the fact that without conception, there is no progeny to continue making progress in other economically relevant traits (Taylor et al., 2018). Creation of effective selection tools requires large volumes of phenotypic data, and because fertility phenotypes are based on multifactorial influences, defining these phenotypes can be challenging (Barth, 2000; Berry et al., 2014). For male fertility, the ability to reproduce first stems from libido, or sex drive. The second factor in male fertility is the physical capacity to copulate. Lame or injured bulls ultimately do not have the physical capacity to breed cows. Finally, semen quality is essential to bull fertility. Sperm abnormalities, poor motility, and/or infectious diseases could all lead to reduced fertility or sterility, affecting the reproductive capacity of a bull.

While bull stud data offers a large volume of high-quality, standardized phenotypic measures of bull semen quality, the data is largely proprietary. Furthermore, bulls that enter into

a stud for collection have previously passed semen quality standards before being eligible for cryopreservation of ejaculate to occur, therefore reducing the variation in samples. In addition, over 90% of all beef cattle producers still predominately use natural service in their breeding programs (USDA, 2017). As an example, the U.S. Department of Agriculture National Agricultural Statistics Service reported 31.4 million head of beef cows and heifers calving during the spring 2021 season (USDA, 2021). Of these 31.4 million cows and heifers, 29.99 million head were likely mated from natural service sires (USDA, 2020). Producers typically mate 15 cows to each yearling bull, and 22 cows per mature bull (USDA, 2020), resulting in the average bull breeding 18 cows per year. With these assumptions in place, approximately 1.7 million bulls are needed annually to serve the U.S. beef cow population. Thus, these natural service sires will be the most plentiful source of male fertility information on large numbers of animals. Breeding soundness exams (BSE) could contribute much needed phenotypic data to develop genetic selection tools to increase bull fertility because they are both commonly collected and could be submitted by producers to genetic evaluation providers (Taylor et al., 2018).

Male Fertility's Effects on U.S. Beef Cattle Industry

Male fertility is arguably more important for the beef industry than female reproduction. Sire selection can have a long-term impact on an operations' herd and production goals. Ultimately, in operations that retain their own replacements, approximately 87.5% of the genetic makeup of the herd will be derived from the previous three herd bulls (Massey, 1993; Bullock and Moser, 2021). Regardless of whether a sire is used for both natural service or artificial insemination (AI), a sire will have significantly more progeny over the course of their lifetime than a dam. On average, bulls are responsible for breeding 15 to 25 females per season (USDA, 2020) in a natural service breeding program, and can be mated to thousands of cows through the

use of AI. Trenkle and Willham (1977) estimated fertility is over ten times as economically important as carcass quality and five times as important as rate of gain. Fertility has the largest impact on offsetting maintenance costs. In addition, lengthening of a calving season has a large, negative economic impact on a cowherd (Barth, 2000). Barth (2000) projected that the most dramatic economic loss to the cattle industry, when sub-fertile bulls are involved, is the reduction in first service conception rate. Furthermore, it has been estimated that for every estrous cycle a cow remains open during the breeding season, there is a 50-to-60-pound reduction in the following year's offspring's weaning weight (Barth, 2000).

Rationale for Male Fertility Expected Progeny Difference

Due to the economic importance of male fertility to the beef industry, development of selection tools to assist with correctly ranking bulls for their fertility or genetic potential for fertility could have substantial economic benefits. The dairy industry has embraced this concept, and through the development of sire conception rate (SCR) a phenotypic index, has been able to make improvement in bull fertility. Sire conception rate was developed through the adaptation of the estimated relative conception rate (ERCR) that was provided to the dairy industry by Dairy Records Management Systems (USDA, 2008). Sire conception rate was implemented by the USDA Animal Improvement Programs Laboratory (Beltsville, MD; Norman et al., 2008) in August of 2008 and was the culmination of research reported by Kuhn et al. (2006, 2008) and Kuhn and Hutchinson (2008). Sire Conception Rate is a phenotypic bull fertility evaluation based on inseminations of conventional semen; and is described as a phenotypic bull fertility evaluation based on the difference in probability that a unit of semen from a specific bull will result in a pregnancy in comparison to the mean of all other bulls that could have been used for that mating (Norman et al., 2011). The use of SCR as an AI conception ranking tool has allowed

not only more accurate selection decisions to be made based off of fertility, but has also allowed expansion of management tools within the AI industry to overcome certain compensable semen traits (Taylor et al.; 2018; McWhorter et al. 2020). The National Association of Animal Breeders (NAAB) 2022 annual report further shows the exponential growth of beef on dairy matings, with a year over year increase of 457,000 units of beef semen used within the dairy industry (NAAB 2022). McWhorter et al. (2020) evaluated 233,379 service records from 1,344 Angus (AN) bred to 163,919 Holstein (HO) cows in 2020 to evaluate SCR's usage for evaluating beef service sires within the dairy industry. This study reported that the AN bulls mated to HO cows exhibited similar SCR as HO bulls, whereas beef bulls had 1/3 of the matings in comparison to their HO counterparts (McWhorter et al., 2020). Furthermore, McWhorter et al. (2020) reported reliability for SCR of the AN sires evaluated averaged 64.5%, with a maximum reliability of 99% when based off of 25,217 matings.

However, using SCR as a stand-alone evaluation tool for determining fertility is challenging due to the multifactorial composition of bull fertility (Ortega et al., 2018; Taylor et al., 2018). First, SCR is calculated from confirmation of pregnancy at 70 days after insemination (Norman et al., 2011; Ortega et al., 2018;); a vast array of processes associated with pregnancy establishment and recognition occur during this time period, and therefore can have large effects on SCR. Additionally, SCR is based off of AI records reported by Dairy Herd Improvement Association (DHIA) and updated on a regular basis (McWhorter et al., 2020). This system provides both opportunities and challenges for beef sires, as bulls already within the AI industry could be tested over a large population of females. Furthermore, variation in phenotypes collected for calculation of SCR have been realized, as this index does not account for bulls with poor semen quality attributes (Ortega et al., 2018). Therefore, bulls that have inferior semen

quality are removed from the population due to failing to pass semen freezing requirements. Though this realized variation in phenotypic records raises concerns, results from Penagarican et al. (2012) and Rezende et al. (2018) indicated that there is a difference in conception rate over 10% when comparing dairy bulls with high and low fertility as indicated by SCR. This point could be further compounded as common matings to beef bulls within a dairy system are analyzed. In a dairy system, beef bulls are often bred to cows that have problems conceiving, so the question arises if we are truly giving beef bulls the same level of evaluation as their HO counterparts (Taylor et al., 2018: McWhorter et al., 2020). Moreover, SCR does a great job of representing AI sires, which in the dairy industry covers a mass majority of the mating options (Taylor et al., 2018); however, within the beef industry over 95% of conception occurs through natural service (USDA, 2020).

Though tools like SCR have had success in the dairy industry, the question remains of what traits to measure while assembling a fertility selection index or making selection decisions in general for beef bulls. This gap in production style leaves large pitfalls for utilization of SCR within the beef industry.

Breeding Soundness Exam

A breeding soundness examination (BSE) is an evaluation of the physical fitness of a bull and an evaluation of his sperm's capabilities to perform fertilization (Barth, 2000). Evaluations of fitness can identify bulls that do not have the correct physiology to be satisfactory breeders. The exam includes observation of genitalia, eyes, and structural soundness in conjunction with measurement of scrotal circumference (SC); and semen evaluation. These examinations provide a practical and cost-effective solution to identify and cull sub-fertile bulls within the population. The economic benefits of implementing a BSE have been reported by multiple entities.

Menegassi et al (2011) conducted a bioeconomic study of BSEs on beef cattle production in Brazil and reported a cost benefit ratio of 1:36. Chenoweth (2000) reported similar results with a cost benefit ratio of 1:17 when evaluating beef cattle in the United States. Although substantial economic value has been demonstrated, producers continue to underutilize this management tool. A USDA survey conducted in 2017 revealed that only 66.8% of producers put newly purchased, leased or borrowed bulls through a BSE before turnout (USDA, 2020). This lack of utilization becomes more alarming when considering the proportion of sub-fertile animals in the population. Kennedy et al. (2002) conducted BSEs on a population of 3,648 yearling bulls and reported that 23.8% were sub-fertile; due to poor semen quality, inadequate scrotal circumference, or physical abnormalities. Caroll et al. (1963) found similar results when analyzing the results of BSE from a population of 10,940 bulls; one in five bulls in their study were sub-fertile due to semen quality issues or inability to service cows (due to skeletal or reproductive tract injury).

Scrotal Circumference

Scrotal circumference (SC) is a simple measurement recorded during a BSE that requires the testes to be pushed firmly to the bottom of the scrotum, while using a circular tape to measure the circumference of the paired testes at the largest circumference (Kastelic and Thundathil, 2008; BSE, 2018). Scrotal circumference is often used as an indicator trait for age at puberty and as a prediction tool to estimate sperm output and quality (Coulter and Foote, 1975; Cammack et al., 2009). On average, beef bulls produce 11x10^9 spermatozoa per gram of testicular parenchyma (Senger, 2012). Significant correlations between SC and testis weight as well as SC and semen output have been reported, ranging between 0.86 and 0.95 and 0.91 and 0.98, respectively (VanDenmark, 1956; Hahn et al., 1969; Coulter and Foote, 1975).

Willett and Ohms (1957) were among the first to correlate phenotypic semen output with SC in young bulls (0.94 in a young population of bulls undergoing an exhaustion test). Hahn et al. (1969) reported strong, positive phenotypic correlations (0.81) between SC and semen output when studying weekly ejaculations of dairy bulls in a collection facility. Findings from Gipson et al. (1985) also showed significant differences ($P>0.05$) between low SC (SC<32cm) and high SC (SC>35 Hereford and >38cm Simmental bulls) in other semen quality traits including percent live sperm, sperm number, and sperm motility indicating bulls with larger scrotal circumference had high quality semen.

Heritability estimates for SC have indicated it is a moderate-to-highly heritable trait, with estimates ranging from 0.41 to 0.71 (Evans et al. 1991; Corbet et al., 2013). Furthermore Corbet et al. (2013), in studying a population of tropical composite bulls, estimated SC heritability at 6, 12, 18, and 24 months of age with estimates of 0.41,0.46,0.43 and 0.44, thus illustrating that increase in age does not seem to change the heritability estimate. Therefore, due to the high heritability estimate, ease of recording this trait, genetic selection programs have been successful in improving SC (Martin et al., 1992; Martinez-Velazquez, 2003; Cammack et al. 2009).

The improvement in SC over time, in conjunction with the ease of collecting trait measurements, has prompted questions connecting SC to female fertility traits. Brinks et al. (1978) reported a correlation between sire SC and age of puberty in heifers (AP) of (-0.71). Moser et al. (1996) found SC expected progeny difference (EPD) was a more effective tool in reducing age of puberty in females than selection of phenotypic SC. More recent studies have contested this theory showing lower correlations between SC and female fertility traits such as heifer pregnancy (HP), such as Martin et al. (1992) whom reported an estimate at (-0.39). Other researchers, including Boldt et al. (2018), Evans et al. (1999) and McAllister et al (2011); found

that the genetic correlation between SC and heifer pregnancy (HP) was not significantly different from zero. With variations in literature estimates, further research is needed to quantify not only relationships between male and female fertility, but also the relationship of SC as a male fertility indicator and its correlation with economically relevant male fertility traits (Hahn et al., 1976; Cammack et al., 2009). A complete list of reported heritability estimates for SC from the literature can be found in Table 1.

Heritability of Semen Quality Factors

Motility

Motility refers to the ability of mature sperm cells to move progressively in a forward direction (Senger, 2012). Assessment of motility provides the easiest way to determine the viability of sperm (Barth, 2000). Motility is also referred to as progressive motility (PROG) by studies that utilized a computer-assisted semen analyzer (CASA), and is a phrase used to describe when sperm cells travel in a linear fashion or make large circular patterns (Butler et al., 2021). During a BSE, MOT is evaluated and scored as a percentage of ejaculate when viewed on a slide warmed to 37 °C (Barth, 2000). Spermatozoa are then counted and classified, based on a subset of ejaculate sample while being viewed under a microscope (Barth and Waldner, 2002). Due to the high intensity work of conducting BSE on groups of bulls, this evaluation can become somewhat subjective and large variation can result between observers (Chenoweth, 2005). The Society for Theriogenology's standards for BSE motility scores classification system ranks MOT in the following categories: 80 to 100% progressively motile sperm is classified as very good (VG), 60 to 79% is good (G), 40 to 59 percent is classified as fair (F), and below 40% progressively motile sperm is classified as poor (P; Barth, 2000). In order for a bull to pass a

breeding soundness exam, he must have greater than 30% progressively motile sperm (Barth, 2000).

Heritability estimates for motility (MOT), percentage of progressive spermatozoa (PROG), and motility score (MOSC) exhibit large variation between studies. Using a population of 549 beef bulls, Smith et al. (1989) reported a heritability estimate of 0.08 ± 0.07, whereas Christmas et al. (2001), Gredler et al. (2007), and Garmyn et al. (2011) reported heritability estimates ranging from 0.04-0.07 in populations of yearling beef bulls ranging in populations sizes from 301 to 1282 head. Conversely, Kealy et al. (2006), when studying a population of 841 Line 1 Hereford bulls, estimated heritability to be 0.22. One explanation for the variation in these estimates; could be the increased inbreeding coefficient in the Line 1 population. Corbet et al. (2013) estimated the PROG heritability at 0.15 for a population of Brahman and tropical composite bulls. The findings from Corbet et al (2013) also indicate that puberty could have effects on PROG, due to the decrease in heritability estimate as age increases, as shown by an increase in age from 12, to 18, to 24 months of age corresponded with a decrease in PROG estimate from 0.44, 0.15, to 0.05 respectively. Management of bulls was the same throughout the duration of the study, thus indicating that variation in estimates could be attributed not to management differences, but rather maturity. Druet et al. (2009) estimated heritability of MOT at 0.43 ±0.08 using data from a population of 12 to 18-month-old Holstein bulls. Motility score (MOSC) is a subjective rating that depends on a scale, which can vary according to the specific standards of the collection protocol; with a higher MOSC being more desirable. Ducrocq and Humboldt (1995) measured MOSC on a 0 to 4 scale while studying a population of 2,387 Normande bulls, finding a heritability estimate of 0.23. Suchocki and Szyda (2015) found similar findings with an estimate for MOSC of 0.26, while measuring MOSC on a 1 to 3 scale.

Differences in estimates could be attributed to not only size in populations studied, but additionally models used for analysis. Smith et al. (1989) utilized a least square means for their analysis, while Christmas et al. (2001), Kealey et al. (2006), and Corbet et al. (2013), utilized Reml for their analysis. Variations in MOSC heritability estimates could be attributed to differences in fixed effects included in the various models, in addition to the scoring protocols not being uniform between studies.

Morphology

Morphology describes the shape, structure and size of sperm cells within a sample of semen; classification of morphology identifies abnormalities that can have detrimental effects on the fertility of a bull. In order for a bull to be classified as a Satisfactory Potential Breeder, total sperm abnormalities (ABNO) must be less than 30% and less than 20% can have head defects (BSE, 2018). Studies report either percent abnormalities or percent normal sperm, in agreement with standard bull breeding evaluation standards (Barth, 2000; Chenoweth, 2005; BSE, 2018).

Classification of sperm defects can be described in multiple ways, including differentiation between compensable and uncompensable semen defects (Kastelic and Thudathil, 2008). Compensable abnormalities cause impaired sperm motility, or can reduce the probability of sperm successfully moving through the female tract (Saacke et al., 2000; Chenoweth, 2005). Compensable semen traits can be overcome by a change in site of deposition or, more commonly, an increase in sperm dosage (Saacke et al., 2000; Chenoweth, 2005). With this in mind, compensable semen traits have smaller impact within systems that utilize AI, as both site of deposition (cervically during AI vs natural service deposition vaginally) and dosage can be monitored to alter conception rate (PR) (Senger, 2012). In contrast, uncompensable abnormalities cannot be overcome through an increase in sperm dosage, and are often times

undiagnosed through typical semen evaluation protocols (Saacke et al., 2000). Examples of uncompensable abnormalities include spermatozoa with subtly misshapen heads, or those that have nuclear vacuoles on otherwise normally shaped heads, as these sperm are able to transverse the female reproductive tract and penetrate the zona pellucida, however pregnancy initiation from these cells have been shown to yield lower quality embryos and lower fertilization rates (Saacke et al., 2000). Therefore semen defects that cause failure in fertilization or early pregnancy loss regardless of dosage are classified as uncompensable (Saacke et al., 1994). As described by Saacke et al. (1994) and Rodriguez-Martinez' and Barth (2007), increasing the number of sperm cells in an ejaculation or inseminate from males producing incompetent sperm that are incapable of reaching the ovum and initiating fertilization would not improve reproductive efficiency.

Perhaps the most widely accepted classification system of sperm abnormalities is the differentiation between primary and secondary abnormalities (Barth, 2000). In this system, sperm abnormalities are classified by perceived origin of defect within the process of spermatogenesis or sperm maturation. Therefore, defects deemed primary have their origins within the testicle during spermatogenesis and were originally thought to be linked to direct insult to the seminiferous epithelium (Barth, 2000; Chenoweth, 2005). Secondary abnormalities originate within the epididymis during sperm maturation and transport (Barth 2000). Though widely accepted, this classification system's open-ended approach leaves room for discrepancies between semen evaluators in regard to assessing origin of defects that can be caused by disruption in both spermatogenesis or maturation (Barth, 2000; Chenoweth, 2005). Proximal droplets and detached head defects both provide a prime example of this issue, as both abnormalities can be linked to disruption in the testicles or epididymis (Barth, 2000; Chenoweth,

2005). Furthermore, misinterpretation of this system has led to primary abnormalities being viewed as more adverse defects in comparison to secondary abnormalities, along with the misconception that the latter were not as consequential to fertility (Chenoweth, 2005).

These discrepancies in classification has led to other systems being proposed to better describe sperm abnormalities, including classifying sperm defects as major and minor defects (Chenoweth 2005). Under this system, major defects are those proven to be associated with major fertility impairment and includes sperm defects such as proximal droplets, crater/diadem defect, acrosome defect, and coiled tail (dag defect; Chenoweth, 2005, Enciso et al., 2011). Minor defects under this description included looped tails, detached sperm heads, and distal droplets (Parkinson, 2004; Chenowth, 2005; Enciso et al., 2011). Moreover, under the direction of the Society of Theriology recommendations, new standards indicate that abnormalities should be identified by location of defect, including head, midpiece, and tail, instead of a primary/secondary or major/minor system (BSE 2018). Because this review focuses primarily on BSE data and supporting research data was collected under BSE classification of abnormalities being listed as primary or secondary, subsequent classifications and discussions will focus on these topics.

Abnormalities

Total abnormalities or percent abnormalities (ABNO) is the proportion of sperm cells contained in an ejaculate sample that contain irregularities or undesirable characteristics. It is the sum of primary (PRIM) and secondary (SEC) abnormalities. Percent normal sperm cells (PNS) is the inverse of ABNO, and in general, studies report one of the two. Smith et al. (1989) reported the highest heritability estimate for ABNO among the literature with a value of 0.31, while studying a population of Angus, Red Angus, and Hereford bulls. Later studies have lower and a

wider variation of estimates for ABNO ranging from 0.15 to 0.29 including Ducroc and Humbolt (1995), Christmas et al. (2001), Druet et al. (2009), Garmyn et al. (2011) and Silva et al. (2011). Differences in heritability estimates could be attributed to multiple things including models used for analysis of data during each study. Smith et al. (1989) utilized least square means to calculate their heritability estimates, while Ducroc and Humbolt (1995), Christmas et al. (2001), Druet et al. (2009), and Garmyn et al. (2011) utilized ASReml for their estimates. Additional explanations for the variation in literature could be attributed to breed as Silva et al. (2011) studied a population of Nellore bulls, estimated ABNO at 0.15, while conversely Ducrocq and Humboldt (1995) utilized data collected from a population of Normande bulls and estimated ABNO at 0.19.

Percent normal sperm heritability estimates also range widely among literature. Smith et al. (1989) and Gredler et al. (2007) reported estimates for PNS or 0.07 and 0.10, respectively, with large standard deviations. Contrarily, Yilmaz et al. (2004), Kealey et al. (2006), and Corbet et al. (2013) had higher heritability estimates for PNS ranging from 0.35 to 0.47. Possible explanations for the difference in estimates include population sizes, as both Smith et al. (1989) and Gredler et al. (2007) studied populations with under 600 head of bulls, whereas, Yilmaz et al. (2004), Kealey et al. (2006), and Corbet et al. (2013) worked with data sets with populations of over 700 head of bulls. Model variation and statistical methodology could also account for the spread in heritability estimates as Smith et al. (1989) used least square means while in contrast Yilmaz et al. (2004), Kealey et al. (2006), and Corbet et al. (2013) utilized variations of Reml to calculate their estimates.

Primary abnormalities

Primary abnormalities are sperm irregularities that originate within the testis during the process of spermatogenesis and impair fertilization (Barth, 2000; Chenoweth, 2005; BSE, 2018). Major or PRIM abnormalities include knobbed acrosome, crater/diadem defect, strongly folded or coiled tails (also known as a "Dag" defect), and tail stump defect (Chenoweth, 2005; BSE, 2018). Other criteria that help in identifying PRIM or major defects include that the defect in question occurs in a substantial proportion (>10%) of the sperm population, are consistent in occurrence, and that these abnormalities occur in the absence of a clinically or environmentally distinguishable cause (Chenoweth, 2005). Heritability estimates surrounding PRIM range from 0.27 to 0.35 (Smith et al., Christmas et al., 2001; Kealey et al., 2006; Garmyn et al., 2011) indicating that it is moderately heritable. Variation in estimates could be attributed to breed of population analyzed in addition to method for statistical analysis, as Smith et al. (1989) studied a mixed population of Red Angus, Hereford, and Angus bulls; while Kealey et al. (2006) utilized a population of line 1 Hereford cattle, and Christmas et al. (2001) and Garmyn et al. (2011) focused solely on Angus bulls. Heritability estimates for specific primary abnormalities varies between studies. Estimates for abnormal proximal cytoplasmic droplets ranges from 0.19 to 0.37 (Kealey et al., 2006; Druet et al., 2009). Druet et al. (2009) estimated the heritability of abnormal tails at 0.19, while Kealey et al. (2006) distinguished coiled tails finding an estimate of 0.34. Differences between these estimates could be accounted to population studied as Druet et al. (2009) utilized stud data taken from Holstein bulls, while Kealey et al. (2006) utilized BSE records from yearling Hereford bulls. Variation in estimates for tail defects could be attributed to differences in classification protocols for tail defects, as Kealey et al. (2006) differentiated between coiled tails and bent tails. Kealey et al. (2006) findings indicate coiled tails to be

moderately heritable (0.34) however, their estimate for bent tails had a large standard error making their estimate no different from zero. Conversely, Druet et al. (2009) combined classification of these two abnormalities together and could therefore account for the much lower heritability estimate for total tail abnormalities.

Secondary abnormalities

Secondary abnormalities (SEC) describe sperm abnormalities that are derived from the epididymis during spermatogenesis (Parkinson, 2004; Chenoweth, 2005). Also known as minor defects, SEC are thought to be more variable, less consequential, and are thought to be effectively compensated for with increasing sperm dosage (in an AI system) (Chenoweth, 2005; Graham and Moce, 2005; BSE, 2018). Examples of SEC include small normal heads, abaxial implantation, and distal droplets (Chenoweth, 2005; BSE, 2018). Due to formation of SEC within the epididymis, abnormalities of this nature were thought to be largely environmental (Chenoweth, 2005; BSE 2018; Hartman, 2020). However, current literature offers a range of estimates from 0.18 to 0.35, indicating SEC as low to moderately heritable (Christmas et al., 2001; Kealey et al., 2006; Garmyn et al., 2011; Butler et al.,2021). Smith et al. (1989) estimated the heritability of SEC at 0.02, however this estimate had a standard error of 0.05, and was calculated using a least square method, while later research studies utilized Reml. Conversely, variation in estimates from these later studies could be attributed to differences in age of bulls utilized in analysis. Christmas et al. (2001), Kealey et al. (2006), Garmyn et al. (2011), utilized BSE records from bulls averaging in age from 383 to 387 days, while Butler et al. (2021) utilized stud records from bulls with an average age of 1135 days. Early research and work within reproductive physiology had indicated that SEC was due to environmental factors, however wide

variation in literature indicates that more research is needed with larger data pools to assess genetic connections of sperm abnormalities considered SEC.

A complete list of heritability estimates reported within the literature for all classifications of motility and morphology can be found in Table 2.

Genetic and Phenotypic Correlations

Scrotal circumference with semen quality measures

Scrotal circumference is a moderate to highly heritable trait (estimates ranging from 0.36 to 0.71; Knights et al., 1985; Evans et al., 1991), with high repeatability (r = 0.98) (Hahn et al., 1969). Many studies have estimated correlations between SC and semen quality traits Smith et al. (1989) was among the first to report a genetic correlation between SC and MOT in a population of Herefords. The genetic correlation was -0.04 with a large standard error of 0.40; this standard error being attributed by Smith to the low estimates of genetic variation in the population of yearling bulls analyzed in this study. More recent literature contradicts Smith's estimate; with a positive genetic relationship between SC and MOT estimated from 0.56 to 0.70 (Christmas et al. 2001; Corbet et al., 2013). Variations in strength of these relationships could reflect breed composition differences between studies, as Christmas et al. (2001) found a moderate, but favorable relationship between SC and MOT in a population of Angus bulls. Corbet et al. (2013), found a stronger relationship between SC and PROG with a value of 0.70 in a population of Brahman bulls and 0.56 in a set of tropical composite cattle, all of which were maintained under similar management. Estimates of phenotypic correlations between SC and MOT are also found to be moderate but positive, ranging from 0.47 to 0.56 (Gipson et al., 1985; Corbet et al. 2013). The variation in the phenotypic correlations could be an indication of breed composition and population size differences as Gipson's data was obtained from a set of 729

yearling Hereford and Simmental bulls, while Corbet's data was derived from over 4,063 Brahman and tropical composite bulls. This breed difference could also account for the slight variation between genetic and phenotypic correlations, as Corbet et al. (2013) reported genetic correlations between SC and MOT at 12, 18 and 24 months of age with estimates of 0.70±0.08, 0.79±0.10, and 0.86±0.31, in addition to phenotypic correlations between these traits of 0.47, 0.38. and 0.20. Because the cattle were managed under similar conditions throughout the study, the progressive decline in the strength in relationship between SC and MOT could be due to differences in maturity or puberty. With this observation in mind, the relationship between SC and MOT could relationship be different between different breeds. breed by breed basis, as literature shows a strong relationship among later maturing breeds such as Brahman (Corbet et al. 2013), however further research is need to assess the strength of this relationship.

Genetic correlations between SC and PNS also show variations among studies, ranging from -0.36 to 0.50 (Smith et al. 1989; Corbet et al. 2013). Smith's reported correlation of -0.36, corresponds with an unfavorable relationship between SC and PNS, however this estimate was also reported with a standard error of 0.34, indicating that this correlation is not statistically different from zero (Smith et al., 1989). Corbet et al. (2013) reported a positive correlation between SC and PNS of 0.50 and 0.21 for a Brahman population and tropical composite population of bulls respectively. This wide variation in results between Smith et al. (1989) and Corbet et al. (2013) could be attributed to many factors including differences in models, population size, age of cattle studied, in addition to breed composition. Smith et al. (1989) utilized least square method sire model; conversely, Corbet et al. (2013) utilized a BLUP animal model. Smith et al. (1989) accounted for the fixed effects of year, birth year, age of dam, and breed in his model. Corbet et al. (2013) accounted for these fixed effects in addition to birth

location and dam's contemporary group. A larger impact to account for variation in these correlations could be the combination of breed and age at performance of a BSE, as Smith et al. (1989) utilized data from a population of yearling British breed bulls, while Corbet et al. (2013) studied a population of 18-month old Brahman and Brahman influenced cattle.

Genetic and phenotypic correlations between SC and ABNO, PRIM, and SEC also show variation in correlation estimates among literature. Christmas et al. (2001) reported a correlation of -0.32 between SC and ABNO, indicating a negative, and favorable interaction between the two traits, inferring that an increase in SC would correspond to fewer abnormalities. Garmyn et al. (2011) reported similar findings to Christmas et al. (2001), although their correlation estimate was lower at -0.23, and the standard error was nearly as large as the estimate, indicating the correlation is not statistically different from zero. Smith et al. (1989) reported correlations between SC and PRIM and SEC to be 0.14±0.22 and 1.22±1.57, respectively. However, considering that Smith et al. (1989) heritability estimate for SEC was not statistically different from zero, the lack of genetic diversity in the population utilized in their study could account for the inconsistent correlation between SC and SEC. Christmas et al. (2001) reported correlations of -0.25 and -0.40 for the relationship between SC and PRIM and SC and SEC, respectively. Kealey et al. (2006) reported more negative, and favorable relationships between SC and PRIM and SC and SEC with estimates of -0.36 and -0.45. Garmyn et al. (2011) reported lower correlations between SC and PRIM and SEC of -0.19 and -0.11, respectively; however, the standard error for these relationships was nearly the same as the reported estimate. Variation in estimates could be attributed to breed and population size differences, as Kealey et al. (2006) utilized a line 1 Hereford population of 851 bulls, while Christmas et al. (2001) and Garmyn et al. (2011) studied larger populations of Angus bulls. Though some literature has indicated

selection for SC could provide indirect selection for semen quality traits (Garmyn et al. 2011), variation among literature indicates more research is needed to assess these relationships. A complete list of genetic and phenotypic correlations between SC and semen quality traits can be found in Table 3.

Semen quality measures

Correlations between PNS and MOT show variation among studies. Smith et al. (1989) reported an estimate of 0.43, indicating a moderate, yet favorable relationship between PNS and MOT; however, the standard error was 0.64. Kealey et al. (2006) reported a similar estimate of 0.51, however did not report standard errors. Corbet et al. (2013) reported a positive and favorable relationship between PNS and MOT of 0.80 and 0.86 in 18-month old Brahman and tropical composite bulls.

Druet et al. (2009) reported negative, and favorable genetic correlations between MOT and ABNO, abnormal head (HEAD), abnormal tail (TAIL), and abnormal cytoplasmic droplets (DROP) of -0.55, -0.56, -0.24, and -0.13, respectively; indicating that abnormalities were associated with low motility. Smith et al. (1989) reported similar estimates between MOT and PRIM and SEC, with estimates of -0.36, and -0.71, respectively. Durcocq and Humboldt (1995) findings were in agreeance with this negative, and favorable relationship as their study reported a genetic correlation of -0.68 between motility score (MOSC) and ABNO. Conversely, Kealey et al. (2006) reported a genetic correlation between MOT and PRIM of 0.57; with no standard error reported. Despite this, the Kealey et al. (2006) estimate of the correlation between MOT and SEC of -0.54 agrees with findings of Smith et al. (1989). Variation among these estimates could be accounted for due the breed differences in populations studied, as both Durcocq and Humboldt (1995) and Druet et al. (2009) utilized data sets taken from dairy sires in collection

facilities, while Smith et al. (1989) and Kealey et al. (2006) utilized BSE records taken from yearling beef bulls.

Literature describing the genetic correlations between total abnormalities and specific abnormality traits is sparse. Druet et al. (2009) is among the few to report estimates between ABNO and HEAD and TAIL; however, as expected, findings were positive and favorable with estimates of 0.71 and 0.78, respectively. Conversely, Druet et al. (2009) reported a correlation of -0.15, indicating a negative and unfavorable relationship between ABNO and DROP; however, this estimate was accompanied by a standard error of 0.34. Relationships between individual abnormalities also showed wide variation in strength and direction, as the genetic correlation between HEAD and TAIL was low, and positively correlated with an estimate of 0.13; while HEAD and DROP was moderate, and negatively correlated with an estimate of -0.43. Druet et al. (2009) reported phenotypic correlations measuring the relationship between ABNO and HEAD, TAIL, and DROP were 0.61, 0.77, and 0.36. The genetic and phenotypic correlations between ABNO and HEAD, and TAIL are in agreeance, however the wide distribution between the genetic and phenotypic correlations for ABNO and DROP indicate a larger environmental component impact for cytoplasmic droplets. A complete list of correlations between semen quality traits can be found in Table 4.

Genomic Predictions

The use of genomic prediction has steadily increased in usage and accuracy over time, and in doing so has had dramatic impacts on the prediction of polygenic traits within agriculture and human medicine (Adbollahi-Arpanahi et al. 2017; Taylor et al. 2018). Genomic predictions, coupled with assisted reproductive techniques, have allowed great advancements in female fertility within the dairy industry, through increased accuracy of prediction, while significantly

reducing generation interval (Garcia-Ruiz et al., 2016). Despite great advancements in prediction of female fertility, beef bull fertility has been primarily neglected (Adbollahi-Arpanahi et al. 2017; Taylor et al. 2018). Genomic prediction allows the use of information from a bull's entire genome to increase accuracy of selection and prediction regarding male fertility. Coupling genomic information with biological markers and phenotypic records would allow great advancements to be made within the field of bull fertility and ultimately reduce cost for producers while increasing genetic progress.

Genome-wide association studies have identified not only genomic regions but also individual genes association with male fertility and other multiple complex traits (Nicolini et al., 2018). Furthermore, some prediction models can incorporate weighting of individual variants to place more emphasis on these individual markers within the prediction process, thus allowing more accuracy and robustness to be obtained within these models (Abdollahi-Arpanahi et al., 2017). Genomic studies that have utilized beef bulls are few, however, studies utilizing dairy bulls have found several single nucleotide poly morphisms (SNPs) near or within genes related to male fertility traits.

Individual genes that are related to spermatogenesis have been identified including PIWIL3, located on chromosome 17, which has been linked to spermatozoa development in Holstein cattle (Nicolini et al., 2018). Gene PIWIL3 is responsible for encoding a member of the PIWI family, which is a group of germ specific proteins that are essential for spermatogenesis and control of post-transcriptional events ahead of translation. Additionally, TMEM119, is another gene located on chromosome 17 that has been linked to spermatogenesis. TMEM119, encodes a transmembrane protein that is actively involved in osteoblast differentiation, and ultimately is expressed in spermatocytes and spermatids in developing testis, with a mutation of

this gene being linked to reduced testis weight and sperm output (Mizuhashi et al. 2015; Nicolini et al. 2018). Han and Penagricano (2016) reported multiple genes with potential involvement in spermatogenesis including genes CKB and TDRD, both of which are located on chromosome 21. The gene CKB is responsible for encoding an enzyme called creatine kinase, which when found in elevated levels, has been linked to severe oligospermia and infertility in males (Gergely et al., 1999). In similar sense, TDRD encodes a helicase responsible for protecting the male germline during spermatogenesis by silencing transposable elements (Shoji et al. 2009).

Multiple genes have been linked to motility, including CDH18, SLC25A31, and KCNU1 (Ferencakivoc et al., 2017). Ferencakivoc et al. (2017) identified SCLC25A31, while studying inbreeding depression within a population of Austrian Fleckvieh bulls, finding that SCLC25A31 is connected to regulation of energy generation and consumption in the distal flagellum of spermatozoa and therefore influences motility. Additionally, Ferencakivoc et al. (2017) identified CDH18, which is a member of cadherin superfamily of integral membrane proteins that helps mediate calcium dependent cell to cell adhesion and significantly impacts motility of sperm (Pacheco et al., 2011). The KCNU1 gene is located on chromosome 27, and is known to encode testis-specific potassium channels; these potassium channels are known to be important for sperm motility and morphology (Schrieber et al., 1998; Ferencakivoc et al., 2017). Rezende et al. (2018) while studying a population of Jersey cattle identified SNPs within or near genes ZMYND10, SCL25A20, and DNAH3 which are all thought to influence motility. ZMYND10, located on chromosome 22, is expressed exclusively in the testis and plays a vital role in cilia integrity, while being linked to sperm dysmotility and male infertility (Moore et al.; 2013). The gene SCL25A20 is involved with ATP production and cell energy metabolism, while DNAH3 encode axonemal dynein heavy chains that are associated with the assembly of inner and outer

arms of sperm flagella and are associated with poor sperm motility (Rezende et al., 2018; Meng et al., 2024). Rezende et al. (2018) also identified a SNP on chromosome 11 with gene COX7A2L; which is responsible for encoding cytochrome c oxidate, which in turn is responsible for energy generation and promoting assembly for a respiratory super complex in addition to be speculated as being involved in motility.

Previous literature shows multiple candidate genes and SNPs related to percentage of living spermatozoa, including a SNP on chromosome 1 that is associated with the glutathione peroxidase 5 (GPX5) gene (Ferencakivoc et al., 2017). Gene GPX5 is proposed to be involved with encoding the Li 75p, an epididymal secretory sperm binding protein that assists with protecting the spermatozoa membrane during oxidative stress and preventing premature acrosome reaction, thus affecting the percentage of normal spermatozoa seen during collection (Hall et al., 1998; Ferencakovic et al., 2017). Furthermore Yin et al. (2005) identified the gene NYD-SP5 which is a testis growth promoter that targets IQCH and plays a role in regulation of spermatogenesis. Other genes including SPESP1 and SPATA18 where identified by Ferencakovic et al. (2017) and found to have significant impact on male fertility and morphology. The gene SPESP1 is highly expressed in the testis, and is a sperm equatorial segment protein that localizes the acrosome during post-meiotic stages of spermatogenesis and therefore helps secure the round, elongated spermatid shape found in ejaculated spermatozoa (Wolokowicz et al., 2008). Ferencakovic et al. (2017) found a negative interaction with the gene SPATA18 which encodes a “mitochondria eating protein”- p53. The protein encoded by SPATA18 is responsible for regulating the repair or degradation of unhealthy mitochondria due to damage; it is found at the highest levels within the testis and the flagellum of spermatozoa (Bornstein et al., 2011).

The dairy industry's use of SCR has enabled GWAS studies to find several genomic regions of interest as well as indicating numerous genes of interest. Han and Penagricano (2016) reported significant connections between multiple genes and SCR including KAT8, IGF1R, and RIMS1. The gene KAT8 encodes a histone acetylase protein, that regulate chromatin compaction. Han and Penagricano (2016) reported that the genetic region that explained the largest percentage of genetic variance in SCR was chromosome 21, which houses gene IGF1R- a key player in testicular development and spermatogenesis. The intron of gene Regulating Synaptic Membrance Exocytosis 1 (RIMS1) was found to be a the most significant SNP by Han and Penagricano (2016) in correlation to SCR, which makes sense regarding the multiple biological processes RIMS1 acts on including Sertoli cell support, maturation of spermatozoa, and motility; and when found in a low frequency among a population can be associated with poor conception rate. Other researchers have indicated multiple SNPs located near or within genes associated with SCR that vary greatly in practical function such as PDGFD and IP6K1, within the Jersey breed; both of which are directly implicated in testicular development and spermatogenesis (Rezende et al., 2017). Pacheco et al. (2019) reported significant associations between SCR and a genomic region closely related to genes FAM9B and TBL1X, both of which have been tied to testicular function and germ cell differentiation.

The continuing expansion of genomic selection could have major implications for bull fertility and the efficiency of cattle production. The use of GWAS and identification of SNPs that pertain to fertility have made a large impact in the dairy industry and have the potential to positively impact the beef industry (Garcia et al. 2016; Taylor et al. 2018). As the usage of genomic testing within the beef industry coincides with increased accuracy of SNP chips available in the market place, there is substantial opportunity for the beef industry to make

genetic improvement of male fertility traits (Taylor et al. 2018). The identification of the practical application of SNPs not only provides insight into the biology behind male fertility, but also provide basis for building genomic tools for selection. Though development of genomic selection tools has the potential to increase genetic change in male fertility traits, development and further inquiries into beef bull fertility genetic selection must be accompanied by increasing phenotypic trait data collection (Taylor et al. 2018; Berry et al., 2019).

Conclusion

Beef bull fertility is an extremely economically relevant trait that's impact on the efficiency of the beef industry warrants further research. Bull fertility must be improved through continuous advancements in research surrounding male fertility and development of bull selection tools for beef cattle producers (Trenkel and Williams, 1977; Berry et al. 2019). The economic losses due to sub fertile bulls demonstrates the opportunity for improving reproductive efficiency to not only increase genetic gain but also profitability among the cattle industry (Barth, 2000; Berry et al., 2014). The use of selection tools to increase performance of fertility traits has been demonstrated within the dairy industry and could be realized in the beef industry despite differences in production styles (Garcia et al., 2016). Heritability estimates for fertility traits are often low to moderate when estimates are available. The development and further adoption of BSE exams has allowed some exploration into genetic parameter estimation of semen quality traits and other fertility traits among beef sire. However, the literature surrounding this topic is still sparse and wide variations in population sizes and analytic protocols have led to varied estimations. Genetic correlations among semen quality traits reported are moderate and favorable indicating some opportunity for indirect selection to occur. Though adoption of AI is limited among beef producers, the wide utilization of BSE exams provides not only a cost-

effective practice for identifying sub fertile bulls, but its usage among the industry lends to the opportunity to collect important phenotypic data on large populations to support and expand genetic parameter estimations for fertility traits.

Genomic selection will continue to have a widespread impact within the beef industry as adoption of this technique continues to improve accuracy of selection and increase genetic gain among a multitude of traits. Currently, few studies have attempted to locate SNPs related to bull fertility and even fewer have attempted research within beef breeds. The utilization of genomic information in beef bull fertility could have substantial implications, if genomic prediction analysis is coupled with phenotypic trait data to provide meaningful connections for beef cattle producers.

Semen quality and other beef bull fertility traits significantly impact the efficiency of the U.S. beef herd and improvements in performance while increasing accuracy of selection could have major production applications while helping solve fertility questions among other species. Expansion of research in this field is needed due to limited literature and significant improvement needed not only within the U.S. beef herd, but the world.

Table 1 Reported heritability estimates for scrotal circumference. * indicates no reported standard error.

Trait	n	Estimate	Standard Error	Breed	Source
Scrotal Circumference, 6 months	2424	0.41	0.08	Tropical Composite	Corbet et al. (2013)
Scrotal Circumference, 6 months	717	0.36	0.06	Angus	Knights et al. (1984)
Scrotal Circumference, 6 months	4233	0.53	0.06	Hereford	Bourdon and Brinks (1985)
Scrotal Circumference, 12 months	549	0.4	0.09	Hereford, Angus, Red Angus	Smith et al. (1989)
Scrotal Circumference, 12 months	1282	0.56	*	Angus	Christmas et al. (2001
Scrotal Circumference, 12 months	1281	0.46	0.09	Angus	Garmyn et al. (2011)
Scrotal Circumference, 12 months	2424	0.46	0.09	Tropical Composite	Corbet et al. (2013)
Scrotal Circumference, 18 months	17648	0.4	0.02	Nellore	Silva et al. (2011)
Scrotal Circumference, 18 months	2424	0.43	0.09	Tropical Composite	Corbet et al. (2013)
Scrotal Circumference, 24 months	2424	0.44	0.09	Tropical Composite	Corbet et al. (2013)

Table 2 Reported heritability estimates for semen quality traits. * indicates no reported standard error

Trait	n	Estimate	Standard Error	Breed	Source
Spermatozoa motility	717	0.13	0.06	Angus	Knights et al. (1984)
	549	0.08	0.07	Hereford, Angus, Red Angus	Smith et al. (1989)
	2387	0.3	0.09	Normande	Ducrocq and Humbolt (1995)
	1282	0.07	*	Angus	Christmas et al. (2001
	841	0.22	0.09	Line 1 Hereford	Kealy et al. (2006)
	515	0.43	0.08	Holstein	Druet et al. (2009)
	1281	0.05	0.03	Angus	Garmyn et al. (2011)
	2424	0.15	0.05	Tropical Composite	Corbet et al. (2013)
	1212	0.31	0.06	Holstein	Suchoki and Syzda 2015
	787	0.37	0.03	Beef & Dairy	Berry et al. (2019)
Progressive Motility	515	0.13	0.13	Holstein	Druet et al. (2009)
	2424	0.15	0.05	Tropical Composite	Corbet et al. (2013)
Motility Score	2387	0.23	0.08	Normande	Ducrocq and Humbolt (1995)
	301	0.04	0.01	Beef/Dairy Cross	Gredler et al. 2007
	1212	0.26	0.05	Holstein	Suchoki and Syzda 2015
Percent Normal spermatozoa	549	0.07	0.06	Hereford, Angus, Red Angus	Smith et al. (1989)
	765	0.47	0.07	Angus	Yilmaz et al. (2004)
	841	0.35	0.1	Line 1 Hereford	Kealy et al. (2006)
	301	0.1	0.03	Beef/Dairy Cross	Gredler et al. 2007
	2424	0.41	0.1	Tropical Composite	Corbet et al. (2013)
Abnormal spermatozoa percentage/Total Abnormalities	2387	0.19	0.07	Normande	Ducrocq and Humbolt (1995)
	1282	0.29	n/a	Angus	Christmas et al. (2001
	515	0.25	0.1	Holstein	Druet et al. (2009)
	17648	0.15	0.01	Nellore	Silva et al. (2011)
	1281	0.25	0.07	Angus	Garmyn et al. (2011)
	549	0.31	0.09	Hereford, Angus, Red Angus	Smith et al. (1989)
Primary Abnormalities	1282	0.35	*	Angus	Christmas et al. (2001)
	841	0.3	0.1	Line 1 Hereford	Kealy et al. (2006)
	1281	0.27	0.07	Angus	Garmyn et al. (2011)
Secondary abnormalities	549	0.02	0.05	Hereford, Angus, Red Angus	Smith et al. (1989)
Secondary abnormalities	1282	0.26	*	Angus	Christmas et al. (2001
	841	0.33	0.09	Line 1 Hereford	Kealy et al. (2006)
	*	0.18	0.04	Angus	Butler et al. (2020)
	1281	0.23	0.08	Angus	Garmyn et al. (2011)
Percentage of spermatozoa with abnormal head	515	0.35	0.12	Holstein	Druet et al. (2009)
	841	0	0.08	Line 1 Hereford	Kealy et al. (2006)
Percentage of spermatozoa with abnormal tail	515	0.19	0.12	Holstein	Druet et al. (2009)
Percentage of spermatozoa with abnormal cytoplasmic droplet	515	0.19	0.08	Holstein	Druet et al. (2009)
Percentage of spermatozoa with abnormal cytoplasmic droplet	841	0.37	0.11	Line 1 Hereford	Kealy et al. (2006)
Percentage of spermatozoa with abnormal midpiece	841	0.16	0.09	Line 1 Hereford	Kealy et al. (2006)
Percentage of spermatozoa with bent tail	841	0.03	0.07	Line 1 Hereford	Kealy et al. (2006)
Percentage of spermatozoa with coiled tail	841	0.34	0.09	Line 1 Hereford	Kealy et al. (2006)

Table 3 Reported phenotypic(r_p) and genetic (r_g) correlations between scrotal circumference and semen quality traits. * indicates missing value

Correlations	n	rp	rg	Breed	Reference
Scrotal Circumference and Motility	549	0.13	-0.04	Hereford, Angus, Red Angus	Smith et al. 1989
	1282	*	0.56	Angus	Christmas et al. 2001
	1281	0.11	0.36	Angus	Garmyn et al. 2011
	2424	0.42	0.56	Tropical Composite	Corbet et al. 2013
Scrotal circumference and Percent of Normal Sperm	841	*	0.33	Line 1 Hereford	Kealy et al. 2006
	549	*	-0.36	Hereford, Angus, Red Angus	Smith et al. 1989
Scrotal Circumference and Percentage of Normal Sperm at 12 months of age	1639	0	0	Brahman	Corbet et al. 2013
	2424	0.55	0.31	Tropical Composite	Corbet et al. 2013
Scrotal Circumference and Percentage of Normal Sperm at 18 months of age	1639	0.5	0.31	Brahman	Corbet et al. 2013
	2424	0.21±0.16	0.22	Tropical Composite	Corbet et al. 2013
Scrotal Circumference and Percentage of Normal Sperm at 24 months of age	1639	0.22 ±.19	0.12	Brahman	Corbet et al. 2013
	2424	0.20 ±0.14	0.34	Tropical Composite	Corbet et al. 2013
Scrotal Circumference and Primary Abnormalities	841	*	-0.36	Line 1 Hereford	Kealy et al. 2006
	1281	-0.1	-0.19±0.17	Angus	Garmyn et al. 2011
	1282	*	-0.25	Angus	Christmas et al. 2001
Scrotal Circumference and Secondary Abnormalities	1281	-0.05	-0.11±0.19	Angus	Garmyn et al. 2011
	1282	*	-0.4	Angus	Christmas et al. 2001
	841	*	-0.45	Line 1 Hereford	Kealy et al. 2006
Scrotal circumference and Total abnormalities	841	-0.11	0.23±0.18	Angus	Garmyn et al. 2011

Table 4 Reported phenotypic (r_p) and genetic (r_g) correlations between semen quality traits. * indicates missing value

Correlations	n	rp	rg	Breed	Reference
Motility and abnormal sperm	515	-0.2	-0.55	Holstein	Druet et al. 2009
Motility and Mass Activity	2424	0.84	0.98	Tropical Composite	Corbet et al. 2013
Motility and Percentage of living spermatozoa	515	0.4	0.58	Holstein	Druet et al. 2009
	787	0.54	0.89	Beef & Dairy	Berry et al. 2019
Motility and percentage of normal spermatozoa	549	0.38	0.43	Hereford, Angus, Red Angus	Smith et al. 1989
	841	*	0.51	Line 1 Hereford	Kealy et al. 2006
	2424	0.56	0.77	Tropical Composite	Corbet et al. 2013
Motility and Percentage of spermatozoa with an abnormal head	515	0.17	-0.56	Holstein	Druet et al. 2009
Motility and percentage of spermatozoa with an abnormal tail	515	-0.11	-0.24	Holstein	Druet et al. 2009
	549	-0.31	-0.36	Hereford, Angus, Red Angus	Smith et al. 1989
Motility and Primary Abnormalities	841	*	0.57	Line 1 Hereford	Kealy et al. 2006
Motility and Progressive Motility	515	0.48	0.74	Holstein	Druet et al. 2009
Motility and Motility Score	515	0.66	0.88	Holstein	Druet et al. 2009
Motility and Secondary Abnormalities	549	-0.22	0.71	Hereford, Angus, Red Angus	Smith et al. 1989
	841	*	-0.54	Line 1 Hereford	Kealy et al. 2006
Motility score and percentage of living spermatozoa	2387	0.73	0.83	Normande	Ducrocq and Humbolt 1995
	515	0.31	0.61	Holstein	Druet et al. 2009
Motility score and percentage of normal spermatozoa	301	0.55	0.9	Beef/Dairy Cross	Gredler et al. 2007
Motility score and percentage of spermatozoa with an abnormal head	515	-0.15	-0.02	Holstein	Druet et al. 2009

Motility Score and Total Abnormalities	2387	-0.34	-0.68	Normande	Ducrocq and Humbolt 1995
	515	-0.16	-0.4	Holstein	Druet et al. 2009
Number of spermatozoa and abnormal spermatozoa	515	-0.05	-0.09	Holstein	Druet et al. 2009
Number of spermatozoa and motility	515	-0.03	-0.12	Holstein	Druet et al. 2009
	787	0.13	0.36	Beef & Dairy	Berry et al. 2019
Number of spermatozoa and motility score	717	*	-1.04	Angus	Knights et al. 1984
Number of spermatozoa and motility score	301	0.06	0.5	Beef/Dairy Cross	Gredler et al. 2007
Number of spermatozoa and motility score	515	0.01	-0.24	Holstein	Druet et al. 2009
Number of spermatozoa and percentage of living spermatozoa	515	0.03	-0.18	Holstein	Druet et al. 2009
Number of spermatozoa and percentage of normal spermatozoa	301	0.07	0.54	Beef/Dairy Cross	Gredler et al. 2007
Number of spermatozoa and percentage of spermatozoa with an Abnormal cytoplasmic droplet	515	-0.05	0.33	Holstein	Druet et al. 2009
Number of spermatozoa and percentage of spermatozoa with an Abnormal head	515	-0.02	-0.38	Holstein	Druet et al. 2009
Number of spermatozoa and percentage of spermatozoa with an Abnormal tail	515	-0.03	0.14	Holstein	Druet et al. 2009

References

Abdollahi-Arpanahi, R., G. Morota, and F. Penagaricano. 2017. Predicting bull fertility using genomic data and biological information. J. Dairy. Sci. 100: 9656-9666.

Barth, A.D, and C.L. Waldner. 2002. Factors affecting breeding soundness classification of beef bulls examined at the Western College of Veterinary Medicine. Can Vet J. 43:274-284.

Barth, A. D. 2000. Bull Breeding Soundness Evaluation, 2nd ed. Saskatoon, Saskatchewan, (CA): West. Can. Assoc. Bovine Pract.

Berry, D.P., B. Eivers, G. Dunne, S. McParland. 2019. Genetics of bull semen characteristics in a multi-breed cattle population. Therio. 123:202-208.

Berry, D.P., E. Wall, J.E. Pryce. 2014. Genetics and genomics of reproductive performance in dairy and beef cattle. Animal Consortium. 8:105-121.

Berry, D.P., R.D. Evans, S. Mc Parland. 2010. Evaluation of bull fertility in dairy and beef cattle using cow field data. Therio. 75:172-181.

Bornstein, C., R. Brosh, A. Molchadsky, S. Madar, I. Kogan-Sakin, I. Goldstein, D. Chakravarti, E. R. Flores, N. Goldfinger, R. Sarig, and V. Rotter. 2011. SPATA18, a spermatogenesis-associated gene, is a novel transcriptional target of p53 and p63. Mol. Cell. Biol. 31:1679–1689. https://doi.org/10.1128/MCB.01072-10.

Bourdon, R.M., and J.S. Brinks, 1986. Scrotal circumference in yearling Hereford bulls: Adjustment factors, heritabilities and genetic and environmental phenotypic relationships with growth traits. J. Anim. Sci. 62:958.

Brinks, J.S., M.J. McInerney, and P.J. Chenowth. 1978. Relationship of age at puberty in heifers to reproductive traits in young bulls. Proc. West. Sect. Am. Soc. Anim. Sci. 29:28.

Boldt, R.J., S.E. Speidel, M.G. Thomas, and R.M. Enns. 2018. Genetic parameters for fertility and production traits in Red Angus cattle. J. Anim. Sci. 96:4100-4111.

Bullock, D. and D.W. Moser. 2021. The importance of sire selection. Beef Sire Selection Manual. 3rd edition. National Beef Cattle Evaluation Consortium.

Butler, M. L., A.R. Hartman, J.M. Bormann, R.L. Weaber, D.M. Grieger, M.M. Rolf. 2021. Genetic parameter estimation for beef bull semen attributes. J. Anim. Sci. 99:1-11. doi.org/10.1093/jas/skab013

Cammack, K.M., M.G. Thomas, and R.M. Enns. 2009. Review: Reproductive traits and their heritabilities in beef cattle. Pr. Anim. Sci. 25: 517-528.

Chenoweth, P.J., 1980. Bull fertility. Modern veterinary practices. 61: 987-991.

Chenoweth, P.J., 1981. Libido and mating behavior in bulls, boars, and rams. A review. Therio. 16: 155-177.

Chenoweth, P.J. 2005. Genetic sperm defects. Theriogenology. 64:457-468.

Chenoweth, P.J. 2002. Bull breeding soundness exams and beyond. In: Proceedings The Applied Reproductive Strategies in Beef Cattle Workshop. 5-6 Sept 2002. Manhattan, Kansas. pp. 174-181.

Christmas, R.A., D.W. Moser, M.F. Spire, J.M. Sargeant and S.K. Tucker. 2001. Genetic relationships among breeding soundness traits in yearling bulls. Kansas Agricultural Experiment Station Research Reports: Vol. 0: Iss. 1. doi.org/10.4148/2378-5977.1712

Coulter G.H. and R.H. Foote. 1975. Relationship of testicular weight to age and scrotal circumference of Holstein bulls. J. Dairy Sci. 59:730-732.

Coulter G.H. and R.H. Foote. 1979. Bovine testicular measurements as indicators of reproductive performance and their relationship to productive traits in cattle. Therio. 11:297-311.

Coulter G.H., T. Rounsaville, and R.H. Foot. 1976. Heritability of testicular size and consistency in Holstein bulls. J. Anim. Sci. 43: 9-12.

Druet, T., S. Fritz, S. Sellem, B. Basso, O. Ge, L. Salas-Cortes, P. Humblot, X. Druart, and A. Eggen. 2009. Estimation of genetic parameters and genome scan for 15 semen characteristics traits of Holstein bulls. J. Anim. Breed. Genet. 136: 269-277.

Ducrocq, V. and P. Humblot. 1995. Genetic characteristics and evolution of semen production of young Normande bulls. Livest. Prod. Sci. 41: 1-10.

Enciso M., H. Cisale, S. D. Johnston, J. Sarasa, J. L. Fernández, J. Gosálvez. 2011. Major morphological sperm abnormalities in the bull are related to sperm DNA damage. Theriogenology. 76(1):23-32. doi:10.1016/j.theriogenology.2010.12.034

Evans, J.L., B.L. Golden, R.M. Bourdon, and K.L. Long. 1999. Additive genetic relationships between heifers pregnancy and scrotal circumference in Hereford cattle. J. Anim. Sci. 77:2621-2628.

Ferenčaković, M., J. Sölkner, M. Kapš, and I. Curik. 2017. Genome-wide mapping and estimation of inbreeding depression of semen quality traits in a cattle population. J. Dairy Sci. 100: 4721-4730

Garcia-Ruiz, A., J.B. Cole, P.M. VanRaden, G.R. Wiggans, F.J. Ruiz-Lopez, C.P. Van Tassell. 2016. Changes in genetic selection differentials and generation intervals in U.S. Holstein dairy cattle as a result of genomic selection. Proceedings of the National Academy of Sciences USA 113 E3995-E4004.

Garmyn, A. J., D.W. Moser, R.A. Christmas, and J.M. Bormann. 2011. Estimate of genetic parameters and effects of cytoplasmic line on scrotal circumference and semen quality traits in Angus bulls. J. Anim. Sci. 89:693-698. doi:10.2527/jas.2010-3534

Gergely, A, J. Szollosi, G. Falkai, B. Resch, L. Kovacs, G. Huszar. 1999. Sperm creatine kinase activity in normospermic and oligozospermic Hungarian men. J Assist Reprod Genet. 16(1):35–40

Gipson, T.A., D.W. Vogt, J.W. Massey, M.R. Ellersieck. 1985. Associations of scrotal circumference with semen traits in young beef bulls. Therio. 24:217-225.

Graham, J. K., and E. Mocé. 2005. Fertility evaluation of frozen/thawed semen. Theriogenology. 64(3):492-504. doi:10.1016/j.theriogenology.2005.05.006

Gredler, B. C. Fuerst-Waltl, H. Schwarzenbacher, and J. Solkner. 2007. Genetic parameters for semen production traits in Austrian dual-purpose Simmental bulls. Repro. Domest. Anim. 42: 326-328.

Hahn, J., R.H. Foote, and G.E. Seidel, J.R. 1969. Testicular growth and related sperm output in dairy bulls. J. Anim. Sci. 29:41-47.

Hall, L., K. Williams, A. C. Perry, J. Frayne, and J.A. Jury. 1998. The majority of human glutathione peroxidase type 5 (GPX5) transcripts are incorrectly spliced: implications for the role of GPX5 in the male reproductive tract. Biochem J. 333: 5-9.

Han, Y., and F. Peñagaricano. 2016. Unravelling the genomic architecture of bull fertility in Holstein cattle. BMC genetics 17: 143.

Kastelic, J.P., J.C. Thundathil. 2008. Breeding soundness evaluation and semen analysis for predicting bull fertility. Reprod Dom Anim. 43 (Suppl. 2) 368-373. doi:10.1111/j.1439-0531.2008.01186.x

Kealy, C.G., M.D. MacNeil, M.W. Tess, T.W. Geary, and R.A. Bellows. 2006. Genetic parameter estimates for scrotal circumference and semen characteristics of line 1 Hereford bulls. J. Anim. Sci. 84:283-290. Doi:10.2527/2006.842283x

Kennedy, S.P., J.C. Spitzer, F.M. Hopkins, H.L. Higdon III, W.C. Bridges Jr. 2002. Breeding soundness evaluations of 3648 yearling beef bulls using the 1993 Society for Theriogenology guidelines. Theriogenology 58:947-961, 2002

Martinez-Velazquez, G., K.E. Gregory, G.L. Bennett, L.D. Van Vleck. 2003. Genetic relationships between scrotal circumference and female reproductive traits. J. Anim. Sci. 83: 395-400

Martin, L.C., J.S. Brinks, R.M. Bourdon and L.V. Cundiff. 1992. Genetic effects on beef heifer puberty and subsequent reproduction. J. Anim. Sci. 70:4006-4017.

Massey, J. 1993. Understanding and using sire summaries: BIF fact sheet. University of Missouri Extension.

McAllister, C.M., S.E. Speidel, D.H. Crews Jr., and R.M. Enns. 2011. Genetic parameters for intramuscular fat percentage, marbling score, scrotal circumference, and heifer pregnancy in Red Angus cattle. J. Anim. Sci. 89:2068-2072.

McWhorter, T.M., J.L. Hutchinson, H.D. Norman, J.B. Cole, G.C. Fok, D.A.L. Lourenco, P.M. VanRaden. 2020. Investigating conception rate for beef service sires bred to dairy cows and heifers. J. Anim. Sci. 103:10374-10382

Menegassi, S.R.O, Julio Otavio Jardim Barcellos, Vinicius do Nascimento Lampert, Joao Batista Souza Borges, Vanessa Peripolli. 2011. Bioeconomic impact of bull breeding soundness examination in cow-calf systems. Brazilian Society of Animal Science. 40:441-447.

Meng, G.Q., Wang, Y., Luo, C., Tan, Y.M., Li, Y., Tan, C., Tu, C., Zhang, Q.J., Hu, L., Zhang, H. and Meng, L.L., 2024. Bi-allelic variants in DNAH3 cause male infertility with asthenoteratozoospermia in humans and mice. *Human Reproduction Open*, *2024*(1), p.hoae003.

Mizuhashi, K., T. Chaya, T. Kanamoto, Y. Omori, and T. Furukawa. 2015. Obif, a transmembrane protein, is required for bone mineralization and spermatogenesis in mice. PloS One. 10: e0133704.

Moser, D.W., J.K. Bertrand, L.L. Benyshek, M.A. McCann, T.E. Kiser.1996. Effects of selection for scrotal circumference in Limousin bulls on reproductive and growth traits of progeny. J. Anim. Sci. 74:2052-2057.

Nicolini, P., R. Amorín, Y. Han, and F. Peñagaricano. 2018. Whole-genome scan reveals significant non-additive effects for sire conception rate in Holstein cattle. BMC Genomics. 19: 14.

Norman, H.D., J.L. Hutchison, and P.M. VanRaden. 2011. Evaluations for service-sire conception rate for heifer and cow inseminations with conventional and sexed semen. J. Dairy Sci. 94:6135-6142.

Norman, H.D., J.L. Hutchison, J.R. Wright. 2008. Sire conception rate: New national AI bull fertility evaluation. AIPL Research Report. Sire Conception Rate (AIPL Res. Rep. SCR1 (7-08) (arsusda.gov)

Ortega, M.S., J.G.N. Moraes, D.J. Patterson, M.F. Smith, S.K. Behura, S. Poock, and T.E. Spencer. 2018. Influences of sire conception rate on pregnancy establishment in dairy cattle. Bio. Repro. 99:1244-1254.

Pacheco, S. E., E. A. Houseman, B. C. Christensen, C. J. Marsit, K. T. Kelsey, M. Sigman, and K. Boekelheide. 2011. Integrative DNA methylation and gene expression analyses identify DNA packaging and epigenetic regulatory genes associated with low motility sperm. PloS one. 6: e20280.

Palasz A.T., W.F. Cates, A.D. Barth and R.J Mapletoft. 1994. The relationship between scrotal circumference and quantitative testicular traits in yearling beef bulls. Soc. Therio. 42:715-726.

Parkinson, T.J. 2004. Evaluation of fertility and infertility in natural service bulls. Vet. J. 168:215-229.

Rezende, F. M., J. P. Nani, and F. Peñagaricano. 2019. Genomic prediction of bull fertility in US Jersey dairy cattle. J Dairy Sci. 102: 3230-3240.

Saacke, R.G. 2008. Sperm morphology: its relevance to compensable and uncompensable traits in semen. Therio. 70:473-478.

Saacke, R.G., J.C. Dalton, S. Nadir, R.L. Nebel, J.H. Bame. 2000. Relationship of seminal traits and insemination time to fertilization rate and embryo quality. Anim. Reprod Sci. 2, 663-667.

Saacke, R.G., S. Nadir, R.L. Nebel. 1994. Relationship of semen quality to sperm transport, fertilization, and embryo quality in ruminants. Therio. 41, 45-50.

Schreiber, M., A. Wei, A. Yuan, J. Gaut, M. Saito, and L. Salkoff. 1998. Slo3, a novel pH-sensitive K+ channel from mammalian spermatocytes. J Bio Chem. 273: 3509-3516.

Senger, P.L. 2012. Pathways to pregnancy and parturition, 3rd ed. Redmond (OR): Current Conceptions, Inc.

Shoji M., T. Tanaka, M. Hosokawa, M. Reuter, A. Stark, Y. Kato, G. Kondoh, K. Okawa, T. Chujo, T. Suzuki. 2009. The TDRD9-MIWI2 complex is essential for piRNA mediated retrotransposon silencing in the mouse male germline. Dev Cell.;17(6):775–87.

Silva, M.R., V.B. Pedrosa, J.C.B. Silva, J.P. Eler, J.D. Guimaraes, and L.G. Albuquerque. 2011. Testicular traits as selection criteria for young Nellore bulls. J. Anim. Sci. 89: 2061-2067.

Smith, B.A., J.S. Brinks and G.V. Richardson. 1989. Estimation of genetic parameters among breeding soundness examination components and growth traits in yearling bulls. J. Anim. Sci. 67:2892-2896.

Suchocki, T., J. Szyda. 2015. Genome-wide association study for semen production traits in Holstein-Friesian bulls. J. Dairy Sci. 98:5774-5780.

Taylor, J.F., R.D. Schnabel, and P. Sutovsky. 2018. Review: Genomics of bull fertility. Anim. Cons. 12:51, 172-183.

Taylor, J.F., R.D. Schnabel, and P. Sutovsky. 2018. Identification of genomic variants causing sperm abnormalities and reduced male fertility. Anim. Repr. Sci. 194:57-62.

Trenkle, A. and R. L. Willham. 1977. Beef production efficiency: The efficiency of beef production can be improved by applying knowledge of nutrition and breeding. Science 198:1009-1015.

Rezende, F.M. G.O. Dietsch, and F. Penagaricano. 2018. Genetic dissection of bull fertility in U.S. Jersey dairy cattle. Anim. Gen.49:393-402.

USDA. 2020. Part II:reference of beef cow-calf management practices in the United States. United States Department of Agriculture National Animal Health Systems Monitoring System Beef Cow-Calf studies. Ft. Collin (CO). Available at: www.aphis.usda.gov beefcowcalf/downloads/beef2017/Beef2017_dr_PartI.pdf [accessed March 7,2021]

USDA-NASS. 2021. July Annual Cattle Report. National Agricultural Statistic Service, United States Department of Agriculture. Cattle 07/23/2021 (usda.gov). ISSN: 1948-9099

VanDemark, N.L. 1956. Quantitative aspects of semen production in bulls. IInd Int. Congr. On An. Reprod., Cambridge, Plenary Papers:80.

Willett, E.L. and J.I. Ohms. 1957. Measurement of testicular size and its relation to production of spermatozoa by bulls. 1559-1569.

Yilmaz, A. M.E. Davis, and R.C.M Simmen. 2004. Estimation of (co)variance components for reproductive traits in Angus beef cattle divergently selected for blood serum IGF-I concentration. J Anim. Sci. 82: 2285-2292.

Yin, L. L., J. M. Li, Z. M. Zhou, and J. H. Sha. 2005. Identification of a novel testis-specific gene and its potential roles in testis development/spermatogenesis. Asian J Andro. 7: 127-137.