Proceedings, Applied Reproductive Strategies in Beef Cattle
September 6-7, 2023; Cheyenne, WY

MALE FERTILITY IN BEEF CATTLE

Danielle M. Stock, Jennifer M. Bormann, Megan M. Rolf

Kansas State University, Manhattan, Kansas

Introduction

Reproductive performance and fertility are critical to the economic profitability of a beef operation. Fertility is broadly defined as the ability to conceive viable offspring, but males and females must be sufficiently fertile to produce a viable embryo (Utt, 2016). A beef herd's overall fertility rate is generally measured by its pregnancy rate or the percentage of cows that successfully became pregnant during their first, second, or third estrus cycle of the breeding season (Hopper, 2014). Conception is impacted by various factors, including age, nutrition, health, and environmental conditions (Chacón et al., 2002; Nichi et al., 2006; Barth, 2007; Koivisto et al., 2009). Furthermore, genetic factors such as the inbreeding coefficient (Karoui et al., 2011) and breed composition(Barth and Waldner, 2002; Koivisto et al., 2009) can impact reproductive traits.

Most genetic selection tools available to beef producers focus on female fertility. Expected progeny differences (EPD) have been created to estimate the probability of pregnancy in first-calf heifers, the probability of calving as a three-year-old given she calved as a first-calf heifer, and the probability that a female will produce a calf every year to at least six years of age (Doyle et al., 2000; RAAA, 2018; AGA, 2022). Several beef breeds have published a scrotal circumference EPD which predicts the ability of an animal to influence scrotal size in their offspring (Angus Beef Bulletin, 2015). However, it does not account for semen production or semen quality measures, which can be major determinants of conception. Heritability estimates and genetic correlations that have been published for scrotal circumference, semen production measures, and semen quality measures illustrate the potential for increasing beef bull fertility.

Genetic Parameters

Tables 1 and 2 outline the reported heritabilities published within the scientific literature for semen production and quality traits, respectively. All studies from scientific literature utilize a best linear unbiased prediction (BLUP) univariate or multivariate animal model. The two exceptions were Smith et al. (1989) and Kriese et al. (1991), who analyzed their data with a sire model and least square procedures. Each study's model had varying fixed effects, but most included bull age, season, and year. Studies that utilized information from artificial insemination (AI) centers generally included fixed effects such as the day of the week when semen collection occurred, ejaculate number, and semen collector.

Scrotal Circumference

Scrotal circumference is correlated with daily spermatozoa production, semen quality, paired testis weight, and offspring reproductive performance (Lunstra et al., 1978; Coulter and Foote, 1979; Brito et al., 2002; Barth, 2007). The SC is measured by gently forcing the testes to the bottom of the scrotum and placing the measuring tape level with the skin around the widest part of the scrotum (Hopper, 2014). Heritability estimates in the literature for SC range from 0.36 to 0.75. In studies examining British-type yearling bulls, moderate heritability estimates were reported ranging from 0.36 to 0.56 (Neely et al., 1982; Knights et al., 1984; Kriese et al., 1991; Christmas et al., 2001). Scrotal circumference in *Bos indicus* bulls has been reported as moderately to highly heritable. Carvalho et al. (2023) estimated a SC heritability of 0.75 in 18-month-old Nellore bulls. Another study in Nellore bulls estimated a moderate heritability for SC (Silva et al., 2013). The Corbet et al. (2013) study estimated SC heritabilities in 6, 12, 18, and 24-month-old Brahman and Tropical composite bulls and reported similar heritability estimates within each breed. Therefore, age may have less effect on SC heritability than breed origin.

Semen Production Traits

Volume is the total amount of semen in an ejaculate, measured in millimeters (Butler et al., 2021). Most studies reported low heritability estimates for volume. Kealey et al. (2006) and Kapš et al. (2000) reported low heritability estimates for volume in semen collected from Line 1 Hereford and Simmental bulls, respectively, during a BSE. Carvalho et al. (2023) published a similar heritability estimate for volume in Nellore yearling bulls. Estimates from beef bulls at AI centers range from 0.11 to 0.32 (Butler et al., 2021; Rostellato et al., 2021; Cesarani et al., 2023). Heritability estimates from AI dairy bull semen range from 0.18 to 0.65 (Ducrocq and Humblot, 1995; Atagi et al., 2017), with most between 0.22 and 0.26 (Mathevon et al., 1998; Druet et al., 2009; Karoui et al., 2011; Suchocki and Szyda, 2015). The higher heritabilities reported in dairy compared to beef cattle could be due to breed. The studies with data from AI centers could have higher estimates than BSE studies because some centers combine multiple ejaculates into one collection day observation.

Semen concentration is the density of sperm cells in an ejaculate, measured in millions/ milliliter. Most estimates for concentration are lowly heritable in beef and dairy AI bull populations. However, one study reported a moderate to high value for concentration heritability in a population of Holstein bulls (Mathevon et al., 1998). The Mathevon et al. (1998) study only had 137 bulls in their population, which is smaller than other populations in the literature. Interestingly, heritability estimates for concentration from AI dairy bulls tended to be higher than estimates from beef bull semen (Knights et al., 1984; Gredler et al., 2007; Butler et al., 2021).

The total number of spermatozoa in an ejaculate is calculated by multiplying the volume and concentration values. The number of spermatozoa is expressed in millions. Taylor et al. (1985) noted that the accuracy of genetic estimates for number of spermatozoa in a multi-trait model could be affected by it being a function of two other traits. Heritability estimates for number of spermatozoa range from 0.03 to 0.38 in beef and dairy studies (Knights et al., 1984; Taylor et al., 1985; Mathevon et al., 1998; Butler et al., 2021). Similar heritability estimates have been reported in Alpine and Saanen goats (Furstoss et al., 2009). Estimate differences could be attributed to population size or model effects.

Semen Quality Traits

Semen motility is the percentage of sperm cells progressively moving forward in an ejaculate. Multiple studies have determined that motility is an essential indicator of fertility in beef (Chenoweth and Lorton, 2021), sheep (David et al., 2015), and humans (Nel-Themaat et al., 2006). Christensen et al. (1999) reported that motility was statistically correlated to non-return rates. Heritability estimates for beef bull motility obtained from yearling bull BSEs had low heritability estimates (Smith et al., 1989; Christmas et al., 2001; Garmyn et al., 2011). Heritability estimates for motility phenotypes obtained at bull semen collection facilities were higher than those recorded from BSEs and ranged from 0.12 to 0.37 (Ducrocq and Humblot, 1995; Mathevon et al., 1998; Kealey et al., 2006; Suchocki and Szyda, 2015; Berry et al., 2019; Butler et al., 2021). The variation in heritability estimates for motility could be due to the subjectivity of the measurement. Other causes could be data collection method, breed differences, or varying fixed effects in the study's model. The heritability of motility is important to bull fertility because if sperm are not motile enough to traverse the female tract, the sperm cannot fertile the ovum (Chenoweth and Lorton, 2021).

Heritability estimates for the percentage of morphologically normal spermatozoa (%Norm) in literature have a wide range of values. Smith et al. (1989) reported a low heritability of 0.07±0.06 from their study of BSEs from Hereford, Angus, and Red Angus bulls. Recent studies reported similar estimates in Angus and Italian Simmental AI bull populations (Butler et al., 2021; Cesarani et al., 2023). Conversely, Kealey et al. (2006) and Corbet et al. (2013) published moderate estimates for %Norm in Line 1 Hereford and Tropical Composite yearling bulls, respectively.

In literature, sperm abnormality traits have been reported in various ways. Primary abnormalities most likely arise during spermatogenesis. Common primary abnormalities are abnormal heads, midpieces, and proximal cytoplasmic droplets (Kealey et al., 2006). Secondary abnormalities are caused by faulty epididymal sperm maturation. Spermatozoa with bent tails, coiled tails, or distal cytoplasmic droplets are considered to have a secondary abnormality. The Kealey et al. (2006) study suggested that genetics could greatly influence secondary abnormalities. Heritability estimates for primary abnormalities in the literature ranged from 0.03 to 0.35 (Smith et al., 1989; Christmas et al., 2001; Garmyn et al., 2011; Butler et al., 2021). Butler et al. (2021) utilized semen collected at an AI center on bulls of various ages. In contrast, the other studies utilized BSE data from yearling bulls. Those same studies reported low heritability estimates for secondary abnormalities (Christmas et al., 2001; Garmyn et al., 2011; Butler et al., 2021).

Major defects decrease fertility when present in an ejaculate. The classification of spermatozoa as a major abnormality includes proximal cytoplasmic droplets, head, and midpiece abnormalities, and any single abnormality with significant presence in the ejaculate (Menon et al., 2011). Minor defects do not significantly impact fertility unless present in a high percentage. Looped tails, distal cytoplasmic droplets, and detached heads would be classified as minor (Menon et al., 2011). Two studies estimated low heritabilities for major and minor abnormalities in Nellore AI bulls. Carvaho et al. (2023) reported an estimate of 0.15 for major abnormalities and 0.04 for minor defects. Silva et al. (2013) reported similar heritability estimates for the percentage of major and minor defects.

In 2016, a differential counting scheme was adopted by the Society of Theriogenology (SFT), which groups defects under the classifications of head, midpiece, and principal piece (tail) abnormalities (Society for Theriogenology, 2018). Duret et al. (2009) reported a moderate heritability estimate for head abnormalities and a low estimate for tail abnormalities.

Heritability estimates for total abnormalities in an ejaculate range from 0.15 to 0.3. Christmas et al. (2001) and Garmyn et al. (2011) reported estimates of 0.29 and 0.25, respectively, for Angus bulls. Estimates of 0.15 and 0.30 were reported in Nellore bulls by Carvalho et al. (2023) and Silva et al. (2013), respectively. Ducrocq and Humblot (1995) published a total abnormality estimate of 0.19 in dairy bulls.

Heritability estimates appear to be highest when abnormalities are classified by anatomical location on the sperm cell or when analyzed as a total amount. However, more research needs to be done on the genetic effects and heritability of sperm abnormalities.

Overall, many of the heritability estimates for semen production and quality traits are low to moderate, but most of the standard errors were small, and the estimates were different from zero, so it is possible to improve male fertility. For example, the Canadian Dairy Industry released a daughter fertility (DF) index for their national breeding program (Fleming et al., 2019) with heritability estimates for the traits within the DF index ranging from 0.02 to 0.07. During the first five years of genomic implementation, the national estimated breeding value (EBV) for the DF index increased by 1.78 EBV points per year (Canadian Dairy Network, 2017). Similar genetic gains could be made in the United States beef population if genetic tools are made available to producers.

Genetic and Phenotypic Correlations

Scrotal Circumference with Semen Production Traits

Table 3 presents the reported correlations between SC and sperm production traits, but the research is limited in the literature. Scrotal circumference is the easiest measurement for veterinarians to take and is less subjective than other measurements taken during a BSE, which is why understanding genetic and phenotypic correlations between SC and ejaculate characteristics is important for improving bull fertility. Barth (2007) published that SC measurements were highly phenotypically correlated with paired testes’ weight and daily sperm production. Kealey et al. (2006) reported favorable genetic correlations between SC and volume and concentration. The favorable correlations are promising for improving male fertility because SC is moderate to highly heritable.

Scrotal Circumference with Semen Quality Traits

Many studies published favorable genetic and phenotypic correlations between SC and semen motility which are presented in Table 3. Corbet et al. (2013) published a strong genetic correlation and moderate phenotypic correlation in 12-month-old Brahman bulls. Christmas et al. (2001) and Kealey et al. (2006) reported favorable, moderate genetic correlations of 0.56 and

0.34, respectively, in British-type bulls. However, Smith et al. (1989) reported a negative genetic correlation of -0.04±0.40 between SC and motility, but the estimate was not different than zero.

Corbet et al. (2013) tested the phenotypic and genetic correlations between SC and %Norm in bulls at 12, 18, and 24 months. The authors reported positive, favorable phenotypic and genetic correlation estimates (Corbet et al., 2013). However, Smith et al. (1989) reported an unfavorable, negative genetic correlation. The difference in results could be because the Smith et al. (1989) estimates were from a small population (549) of yearling Hereford bulls, and the Corbet et al. (2013) utilized a large population of 12, 18, and 24-month-old Brahman and Tropical Composite bulls.

Silva et al. (2013) found negative, low genetic correlations between SC and sperm defects in yearling Nellore bulls. Other studies have reported negative genetic associations between SC and sperm traits, with estimates ranging from -0.19 to -0.36, -0.11 to -0.45, and -0.12 to -0.23, for genetic correlations between SC and primary, secondary, and total sperm defects, respectively (Knights et al., 1984; Kealey et al., 2006; Garmyn et al., 2010). These results suggest that direct selection to increase SC could reduce abnormal spermatozoa, which could improve the semen quality of young bulls and subsequently increase the number of males passing a BSE.

Semen Production Traits

Most phenotypic and genetic correlations reported between volume and concentration are negative and unfavorable because as volume increases, concentration decreases. Druet et al. (2009) and Burren et al. (2019) estimated moderate genetic correlations in dairy AI bulls. A lower estimate was published by Rostellato et al. (2021) in a population of Piemontese bulls. Phenotypic correlations ranged from -0.01 to -0.35 (Berry et al., 2019; Rostellato et al., 2021, respectively). Table 3 presents the reported correlations.

Literature estimates for correlations between number of spermatozoa and volume are varied. Gredler et al. (2007) estimated the strong phenotypic and genotypic correlations in a population of dual-purpose Fleckvieh bulls. Similarly, Butler et al. (2021) estimated phenotypic and genetic correlation to be 0.75 ± 0.08 and 0.66 ± 0.01, respectively. While Rostellato et al. (2021) and Druet et al. (2009) published moderate genetic correlation estimates between number of spermatozoa and volume. The published genetic correlations between concentration and number of spermatozoa are moderate in strength. Druet et al. (2009) reported one of the lower estimates between number of spermatozoa and concentration and it has a large standard error that could be attributed to population size. Higher genetic correlation estimates were published by Gredler et al. (2007), Butler et al. (2021), and Rostellato et al. (2021). Literature estimates for phenotypic correlations range from 0.52 to 0.71 (Gredler et al., 2007; Druet et al., 2009; Butler et al., 2021). The published genetic and phenotypic correlations between number of spermatozoa and volume and concentration should be expected as number of spermatozoa is a function of the two.

Semen Production Traits with Semen Quality

Genetic correlation estimates between volume and initial motility are mostly weak and positive as summarized in Table 3. Relatively few studies have quantified the interrelationships between volume and morphology. Butler et al. (2021) reported a positive genetic correlation between volume and primary abnormalities. While their estimate between volume and secondary abnormalities was negative and weak. Both estimates were not different than zero (Butler et al., 2021). Druet et al. (2009) reported similar results between volume and numerous individual sperm defects. Berry et al. (2009) reported unfavorable, positive phenotypic and genetic correlation estimates between volume and total abnormalities. Conversely, Ducrocq and Humblot (1995) reported favorable weak correlations between the two traits.

Berry et al. (2019) found a low, favorable genetic correlation between concentration and motility. Similarly, Karoui et al. (2011) reported a moderate, positive correlation between the two traits, but the authors did not report a standard error. Butler et al. (2021) reported negative phenotypic correlations between concentration and primary and secondary abnormalities, so as concentration increases, sperm abnormalities would decrease, which is similar to the results seen in SC correlations. Druet et al. (2009) published many genetic correlations between concentration and various sperm defects, but most estimates were not different than zero. Genetic correlations between concentration and percentage of viable spermatozoa have been estimated to be moderate and positive in several studies (Gredler et al., 2007; Druet et al., 2009; Berry et al., 2019).

Atagi et al. (2017) and Butler et al. (2021) both reported positive and favorable genotypic and phenotypic correlations between number of spermatozoa and motility. Phenotypic correlations for number of spermatozoa and semen morphology are low and negative (Druet et al., 2009; Butler et al., 2021). Butler et al. (2021) genetic correlations between number of spermatozoa and primary and secondary abnormalities both had large standard errors. Knights et al. (1984) reported that correlations in their study indicated that selection to increase the number of spermatozoa would be accompanied by an increase in sperm quality. More research is necessary on the effects between semen production traits and sperm morphology because many current estimates are not different from zero.

Semen Quality Traits

Table 3 also includes genetic and phenotypic correlation between semen quality traits. Butler et al. (2021) estimated a strong and favorable genetic correlation between motility and %Norm. In contrast, Smith et al. (1989; 0.43) and Kealey et al. (2006; 0.51) reported only a moderate, favorable correlation between motility and %Norm. Genetic correlations between motility and primary and secondary abnormalities reported in the literature but some estimates are not statistically significant (Smith et al., 1989; Butler et al., 2021). Druet et al. (2009) reported motility had negative, favorable genetic correlations with head, tail, and total sperm abnormalities. These results indicate that lower motility is associated with a higher percentage of abnormal sperm cells; however, selecting to increase motility could decrease the number of abnormal sperm in an ejaculate.

Current State of Male Fertility Selection Tools

The only available male fertility selection tool for beef producers is the SC EPD. The SC EPD evaluation predicts the difference in an animal’s ability to transmit scrotal circumference to its male offspring compared to other animals (AGA, 2022; AAA, 2023). Moser et al. (1996) reported that Limousin bulls with higher SC EPDs tended to have fewer abnormalities in their semen, and their daughter reached puberty at significantly earlier ages when compared to bulls with lower SC EPDs. Butler et al. (2021) utilized the BLUPF90 family of programs (Misztal et al., 2014) to correlate SC EPDs, provided by the American Angus Association, with beef bull fertility EBVs to determine if SC could be a potential indicator of beef bull fertility. The authors reported that SC was not a good predictor of fertility due to low correlations (Butler et al., 2021).

The literature provides evidence that genetic selection tools could impact beef bull fertility. However, there are few male fertility selection tools currently available within the industry. These tools could allow producers to make selection decisions on younger animals for reproduction traits which require an animal to be at least 12 months old or older to record a phenotype. Additionally, utilizing genomic technology could give producers more predictive power and more confidence when incorporating young, unproven sires into their breeding programs.

Conclusion

Due to its economic importance, additional research into beef bull fertility is warranted. Increased bull fertility could increase beef production, improve an individual herd’s efficiency, and provide insight into male fertility traits in other species. Furthermore, improvements to bull fertility could be expedited with genetic selection tools. If beef producers could utilize phenotypic measures from BSEs to make selection decisions for improved male fertility, it would improve efficiency, save on labor and resources, and increase profitability (Rodgers et al., 2012).

Table 1. Reported heritabilities for semen production traits which define bull fertility. *Indicates semen ejaculate records instead of individual animals.

Trait	n	Estimate	Standard Error	Breed	Reference
Concentration	2617	0.25	0.03	Swiss Cattle	Burren et al. (2019)
	1626	0.09	0.02	Angus	Butler et al. (2021)
	515	0.19	0.05	Holstein	Druet et al. (2009)
	301	0.14	0.04	Fleckvieh	Gredler et al. (2007)
	717	0.13	0.06	Angus	Knights et al. (1984)
	137	0.52	--	Holstein	Mathevon et al. (1998)
	1212	0.34	0.068	Holstein-Friesian	Suchocki and Szyda (2015)
Number of Spermatozoa	1626	0.08	0.02	Angus	Butler et al. (2021)
	758	0.15	0.04	Apline Goats	Furstoss et al. (2009)
	535	0.25	0.02	Saanen Goats	Furstoss et al. (2009)
	717	0.24	0.05	Angus	Knights et al. (1984)
	137	0.38	--	Holstein	Mathevon et al. (1998)
	2351	0.03	--	Holstein	Taylor et al. (1985)
Scrotal Circumference (6 months)	1608	0.46	0.08	Brahman	Corbet et al. (2013)
	2388	0.41	0.08	Tropical Composite	Corbet et al. (2013)
Scrotal Circumference (12 months)	1282	0.56	--	Angus	Christmas et al. (2001)
	1447	0.65	0.08	Brahman	Corbet et al. (2013)
	2092	0.46	0.06	Tropical Composite	Corbet et al. (2013)
	717	0.36	0.06	Angus	Knights et al. (1984)
	10511	0.53	--	Hereford	Kriese et al. (1991)
	578	0.44	0.24	Hereford	Neely et al. (1982)
Scrotal Circumference (18 months)	18435	0.75	--	Nellore	Carvalho et al. (2023)*
	1409	0.75	0.09	Brahman	Corbet et al. (2013)
	2081	0.43	0.09	Tropical Composite	Corbet et al. (2013)
	51161	0.4	0.02	Nellore	Silva et al. (2013)*
Scrotal Circumference (24 months)	1403	0.75	0.09	Brahman	Corbet et al. (2013)
	2067	0.44	0.09	Tropical Composite	Corbet et al. (2013)
Volume	2065	0.159	0.022	Holstein	Atagi et al. (2017)
	1626	0.11	0.02	Angus	Butler et al. (2021)
	15882	0.05	--	Nellore	Carvalho et al. (2023)*
	622	0.32	0.11	Italian Simmental	Cesarani et al. (2022)
	515	0.22	0.05	Holstein	Druet et al. (2009)
	1644	0.65	--	Normande	Ducrocq and Humblot (1995)
	955	0.04	--	Simmental	Kapš et al. (2000)
	502	0.22	--	Holstein	Karoui et al. (2011)
	840	0.09	0.08	Line 1 Hereford	Kealey et al. (2006)
	137	0.24	--	Holstein	Mathevon et al. (1998)
	693	0.219	--	Piemontese	Rostellato et al. (2021)
	1212	0.26	0.062	Holstein-Friesian	Suchocki and Szyda (2015)

Table 2. Reported heritabilities for semen quality traits which define bull fertility. *Indicates semen ejaculate records instead of individual animals.

Trait	n	Estimate	Standard Error	Breed	Reference
Initial Motility	794	0.37	0.03	Beef and Dairy	Berry et al. (2019)
	1626	0.12	0.03	Angus	Butler et al. (2021)
Motility	1282	0.07	--	Angus	Christmas et al. (2001)
	1245	0.05	0.03	Angus	Garmyn et al. (2011)
	137	0.31	--	Holstein	Mathevon et al. (1998)
	423	0.08	0.07	Hereford, Angus, & Red Angus	Smith et al. (1989)
	1212	0.31	0.06	Holstein-Friesian	Suchocki and Szyda (2015)
Motility Score	1644	0.35	--	Normande	Ducrocq and Humblot (1995)
	841	0.22	0.09	Line 1 Hereford	Kealey et al. (2006)
Percentage of Normal Spermatozoa	549	0.07	0.06	Hereford, Angus, & Red Angus	Smith et al. (1989)
	1626	0.09	0.04	Angus	Butler et al. (2021)
	622	0.16	0.10	Italian Simmental	Cesarani et al. (2022)
	837	0.35	0.10	Line 1 Hereford	Kealey et al. (2006)
	970	0.41	0.10	Tropical Composite	Corbet et al. (2013)
Primary Abnormalities	1626	0.03	0.03	Angus	Butler et al. (2021)
	1282	0.35	--	Angus	Christmas et al. (2001)
	1238	0.27	0.07	Angus	Garmyn et al. (2011)
	839	0.3	0.10	Line 1 Hereford	Kealey et al. (2006)
	549	0.31	0.09	Hereford, Angus, & Red Angus	Smith et al. (1898)
Secondary Abnormalities	1626	0.18	0.04	Angus	Butler et al. (2021)
	1282	0.26	--	Angus	Christmas et al. (2001)
	1238	0.23	0.08	Angus	Garmyn et al. (2011)
	838	0.33	0.09	Line 1 Hereford	Kealey et al. (2006)
	549	0.02	0.05	Hereford, Angus, & Red Angus	Smith et al. (1898)
Major Sperm Abnormalities	14312	0.15	--	Nellore	Carvalho et al. (2023)*
	17648	0.16	0.02	Nellore	Silva et al. (2013)*
Minor Sperm Abnormalities	13743	0.04	--	Nellore	Carvalho et al. (2023)*
	17648	0.04	0.01	Nellore	Silva et al. (2013)*
Percentage of Spermatozoa with Abnormal Head	515	0.35	0.12	Holstein	Druet et al. (2009)
Percentage of Spermatozoa with Abnormal Tail	515	0.19	0.12	Holstein	Druet et al. (2009)
Total Abnormalities	14621	0.3	--	Nellore	Carvalho et al. (2023)*
	1282	0.29	--	Angus	Christmas et al. (2001)
	1644	0.19	--	Normande	Ducrocq and Humblot (1995)
	1238	0.25	0.07	Angus	Garmyn et al. (2011)
	17648	0.15	0.01	Nellore	Silva et al. (2013)*

Table 3. Phenotypic and genetic correlations between semen production and semen quality traits. *Indicates semen ejaculate records instead of individual animals.

n	r_P	r_G	Breed	Reference
Scrotal Circumference and Volume				
626	--	0.2	Hereford	Kealey et al. (2006)
Scrotal Circumference and Concentration				
626	--	0.77	Hereford	Kealey et al. (2006)
Scrotal Circumference and Motility				
1282	--	0.56	Angus	Christmas et al. (2001)
1447	0.47	0.70 ± 0.08	Brahman	Corbet et al. (2013)
626	--	0.34	Line 1 Hereford	Kealey et al. (2006)
423	0.13	-0.04 ± 0.40	Hereford, Angus, & Red Angus	Smith et al. (1898)
Scrotal Circumference (12 month) and Percentage of Normal Spermatozoa				
2092	0.31	0.55 ± 0.13	Tropical Composite	Corbet et al. (2013)
549	0.17	-0.36 ± 0.34	Hereford, Angus, & Red Angus	Smith et al. (1989)
Scrotal Circumference (18 month) and Percentage of Normal Spermatozoa				
1409	0.31	0.50 ± 0.13	Brahman	Corbet et al. (2013)
2081	0.22	0.21 ± 0.16	Tropical Composite	Corbet et al. (2013)
Scrotal Circumference (24 month) and Percentage of Normal Spermatozoa				
1403	0.12	0.22 ± 0.19	Brahman	Corbet et al. (2013)
2067	0.13	0.20 ± 0.14	Tropical Composite	Corbet et al. (2013)
Scrotal Circumference and Primary Abnormalities				
1238	-0.10	-0.19 ± 0.17	Angus	Garmyn et al. (2011)
626	--	-0.36	Line 1 Hereford	Kealey et al. (2006)
549	-0.09	0.14 ± 0.22	Hereford, Angus, & Red Angus	Smith et al. (1989)
Scrotal Circumference and Secondary Abnormalities				
1282	--	-0.32	Angus	Christmas et al. (2001)
1238	-0.11	-0.23 ± 0.18	Angus	Garmyn et al. (2011)
Volume and Concentration				
794	-0.01	-0.40 ± 0.20	Beef and Dairy	Berry et al. (2019)
2617	-0.28 ± 0.01	-0.56 ± 0.05	Swiss Dairy	Burren et al. (2019)
515	-0.02 ± 0.02	-0.55 ± 0.18	Holstein	Druet et al. (2009)
693	-0.35	-0.44	Piemontese	Rostellato et al. (2005)
Volume and Initial Motility				
2065	0.047 ± 0.024	0.165 ± 0.146	Holstein	Atagi et al. (2017)
2617	0.01 ± 0.02	0.19 ± 0.11	Swiss Dairy	Burren et al. (2019)
1819	0.13 ± 0.01	0.23 ± 0.16	Angus	Butler et al. (2021)
Volume and Gross Motility Score				
515	0.01 ± 0.03	-0.17 ± 0.19	Holstein	Druet et al. (2009)
840	--	-0.04	Line 1 Hereford	Kealey et al. (2006)
Volume and Primary Abnormalities				
1626	-0.09 ± 0.01	0.52 ± 0.61	Angus	Butler et al. (2021)

Volume and Secondary Abnormalities				
1626	-0.01 ± 0.01	-0.13 ± 0.17	Angus	Butler et al. (2021)
Volume and Total Abnormalities				
794	0.63	0.66 ± 0.16	Beef and Dairy	Berry et al. (2019)
1644	-0.13	-0.26	Normande	Ducrocq and Humblot (1995)
Volume and Number of Spermatozoa				
1626	0.66 ± 0.01	0.75 ± 0.08	Angus	Butler et al. (2021)
515	0.61 ± 0.03	0.47 ± 0.18	Holstein	Druet et al. (2009)
301	0.70	0.83 ± 0.13	Fleckvieh	Gredler et al. (2007)
693	0.53	0.51	Piemontese	Rostellato et al. (2005)
Concentration and Number of Spermatozoa				
1626	0.61 ± 0.01	0.55 ± 0.13	Angus	Butler et al. (2021)
515	0.71 ± 0.04	0.46 ± 0.18	Holstein	Druet et al. (2009)
301	0.52	0.60 ± 0.07	Fleckvieh	Gredler et al. (2007)
693	0.56	0.56	Piemontese	Rostellato et al. (2005)
Concentration and Motility				
794	0.20	0.29 ± 0.04	Beef and Dairy	Berry et al. (2019)
502	0.33	0.54	Holstein	Karoui et al. (2011)
Concentration and Primary Abnormalities				
1626	-0.03 ± 0.01	--	Angus	Butler et al. (2021)
Concentration and Secondary Abnormalities				
1626	-0.13 ± 0.01	0.04 ± 0.19	Angus	Butler et al. (2021)
Concentration and Percentage of Spermatozoa with Abnormal Cytoplasmic Droplet				
515	-0.08 ± 0.03	-0.09 ± 0.28	Holstein	Druet et al. (2009)
Concentration and Percentage of Spermatozoa with Abnormal Head				
515	-0.02 ± 0.03	-0.23 ± 0.24	Holstein	Druet et al. (2009)
Concentration and Percentage of Spermatozoa with Abnormal Tail				
515	-0.06 ± 0.03	0.33 ± 0.30	Holstein	Druet et al. (2009)
Concentration and Percentage of Viable Spermatozoa				
23614	0.15	0.37 ± 0.23	Beef and Dairy	Berry et al. (2019)
515	0.04 ± 0.03	0.29 ± 0.26	Holstein	Druet et al. (2009)
301	0.27	0.41 ± 0.17	Fleckvieh	Gredler et al. (2007)
Number of Spermatozoa and Initial Motility				
1626	0.16 ± 0.01	0.23 ± 0.18	Angus	Butler et al. (2021)
2065	0.23 ± 0.022	0.205 ± 0.146	Holstein	Atagi et al. (2017)
Number of Spermatozoa and Primary Abnormalities				
1626	-0.10 ± 0.01	0.08 ± 0.73	Angus	Butler et al. (2021)
Number of Spermatozoa and Secondary Abnormalities				
1626	-0.09 ± 0.01	-0.10 ± 0.20	Angus	Butler et al. (2021)
Number of Spermatozoa and Percentage of Spermatozoa with Abnormal Cytoplasmic Droplet				
515	-0.05 ± 0.02	0.33 ± 0.43	Holstein	Druet et al. (2009)
Number of Spermatozoa and Percentage of Spermatozoa with Abnormal Head				
515	-0.02 ± 0.03	-0.38 ± 0.36	Holstein	Druet et al. (2009)

Number of Spermatozoa and Percentage of Spermatozoa with Abnormal Tail				
515	-0.03 ± 0.03	0.14 ± 0.54	Holstein	Druet et al. (2009)
Number of Spermatozoa and Percentage of Viable Spermatozoa				
717	0.79	--	Angus	Knights et al. (1984)
Initial Motility and Percentage of Normal Spermatozoa				
1626	0.20 ± 0.01	0.77 ± 0.09	Angus	Butler et al. (2021)
Motility and Percentage of Normal Spermatozoa				
423	0.38	0.43 ± 0.64	Hereford, Angus, & Red Angus	Smith et al. (1898)
Gross Motility Score and Percentage of Normal Spermatozoa				
837	--	0.51	Line 1 Hereford	Kealey et al. (2006)
Initial Motility and Primary Abnormalities				
1626	-0.21 ± 0.01	0.33 ± 0.20	Angus	Butler et al. (2021)
Initial Motility and Secondary Abnormalities				
1626	-0.15 ± 0.01	0.63 ± 0.82	Angus	Butler et al. (2021)
Motility and Primary Abnormalities				
423	-0.31	-0.36 ± 0.55	Hereford, Angus, & Red Angus	Smith et al. (1898)
Motility and Secondary Abnormalities				
423	-0.22	0.71 ± 0.89	Hereford, Angus, & Red Angus	Smith et al. (1898)
Motility and Percentage of Spermatozoa with Abnormal Cytoplasmic Droplet				
515	-0.07 ± 0.03	0.13 ± 0.23	Holstein	Druet et al. (2009)
Motility and Percentage of Spermatozoa with Abnormal Head				
515	0.17 ± 0.04	-0.56 ± 0.18	Holstein	Druet et al. (2009)
Motility and Percentage of Spermatozoa with Abnormal Tail				
515	-0.11 ± 0.03	-0.24 ± 0.24	Holstein	Druet et al. (2009)

Literature Cited

AAA. 2023. EPD and $Value Definitions. Available from: https://www.angus.org/Nce/Definitions

AGA. 2022. EPD Definition. Available from: https://gelbvieh.org/genetic-technology/epd-info/epd-definitions

Angus Beef Bulletin. 2015. Available from: http://www.angusbeefbulletin.com/ArticlePDF/Scrotal-Circumference-02_15-ABB.pdf.

Atagi, Y., A. Onogi, M. Kinukawa, A. Ogino, K. Kurogi, K. Uchiyama, T. Yasumori, K. Adachi, K. Togashi, and H. Iwata. 2017. Genetic analysis of semen production traits of Japanese Black and Holstein bulls: genome-wide marker-based estimation of genetic parameters and environmental effect trends. Journal of Animal Science. 95:1900. doi:10.2527/jas2016.1186.

Barth, A. D. 2007. Chapter 31 - Evaluation of Potential Breeding Soundness of the Bull. In: The Western Canadian Association of Bovine Practitioners. p. 228–240.

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.

Berry, D. P., B. Eivers, G. Dunne, and S. McParland. 2019. Genetics of bull semen characteristics in a multi-breed cattle population. Theriogenology. 123:202–208. doi:10.1016/j.theriogenology.2018.10.006.

Brito, L. F. C., A. E. D. F. Silva, L. H. Rodrigues, F. V. Vieira, L. A. G. Deragon, and J. P. Kastelic. 2002. Effect of age and genetic group on characteristics of the scrotum, testes and testicular vascular cones, and on sperm production and semen quality in AI bulls in Brazil. Theriogenology. 58:1175–1186. doi:10.1016/S0093-691X(02)00921-4.

Butler, M. L., A. R. Hartman, J. M. Bormann, R. L. Weaber, D. M. Grieger, and M. M. Rolf. 2021. Genetic parameter estimation for beef bull semen attributes. Journal of Animal Science. 99:skab013. doi:10.1093/jas/skab013.

Canadian Dairy Network. 2017. Genetic Gain Before and After Genomics. Available from: https://www.cdn.ca/document.php?id=468

Cesarani, A., F. Corte Pause, J. Hidalgo, A. Garcia, L. Degano, D. Vicario, N. P. P. Macciotta, and G. Stradaioli. 2023. Genetic background of semen parameters in Italian Simmental bulls. Italian Journal of Animal Science. 22:76–83. doi:10.1080/1828051X.2022.2160665.

Chacón, J., E. Pérez, and H. Rodríguez-Martínez. 2002. Seasonal variations in testicular consistency, scrotal circumference and spermiogramme parameters of extensively reared Brahman (Bos indicus) bulls in the tropics. Theriogenology. 58:41–50. doi:10.1016/S0093-691X(02)00679-9.

Chenoweth, P. J., and S. P. Lorton, eds. 2021. Manual of animal andrology. CAB International, Wallingford, Oxfordshire ; Boston, MA.

Christensen, P., P. Brockhoff, and H. Lehn-Jensen. 1999. The Relationship between Semen Quality and the Nonreturn Rate of Bulls. Reprod Domest Anim. 34:503–507. doi:10.1111/j.1439-0531.1999.tb01410.x.

Christmas, R. A., D. W. Moser, M. F. Spire, J. M. Sargent, and S. K. Tucker. 2001. Genetic relationships among breeding soundness traits in yearling bulls. 0:3. doi:10.4148/ 2378–5977.1712.

Corbet, N. J., B. M. Burns, D. J. Johnston, M. L. Wolcott, D. H. Corbet, B. K. Venus, Y. Li, M. R. McGowan, and R. G. Holroyd. 2013. Male traits and herd reproductive capability in tropical beef cattle. 2. Genetic parameters of bull traits. Anim. Prod. Sci. 53:101. doi:10.1071/AN12163.

Coulter, G. H., and R. H. Foote. 1979. Bovine testicular measurements as indicators of reproductive performance and their relationship to productive traits in cattle: A review. Theriogenology. 11:297–311. doi:10.1016/0093-691X(79)90072-4.

David, I., P. Kohnke, G. Lagriffoul, O. Praud, F. Plouarboué, P. Degond, and X. Druart. 2015. Mass sperm motility is associated with fertility in sheep. Animal Reproduction Science. 161:75–81. doi:10.1016/j.anireprosci.2015.08.006.

Doyle, S. P., B. L. Golden, R. D. Green, and J. S. Brinks. 2000. Additive genetic parameter estimates for heifer pregnancy and subsequent reproduction in Angus females. Journal of Animal Science. 78:2091. doi:10.2527/2000.7882091x.

Druet, T., S. Fritz, E. Sellem, B. Basso, O. Gérard, 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. Journal of Animal Breeding and Genetics. 126:269–277. doi:10.1111/j.1439-0388.2008.00788.x.

Ducrocq, V., and P. Humblot. 1995. Genetic characteristics and evolution of semen production of young Normande bulls. Livestock Production Science. 41:1–10. doi:10.1016/0301-6226(94)00029-7.

Fleming, A., C. F. Baes, A. A. A. Martin, T. C. S. Chud, F. Malchiodi, L. F. Brito, and F. Miglior. 2019. Symposium review: The choice and collection of new relevant phenotypes for fertility selection. Journal of Dairy Science. 102:3722–3734. doi:10.3168/jds.2018-15470.

Furstoss, V., I. David, B. Leboeuf, P. Guillouet, P. Boué, and L. Bodin. 2009. Genetic and non-genetic parameters of several characteristics of production and semen quality in young bucks. Animal Reproduction Science. 110:25–36. doi:10.1016/j.anireprosci.2007.12.011.

Garmyn, A. J., D. W. Moser, R. A. Christmas, and J. Minick Bormann. 2011. Estimation of genetic parameters and effects of cytoplasmic line on scrotal circumference and semen quality traits in Angus bulls. Journal of Animal Science. 89:693–698. doi:10.2527/jas.2010-3534.

Gredler, B., C. Fuerst, B. Fuerst-Waltl, H. Schwarzenbacher, and J. Sölkner. 2007. Genetic Parameters for Semen Production Traits in Austrian Dual-Purpose Simmental Bulls. Reprod Domest Anim. 42:326–328. doi:10.1111/j.1439-0531.2006.00778.x.

Hopper, R. M., ed. 2014. Bovine Reproduction: Hopper/Bovine Reproduction. John Wiley & Sons, Inc, Hoboken, NJ, USA. Available from: http://doi.wiley.com/10.1002/9781118833971

Karoui, S., C. Díaz, M. Serrano, R. Cue, I. Celorrio, and M. J. Carabaño. 2011. Time trends, environmental factors and genetic basis of semen traits collected in Holstein bulls under commercial conditions. Animal Reproduction Science. 124:28–38. doi:10.1016/j.anireprosci.2011.02.008.

Kealey, 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 bulls1. Journal of Animal Science. 84:283–290. doi:10.2527/2006.842283x.

Knights, S. A., R. L. Baker, D. Gianola, and J. B. Gibb. 1984. Estimates of Heritabilities and of Genetic and Phenotypic Correlations among Growth and Reproductive Traits in Yearling Angus Bulls1. Journal of Animal Science. 58:887–893. doi:10.2527/jas1984.584887x.

Koivisto, M., M. Costa, S. Perri, and W. Vicente. 2009. The Effect of Season on Semen Characteristics and Freezability in *Bos indicus* and *Bos taurus* Bulls in the Southeastern Region of Brazil. Reproduction in Domestic Animals. 44:587–592. doi:10.1111/j.1439-0531.2008.01023.x.

Kriese, L. A., J. K. Bertrand, and L. L. Benyshek. 1991. Age adjustment factors, heritabilities and genetic correlations for scrotal circumference and related growth traits in Hereford and Brangus bulls. Journal of Animal Science. 69:478. doi:10.2527/1991.692478x.

Lunstra, D. D., J. J. Ford, and S. E. Echternkamp. 1978. Puberty in Beef Bulls: Hormone Concentrations, Growth, Testicular Development, Sperm Production and Sexual Aggressiveness in Bulls of Different Breeds1. Journal of Animal Science. 46:1054–1062. doi:10.2527/jas1978.4641054x.

Mathevon, M., M. M. Buhr, and J. C. M. Dekkers. 1998. Environmental, Management, and Genetic Factors Affecting Semen Production in Holstein Bulls. Journal of Dairy Science. 81:3321–3330. doi:10.3168/jds.S0022-0302(98)75898-9.

Menon, A. G., H. W. Barkema, R. Wilde, J. P. Kastelic, and J. C. Thundathil. 2011. Associations between sperm abnormalities, breed, age, and scrotal circumference in beef bulls. Can J Vet Res. 75:241–247.

Misztal, I., S. Tsuruta, D. A. L. Lourenco, I. Aguilar, A. Lagarra, and Z. Vitezica. 2014. Manual for BLUPF90family of programs. Available from: http://nce.ads.uga.edu/wiki/lib/exe/fetch. php?media=blupf90_all1.pdf

Moser, D. W., J. K. Bertrand, L. L. Benyshek, M. A. McCann, and T. E. Kiser. 1996. Effects of selection for scrotal circumference in Limousin bulls on reproductive and growth traits of progeny. Journal of Animal Science. 74:2052. doi:10.2527/1996.7492052x.

Neely, J. D., B. H. Johnson, E. U. Dillard, and O. W. Robison. 1982. Genetic Parameters for Testes Size and Sperm Number in Hereford Bulls. Journal of Animal Science. 55:1033–1040. doi:10.2527/jas1982.5551033x.

Nel-Themaat, L., G. D. Harding, J. E. Chandler, J. F. Chenevert, P. Damiani, J. M. Fernandez, P. E. Humes, C. E. Pope, and R. A. Godke. 2006. Quality and freezing qualities of first and second ejaculates collected from endangered Gulf Coast Native rams. Animal Reproduction Science. 95:251–261. doi:10.1016/j.anireprosci.2005.09.014.

Nichi, M., P. E. J. Bols, R. M. Züge, V. H. Barnabe, I. G. F. Goovaerts, R. C. Barnabe, and C. N. M. Cortada. 2006. Seasonal variation in semen quality in Bos indicus and Bos taurus bulls raised under tropical conditions. Theriogenology. 66:822–828. doi:10.1016/j.theriogenology.2006.01.056.

RAAA. 2018. The ranchers' guide to EPDs. Available from: https://redangus.org/wp-content/uploads/2018/02/Ranchers_Guide_to_EPDs_2-15.pdf

Rodgers, J. C., S. L. Bird, J. E. Larson, N. Dilorenzo, C. R. Dahlen, A. DiCostanzo, and G. C. Lamb. 2012. An economic evaluation of estrous synchronization and timed artificial insemination in suckled beef cows1. Journal of Animal Science. 90:4055–4062. doi:10.2527/jas.2011-4836.

Rostellato, R., V. Bonfatti, V. A. D. Dias, S. Savoia, V. Spalenza, A. Albera, and P. Carnier. 2021. Estimates of non-genetic effects and genetic parameters for semen traits in Piemontese bulls. Animal. 15:100302. doi:10.1016/j.animal.2021.100302.

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. Journal of Animal Science. 67:2892–2896. doi:10.2527/jas1989.67112892x.

Society for Theriogenology. 2018. New BSE Manual. Available from: https://www.therio.org/page/NewBSEManual?&hhsearchterms=%22bse%22

Suchocki, T., and J. Szyda. 2015. Genome-wide association study for semen production traits in Holstein-Friesian bulls. Journal of Dairy Science. 98:5774–5780. doi:10.3168/jds.2014-8951.

Taylor, J. F., B. Bean, C. E. Marshall, and J. J. Sullivan. 1985. Genetic and Environmental Components of Semen Production Traits of Artificial Insemination Holstein Bulls. Journal of Dairy Science. 68:2703–2722. doi:10.3168/jds.S0022-0302(85)81155-3.

Utt, M. D. 2016. Prediction of bull fertility. Animal Reproduction Science. 169:37–44. doi:10.1016/j.anireprosci.2015.12.011.