ESTIMATION OF GENETIC PARAMETERS OF YEARLING SCROTAL CIRCUMFERENCE AND SEMEN CHARACTERISTICS IN LINE 1 HEREFORD BULLS

by

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ABSTRACT

Objectives of this research were to estimate heritabilities of scrotal circumference and semen traits, and genetic correlations among these traits and birth weight. Line 1 Hereford bulls (n = 841), born in 1963 or from 1967 to 2000, were selected for use by USDA-ARS at Miles City, Montana or for sale. Semen was collected by electro-ejaculation when the bulls were approximately one year of age (mean = 446d) and all samples were evaluated by one person. Traits analyzed were scrotal circumference, color, volume, concentration, swirl, motility, and percents normal, live, abnormal heads, abnormal mid-pieces, proximal distal droplets, bent tails, coiled tails, distal proximal droplets, and primary and secondary abnormalities. Data were analyzed using MTDF-REML. Models included fixed effects for contemporary group, age of dam, age of bull at evaluation, inbreeding of the bull and his dam, and random animal, maternal, permanent maternal environmental, and residual effects. Heritability estimates for scrotal circumference, color, volume, concentration, swirl, motility, and percents normal, live, abnormal mid-pieces, proximal distal droplets, coiled tails, and primary and secondary abnormalities were 0.57, 0.15, 0.09, 0.16, 0.21, 0.22, 0.23, 0.34, 0.17, 0.34, 0.30 0.34, and 0.29, respectively. Estimates of genetic correlations between birth weight and scrotal circumference, color, volume, concentration, swirl, motility, and percents normal, live, abnormal mid-pieces, proximal distal droplets, coiled tails, and primary and secondary abnormalities were 0.36, 0.60, 0.07, 0.58, 0.44, 0.21, 0.20, 0.34, -0.03, -0.52, -0.20, -0.25, and 0.05, respectively. The moderate estimates of heritability for many of the traits indicate potential for favorable selection response. Positive genetic correlations between birth weight and majority of the traits suggest selection to reduce birth weight may compromise semen traits. However, for most traits the expected correlated responses are small. Desirable genetic correlations among scrotal circumference and semen traits suggest selection for one trait would not compromise the other semen traits. Expected correlated responses in semen traits to selection for increased scrotal circumference appear favorable.

CHAPTER 1

LITERATURE REVIEW

Introduction

Economic success of a cow-calf operation is partially determined by number of calves produced for sale, which depends on cow fertility, bull fertility and calf survival (Werth et al., 1991; MacNeil et al., 1994; Tess, 1999). Werth et al. (1991) reported that net income increased as conception rate at first service increased. An increase in conception rate at first service increased overall pregnancy rates, decreased replacement rates, and reduced feed costs because fewer heifers were retained for breeding (Werth et al., 1991; Tess, 1999). Calves were heavier at weaning when a large proportion of them were born in the first 21 days of the calving season (Werth et al., 1991). Heavier calves increased revenue derived from their sale (Tess, 1999). Tess (1999) also concluded decreased conception rates reduced average age of the cowherd. In turn, reducing the average age of the cowherd reduced weaning weight of the calves because of age of dam effects. These factors all caused gross ranch margin to decrease. Subsequent sections of this review focuses on indicators of male fertility as an important contributor to reproductive success and ultimately to economic success of cow-calf production systems.

Fertility of a bull is most easily measured by birth of a live calf, but this measure is impractical because even bulls of low fertility are capable of impregnating a single cow. Fertility of a bull should be established prior to the breeding season. Therefore, many beef producers use breeding soundness evaluations as a practical tool to predict

bull fertility. A breeding soundness evaluation consists of three parts, a physical examination, scrotal circumference measurement, and a semen evaluation (Elmore et al., 1976; Hopkins, 2003).

If a bull meets the requirements of all three parts of the breeding soundness evaluation, then he is classified as a satisfactory potential breeder, but if he does not meet the requirements of any part of the evaluation then he is classified as an unsatisfactory potential breeder or is deferred (Chenoweth et al., 1992). If a bull is classified as deferred, then he can be retested. Yearling bulls are commonly deferred as a result of not having reached puberty at the time of the evaluation (Field and Taylor, 2003). Field and Taylor (2003) state that 30% of bulls tested are classified as unsatisfactory, which means they are expected to produce fewer pregnancies than bulls classified as satisfactory (Hopkins, 2003). Bulls classified as satisfactory are also more likely to produce more calves in the first 21 days of the breeding season than bulls classified as unsatisfactory (Christmas, 2001; Hopkins, 2003). However, results of the breeding soundness evaluation should be used to predict performance of a bull during the current breeding season, rather than as an absolute measure of his fertility.

Phenotypic factors affecting breeding soundness

The physical examination portion of a breeding soundness evaluation covers the entire body, but emphasizes feet, legs, eyes, and internal and external reproductive tract (Gosey, 1996; Sprout et al., 1998). Examination of these physical attributes seeks to ensure that a bull is capable of finding and mounting a cow in estrus (Gosey, 1996).

Scrotal circumference is measured because it is an indirect measurement of potential production of spermatozoa (Latimer et al., 1982; Hopkins, 2003). Quality and amount of spermatozoa producing tissue within the testes can be inferred from scrotal circumference (Elmore et al., 1976; Brinks et al., 1978; Coe, 1999; Hopkins, 2003). Ruttle and Southward (1988) reported bulls classified as satisfactory by a breeding soundness evaluation had larger scrotal circumference than bulls classified as unsatisfactory or that were deferred. Lunstra et al. (1978) showed scrotal circumference is also a good indicator of age at which puberty is attained; as scrotal circumference increased, age of puberty decreased.

As a bull ages, scrotal circumference increases (Coulter and Foote, 1977; Madrid et al., 1988; Ruttle and Southward, 1988). The increases in scrotal circumference with age are one reason that breeding soundness evaluations have different minimum scrotal circumference requirements for different age groups of bulls. Bulls 15 months of age or younger are required to have a scrotal circumference of at least 30 cm. As bulls increase in age by three month increments from 15 months the requirement for scrotal circumference increases by one centimeter until he is greater than 24 months age. Bulls greater than 24 months of age are required to reach a minimum scrotal circumference of 34 cm. Pratt et al. (1991) reported that, on average, Angus bulls must have a scrotal circumference of 23 cm at 230 to 261 days of age in order to reach the 30 cm requirement by one year of age and Hereford bulls must have a scrotal circumference of 26 cm at 230 to 261 days of age in order to reach 30 cm at one year of age. If the minimum required scrotal circumference was raised to 32 cm for yearling bulls, then by 230 to 261 days of age Angus and Hereford bulls would have to attain 25 and 28 cm, respectively (Pratt et

al., 1991). Almost 100% of the Angus bulls and 22 to 88% of the Hereford bulls studied by Pratt et al. (1991) met the 23 and 26 cm requirements in order to attain 30 cm by one year of age. Madrid et al. (1988) reported linear growth in scrotal circumference of Angus bulls between the ages of 11 and 14 months. Hereford bulls were reported to reach a maximum scrotal circumference (average 36.0±0.6 cm) at two years of age, whereas, Angus bulls did not reach a maximum scrotal circumference (average 40.1±0.6 cm) until at least three years of age (Chenoweth et al., 1984). In a study by Ruttle and Southward (1988) scrotal circumference of rams increased until seven years of age.

Coulter et al. (1987) proposed breed-specific minimum requirements for bulls between the ages of 12 and 14 months. These requirements are as follows: Simmental = 33 cm, Angus and Charolais = 32 cm, Hereford and Shorthorn = 31 cm and Limousin = 30 cm. Bulls of different breeds between 370 and 401 days of age, in a study by Pratt et al. (1991), on average exceeded the requirements set by Coulter et al. (1987) for their breed. Angus bulls had an average scrotal circumference of 33.4 cm and Hereford bulls averaged 33.0 cm. All of the breeds in the study by Pratt et al. (1991) also exceeded the requirements for the breeding soundness evaluation of 30 cm.

The breeding soundness evaluation requires a bull have spermatozoa with equal to or greater than 30% progressive motility in order to be classified as a satisfactory breeder (Chenoweth et al., 1992). Having at least 30% progressive motility ensures substantial numbers of spermatozoa are capable of reaching the ova. Motility can be measured two ways, either individual motility or mass motility. Individual motility is determined by observing the forward, progressive movement of individual spermatozoa and mass motility is the overall movement of all the spermatozoa in the viewing field of the

microscope. Mass motility is often described as a swirling cloud. Progressive motility of spermatozoa was found to be a predictor of non-return rate in cows. Correlations between non-return rates and motility of first and second ejaculations to be, 0.43 and 0.39, respectively (Wood et al., 1986). These correlations indicate a relationship that is beneficial to producers; as progressive motility of a bull's spermatozoa increases fewer cows that he serves will return to estrus after being bred.

Sobrero and Rehan (1975) reported spermatozoa from 100 fertile men had, on average, 63% active spermatozoa. Fertility of these men was determined by the number of children they had and that their wives were pregnant at the time of the study. Motility ranged from 10 to 95%, with most falling between 40 to 80%, but no significant relationship was found between motility and number of children. The 40 to 80% motility of spermatozoa was above the 30% required for the bovine breeding soundness evaluation.

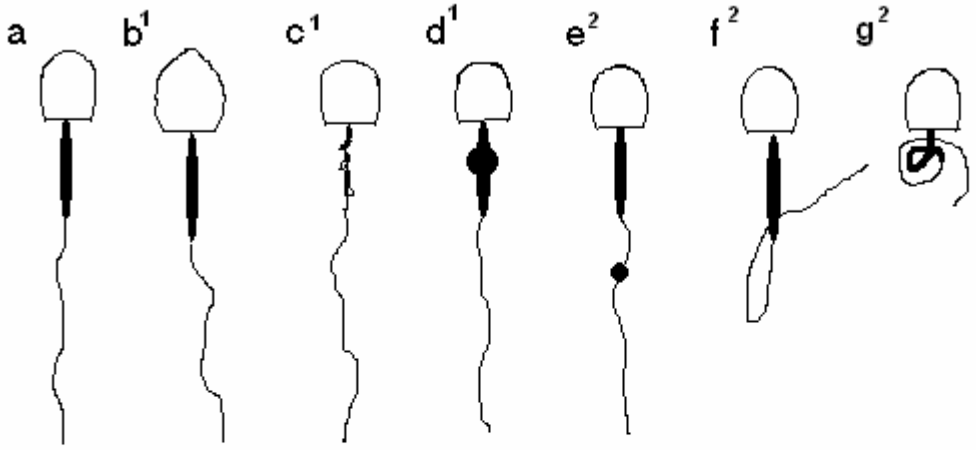
Age or physiological maturity affects motility of spermatozoa. Lunstra and Echternkemp (1982) reported that motility increased rapidly 6 weeks after puberty. Fields et al. (1979) compared semen characteristics of five different breeds of bulls, between the ages of 16 and 20 months. Angus, an early maturing breed, did not show an increase in motility of spermatozoa from 16 to 20 months. This lack of increase may be explained by the finding that Angus bulls reach puberty at 295 days of age (Lunstra and Echternkemp, 1982). Thus, all the Angus bulls evaluated by Fields et al. (1979) had likely reached puberty more than 6 weeks before being evaluated at 16 months. Two Bos indicus breeds, Santa Gertrudis and Brahman, which are later maturing than Angus, had increased motility of spermatozoa from 16 to 20 months, because their sexual maturity

also increased during this time (Fields et al., 1979). The other two groups, Herefords from Montana and Florida, both had 16% and 1% decreased motility of spermatozoa during this time frame, respectively (Fields et al, 1979). However, the bulls remained above 30% progressive motility required by the breeding soundness evaluation after experiencing the decrease (Fields et al., 1979), so the decrease was not as detrimental as first assumed. Fields et al. (1979) attributed the decreased progressive motility of spermatozoa experienced by the Hereford bulls originating in Montana to the hot weather because the bulls were not acclimatized to it. However, Hultnäs (1959) concluded that there was no seasonal effect on motility. Therefore the warmer climate of Florida may not have contributed to the decrease in motility reported by Fields et al. (1979).

Lunstra and Echternkemp (1982) evaluated semen collected from Angus, Hereford, Red Poll, and Brown Swiss bulls every two weeks from 7 to 13 months of age. Progressive motility of spermatozoa increased steadily from the time when spermatozoa were first observed through 13 months. Progressive motility reached 30%, the level required in the breeding soundness evaluation to be classified as satisfactory, by 10 months of age in Angus, Red Poll, and Brown Swiss bulls. However, spermatozoa from Hereford bulls did not reach 30% progressive motility until the bulls were 11.5 months of age.

Semen samples are further evaluated to determine if spermatozoa that are progressively motile have normal morphology, and thus would not be hindered in their ability to fertilize an ovum (Sprout et al., 1998; Hopkins, 2003). Consistent with the requirement for at least 70% normal spermatozoa required by the breeding soundness evaluation (Chenoweth et al., 1992), Field and Taylor (2003) state that fertility of a bull is

affected when 25% or more of the spermatozoa are abnormal. There are two categories for spermatozoa abnormalities (Figure 1), primary and secondary. Primary abnormalities are thought to be permanent and more severe, whereas secondary abnormalities are



Firgure 1. Morphology of spermatozoa
a) normal spermatozoa; b) abnormal head; c) abnormal mid-piece; d) proximal cytoplasmic droplet; e) distal cytoplasmic droplet; f) bent tail; g) coiled tail
1 primary abnormality; 2 secondary abnormality

temporary (Field and Taylor, 2003). Primary abnormalities are most often associated with production of spermatozoa and related to the head of the sperm cell. Secondary abnormalities are associated with storage of spermatozoa and frequently affect the tail. According to the Society for Theriogenology, primary abnormalities are abnormal heads, abnormal mid-pieces, and proximal cytoplasmic droplets, and secondary abnormalities consist of coiled tails, bent tails, and distal cytoplasmic droplets (Chenoweth et al., 1992).

Sobrero and Rehan (1975) reported that percent of spermatozoa with normal heads in fertile men range from 21 to 90% with a mean of 73%. Roughly 7% of the men studied had spermatozoa with less than 60% normal heads, where 67% tested had spermatozoa with between 61 and 80% normal heads (Sobrero and Rehan, 1975). The 70% normal spermatozoa required for the breeding soundness evaluation of cattle falls in the range observed for fertile men.

Proximal cytoplasmic droplets are primary abnormalities and were found to decrease from 30.6 to 16.5% as Angus bulls increased in age from 11 to 13 months (Madrid et al., 1987), which is around the time when Angus bulls might be expected to reach puberty. During the same time frame, percentage of normal spermatozoa increased from 35.6 to 73% (Madrid et al., 1987). Wood et al. (1986) calculated negative correlation coefficients between non-return rate and various abnormalities. Correlation coefficients between non-return rate and abnormalities were: -0.25 for abnormal mid-pieces, -0.28 for bent tails, -0.51 for coiled tails, -0.31 for proximal cytoplasmic droplets, and -0.50 for distal cytoplasmic droplets (Wood et al., 1986). These correlation coefficients indicate that as the percentage of abnormalities decrease the percentage of cows not returning to estrus after being exposed to a bull increases. Thus, the percentage of abnormalities may be a useful predictor of fertility for that collection (Wood et al., 1986).

Wiemer and Ruttle (1987) found the percentage of spermatozoan abnormalities increased in range rams as age increased from one and a half to greater than six years of age. While one obvious difference between this study and the previously discussed

report of Madrid et al. (1987) is the species used, the difference between males around the time they attain puberty and those that are aging is likely also important.

Abnormal tails are a secondary abnormality of spermatozoa, which Omeje and Marire (1990) found was the most prominent abnormality in 4 lines of cocks between 50 and 56 weeks of age. When all abnormalities in cock semen were compared, mid-piece abnormalities were the least frequent, accounting for only 0.67% (Omeje and Marire, 1990).

Laing (1945) reported that a higher fertility group of bulls produced greater volumes of semen than bulls in a lower fertility group. Thus, volume of an ejaculate may be an indicator of fertility. Many factors may influence the volume of an ejaculate, such as, age (Wiemer and Ruttle, 1987; Toe et al., 1994), breed (Bishop et al., 1954; Fields et al., 1979), weight (Omeje and Marire, 1990), and season (Ruttle et al., 1975). Volume of ejaculate varies greatly with species; bulls usually ejaculate 3 to10 ml, where as boars ejaculate 150 to 250 ml of semen per ejaculation (Taylor and Field, 1998). In a study of 100 fertile men Sobrero and Rehan (1975) reported semen volumes ranging from 0.6 to 11.0 ml with an average of 3.31 ml. Almost 75% of the men had semen volumes between 1 to 4 ml per ejaculate.

Rams less than 1.5 years of age produce less semen than rams 6 years of age or older (1.0 ml verses 1.3 ml; Wiemer and Ruttle, 1987). The rams in between the ages of 1.5 and 6 years of age produced 1.1 ml of semen per ejaculate, which did not differ significantly from either the young or old rams.

Weight of an animal has also been shown to affect the volume of semen ejaculated. Omeje and Marire (1990) reported that lighter cocks produced more

spermatozoa than heavier cocks. They acknowledged that their results were not in agreement with previously reported values, because the heavy cocks were too heavy and the extra weight reduced their reproductive capacity affecting the volume of an ejaculate. Rege et al. (2000) reported no effect of weight on volume in 6 to 12 month old rams. Huang and Johnson (1996) evaluated two lines of boars, one selected for increased testis size and the other a control line. The boars represented 10 to 11 generations of selection and no difference was reported between the two lines for the volume of semen per ejaculate.

Ruttle et al. (1975) found the volume of an ejaculate varied with season, using mostly Hereford bulls. Ejaculate volumes were the highest, average of 3.32 ml, in the months of April, May, and June, which were classified as "spring" for this study. During "winter" or the months of January, February, and March bulls had the lowest average volume of 2.26 ml. However, Hultnäs (1959) did not find significant seasonal effects on volume when using 2101 bulls between the ages of 15 and 26 months of the Swedish Red and White breed. There are many differences between the two studies that could account for the opposing results. The studies divided the year differently. Hultnäs (1959) divided the year into 3 seasons, each season being four months, whereas Ruttle et al. (1975) used four seasons of three months each. Ruttle et al. (1975) found a significant difference in volume between winter and spring. All the months included in winter and the first month in spring in the study by Ruttle et al. (1975) were included in the first season (January through April) in the study by Hultnäs (1959). The overlapping of months may have had an effect on the significance of the differences between seasons. The number of bulls used in each study were quite different, Hultnäs (1959) used 2101 bulls whereas Ruttle et

al. (1975) used 41 bulls. The significant difference between seasons reported by Ruttle et al. (1975) with the use of a small population leads to the belief that there is a seasonal effect. The ages of the bulls used could have also affected the results. The bulls used by Ruttle et al. (1975) ranged in age from 1 to 9 years of age, the bulls used by Hultnäs (1959) were 15 to 26 months. Volume increases as age increases, as was discussed earlier. There was probably greater variation in semen volume in the 1 to 9 year old bulls, which contributed to the difference.

Percentage of dead spermatozoa in an ejaculate is important because as percent dead increases, fertility decreases (Bishop et al., 1954). The first ejaculate from bulls usually has more dead spermatozoa than future ejaculates (Bishop et al., 1954). Bishop et al. (1954) reported percent dead to range from 6 to 87% with an average of 22.1%, based on evaluations of seven different breeds of bulls. Age of the bull plays a role in the percentage of live spermatozoa. Rege et al. (2000) reported decreased percent dead spermatozoa as rams increased in age. As a result, the coefficient of variation of percent dead increased as rams increased in age from 6 to 12 months of age. Percent live spermatozoa did not change between 8 and 16 weeks after puberty, instead it remained between 66 and 74% throughout the period (Lunstra and Echternkamp, 1982).

Concentration of spermatozoa is important because more spermatozoa per ejaculate will increase the chance of one reaching and fertilizing an ovum. Laing (1945) reported bulls with higher concentrations of spermatozoa had higher fertility rates. Most pregnancies in humans occurred when the concentration of spermatozoa was between 61 and 80 million cells/ml (Sobrero and Rehan, 1975). Thus, Sobrero and Rehan (1975)

concluded, there is a minimum threshold concentration that a man has to meet, but any increase in concentration above that baseline does not appear to be important to fertility.

Age at time of collection appears to effect the concentration of spermatozoa. Rege et al (2000) and Hultnäs (1959) reported increased concentrations of spermatozoa in ejaculates of rams and bulls, respectively, as age increased. Rams evaluated were between the ages of 9 and 12 months (Rege et al., 2000). Bulls that are earlier maturing, such as Angus (average age at puberty = 295 days), had higher concentrations of spermatozoa than bulls that are later maturing, such as the Hereford (average age at puberty = 326 d), when semen was collected from bulls between the ages of 7 and 13 months (Lunstra and Echternkamp, 1982). However, Madrid et al. (1988) reported conflicting results. As age increased, concentration of spermatozoa increased in the ejaculate of some bulls while it decreased or showed no change in others (Madrid et al., 1988). The lowest concentration was less than 28 x 10^6 spermatozoa/ml and the highest concentrations were 496.0 x 10^6/ml, 598.1 x 10^6/ml and 712.9 x 10^6/ml for 11, 12 and 13 months of age, respectively (Madrid et al., 1988). Bulls representing 14 breeds, mostly Bos taurus, ages 11 to 15 months, exhibited increased concentrations of spermatozoa as age increased (Arteaga et al., 2001). At 11 months only 34.8% of bulls had greater than or equal to 4.0 x 10^6 spermatozoa/ml, which is the concentration used to classify a bull as attaining puberty in this study, but at 15 months 84.7% had greater than or equal to 4.0 x 10^6 spermatozoa/ml (Arteaga et al., 2001).

Season has also been shown to effect the spermatozoa concentration (Ruttle et al., 1975). Samples from 41, mainly Hereford, bulls between the ages of 1 and 9 years showed a seasonal effect. Samples from the summer had the lowest concentration of 491

x 10^6 spermatozoa/ml of ejaculate. Fall collections had the highest concentration of 952 x 10^6 spermatozoa/ml of ejaculate, but did not differ significantly from spring or winter collections (Ruttle et al., 1975). This is important because in higher latitudes most bulls are used during the spring and summer and lower concentrations could affect fertility, since higher concentration is associated with higher fertility (Laing, 1945). As long as the concentration of spermatozoa is higher during the summer than the baseline projected by Sobrero and Rehan (1975), then the producer should not be concerned by the lower concentrations in the summer.

Genetic factors affecting breeding soundness

Breed effects.

Differences in semen characteristics have been observed between breeds. Volume of semen has been shown to differ significantly among breeds (Bishop et al., 1954; Fields et al, 1979). Bishop et al. (1954) compared the volume of semen produced by Friesian, Shorthorn, Ayrshire, Guernsey, Jersy, Hereford, and Red Poll bulls. Ayrshire bulls had the greatest volume with 5.87 ml per ejaculate and Jersy had the smallest amount with 3.77 ml. Average ejaculate over all bulls was 5.02 ml. Fields et al. (1979) reported that yearling Hereford bulls originating in Montana produced less semen per ejaculate at 16 to 20 months of age than Angus, Santa Gertrudis, Brahman, and Hereford yearling bulls originating in Florida. Some of the variation observed by Fields et al. (1979) was due to the environment, since the study was performed during the period from April through August in Florida. High temperature was identified as a factor that affected the bulls from Montana.

Breed also has an effect on spermatozoa concentration (Fields et al., 1979; Lunstra and Echternkamp, 1982). Fields et al. (1979) compared semen characteristics of yearling Angus, Brahman, Santa Gertrudis, and Hereford bulls. The Hereford bulls originated from either Montana or Florida. Spermatozoa concentration varied significantly between breeds with Angus and Hereford bulls originating from Florida having the greatest concentration, Brahman and Santa Gertrudis had the lowest concentrations, and the Hereford bulls originating from Montana were intermediate. Brahman and Santa Gertrudis are later maturing breeds and since the study was conducted when the bulls were between 16 and 20 months of age, the bulls from these breeds were probably just reaching puberty, which resulted in lower concentrations. Concentrations of spermatozoa increased from April to August for all breeds except the Hereford bulls that originated from Montana who had decreased concentration of spermatozoa over the trial. This decrease was attributed to the hot and humid climate of Florida, where the study took place. The bulls from Montana may not have been acclimatized to the environment. However, the difference in concentration between the lines of Hereford cattle is supported by Omeje and Marire (1990) who studied 4 different lines of chickens and found concentration to differ between lines. Huang and Johnson (1996) evaluated differences between lines of boars. Boars selected for increased testis size had more 35 x 10^6 spermatozoa/ml than boars that were not selected for testis size.

Heritability.

Heritability of scrotal circumference has been estimated in several studies, however other measures of male fertility have not been investigated as intensely. Scrotal

circumference heritabilities range from 0.38 to 0.67 (Table 1). Consistent with its moderate heritability and because a breeding soundness evaluation places positive selection pressure on scrotal circumference, using bulls that passed a breeding soundness evaluation resulted in increased scrotal circumference of bulls retained from subsequent generations within the herd (Godfrey et al., 1988). Further, Smith et al. (1989b) reported increased scrotal circumferences in the male progeny as scrotal circumference of the sire increased. Progeny produced by a bull with an above average scrotal circumference and kept as replacements will reach puberty sooner. Bulls that reach puberty at earlier ages and are used as yearlings are also beneficial to the producer because it enables them to reduce the generation interval and accelerate genetic improvement.

Several estimates of the heritability for motility were found (Table 1). Smith et al. (1989a) found the heritability of motility to be 0.08 and Knights et al. (1984) reported a heritability of 0.13, which are both low estimates of heritability. Rege et al. (2000) reported estimated heritabilities for individual spermatozoa and mass motility in rams at 9 and 12 months of age. Motility of individual spermatozoa decreased from 9 to 12 months of age with estimated heritabilities of 0.32 and 0.16, respectively. However, heritabilities estimated for mass motility decreased only slightly from 0.32 to 0.27 over the three-month period. The difference in the heritability estimates from the two studies may be attributed to age differences. The maximum age of the rams used by Rege et al. (2000) was 12 months, whereas the bulls used by Smith et al. (1989a) were yearlings, which implies the bulls ranged in age from 12 to 24 months. Heritability of individual motility decreased by half in three months, so it is plausible that it could have decreased even more as the animals aged. Individual spermatozoa motility estimate for 12 month old

Table 1. Heritability (h^2) estimates for scrotal circumference and semen characteristics

Trait	h^2±SE	Source
Scrotal circumference	0.71±0.13	Evans et al., 1999
	0.65	Quirino and Bergmann, 1998
	0.53±0.06	Bourdon and Brinks, 1986
	0.53	Kriese et al., 1991
	0.49±0.06	Bourdon and Brinks, 1986
	0.45±0.16	Koots et al., 1994a
	0.44±0.24	Neeley et al., 1982
	0.41±0.04	Martines-Velazquez et al., 2003
	0.41±0.06	Lunstra et al., 1988
	0.38±0.16	Latimer et al., 1982
	0.36±0.06	Knights et al., 1984
	0.32±0.10	Morris et al., 1992
Volume		
9 mo	0.07	Rege et al., 2000
12 mo	0.11	Rege et al., 2000
Concentration	0.13	Knights et al., 1984
	0.17	Rege et al., 2000
Motility	0.13	Knights et al., 1984
	0.08	Smith et al., 1989a
Individual motility		
9 mo	0.32	Rege et al., 2000
12 mo	0.16	Rege et al., 2000
Mass motility		
9 mo	0.32	Rege et al., 2000
12 mo	0.27	Rege et al., 2000
Percent normal spermatozoa	0.07	Smith et al., 1989a
Percent abnormal spermatozoa		
9 mo	0.35	Rege et al., 2000
12 mo	0.16	Rege et al., 2000
Primary abnormalities	0.31	Smith et al., 1989a
Secondary abnormalities	0.02	Smith et al., 1989a
Proximal cytoplasmic droplets		
9 mo	0.42	Rege et al., 2000
12 mo	0.3	Rege et al., 2000
Distal cytoplasmic droplets		
9 mo	0.05	Rege et al., 2000
Percent dead spermatozoa		
9 mo	0.17	Rege et al., 2000
12 mo	0.01	Rege et al., 2000

rams and the estimate by Smith et al. (1989a) are classified as lowly heritable, whereas the estimate for mass motility at both 9 and 12 months of age in rams is considered moderately heritable.

Estimates of heritability for morphology have been cited in the literature (Table 1). Smith et al. (1989a) estimated heritability for percent normal spermatozoa to be 0.07. Primary abnormalities and secondary abnormalities had estimated heritabilities of 0.31 and 0.02, respectively (Smith et al., 1989a). Rege et al. (2000) reported a heritability estimate for total spermatozoa abnormalities and then broke the abnormalities down further into proximal and distal cytoplasmic droplets for rams of 9 and 12 months of age. Heritability estimates for rams of 9 months of age were 0.35, 0.42, and 0.05 for total abnormalities, proximal cytoplasmic droplets (a primary abnormality), and distal cytoplasmic droplets (a secondary abnormality), respectively. Estimates for total abnormalities and proximal cytoplasmic droplets decreased to 0.16 and 0.30 over the three month period from 9 to 12 months of age. Heritability estimates for distal cytoplasmic droplets at 12 months of age were not available. The preceding results support the inference that primary abnormalities arise genetically, while secondary abnormalities originate largely as a consequence of environmental effects.

Only one study was found in which heritability of ejaculate volume and percent dead spermatozoa were estimated (Table 1). Rege et al. (2000) found the heritability of volume to be 0.07 and 0.11 in 9 and 12 month old rams, respectively. Heritability estimates for percent dead spermatozoa decreased from being almost moderately heritable to hardly heritable over the three-month period from 9 to 12 months. At 9 months heritability was estimated at 0.17 and then decreased to 0.01 at 12 months of age.

Two studies report estimates of heritability of spermatozoa concentration (Table 1). A study of 717 yearling Angus bulls by Knights et al. (1984) reported an estimate of heritability of 0.13. Rege et al. (2000) estimated a heritability of 0.17 for the concentration for 12-month-old rams. Knowing the heritability of the concentration of spermatozoa may be important to the artificial insemination industry, because they could genetically increase concentration through selection. The higher concentration would allow firms to obtain the same number of units of semen with fewer collections. Also, because higher concentration is related to higher fertility, producers could select bulls with higher concentrations to increase the fertility of their bulls over time. Because these traits are heritable, selection within a herd for increased concentration of spermatozoa would be possible, but progress would be slow due to the low heritability.

Genetic Correlations.

Correlations between scrotal circumference and growth traits have been shown to be positive (Table 2). Genetic correlations between scrotal circumference and birth weight range from 0.02 to 0.10. The average correlation of 0.10 reported in a review paper by Koots et al.(1994b) indicates a fairly weak relationship and implies that selection to increase scrotal circumference will have little effect on birth weight. Estimates of the genetic correlation between weaning weight and scrotal circumference are positive, averaging 0.20, and intermediate between the corresponding

Table 2. Estimates of genetic correlations between scrotal circumference and birth, weaning, and yearling weight

Birth	Weaning	Yearling	Source
NA	0.43	0.05	Neely et al., 1982
0.10	0.00	0.68	Knights et al., 1984
0.04	0.20	0.39	Bourdon and Brinks, 1986
0.02	0.08	0.36	Kriese et al., 1991
0.10	0.30	0.47	Koots et al., 1994b

correlations of scrotal circumference with birth and yearling weights. Estimates of the genetic correlation between yearling weight and scrotal circumference averaged 0.40.

Coulter and Foote (1977) reported a genetic correlation of 0.51 between scrotal circumference and body weight in bulls between the ages of 12 and 17 months. Morris et al. (1992) reported genetic correlations of 0.44 and 0.36, between live weight and scrotal circumference at 11 and 13 months, respectively. These estimates calculated from data collected at approximately one year of age are similar to those for yearling weight and scrotal circumference presented in Table 2. Quirino and Bergmann (1998) evaluated two models for estimation of the genetic correlation between body weight and scrotal circumference. In the first model, scrotal circumference was not adjusted for body weight. In the second model, scrotal circumference was adjusted for body weight. Genetic correlations between body weight at 9, 12, 18 and 24 months of age and unadjusted scrotal circumference were 0.68, 0.70, 0.71 and 0.58. Corresponding estimates when scrotal circumference was adjusted for body weight were 0.64, 0.47, 0.64 and 0.33, respectively. Bourdon and Brinks (1986) estimated two correlations, one with

scrotal circumference adjusted to 365 days of age and the other unadjusted for age. The adjusted correlation (0.44) was greater than the unadjusted estimate (0.39).

Selecting bulls that have above average scrotal circumference may be beneficial to cow-calf producers. Selection for increased fertility through selection for increased scrotal circumference would not be expected to compromise calf survival associated with calving difficulty that resulted from excessive birth weight. Further, producers could straightforwardly increase scrotal circumference of bulls simultaneously with increasing weaning weight and thus potentially increase income from the production system (Werth et al., 1991; Tess, 1999). Finally, estimates of the genetic correlation between scrotal circumference and yearling weight are of moderate magnitude and suggest that yearling weight will increase with selection for increased scrotal circumference or vice versa. Even more striking than the estimates discussed previously, Smith et al. (1989b) reported that for each additional centimeter of scrotal circumference, the birth weight in the progeny decreased and the other growth traits increased.

Genetic correlations of scrotal circumference with various reproductive aspects of a bull's female progeny have also been reported (Brinks et al, 1978; King et al., 1983; Toelle and Robison, 1985; Morris et al., 1992). Female progeny of bulls with greater scrotal circumference were younger at puberty than contemporaries sired by bulls with smaller scrotal circumference (Smith et al., 1989b; Moser et al., 1996; Martines-Velázquez et al., 2003). The genetic correlation of -0.15 was reported by Martines-Velázquez et al. (2003) between scrotal circumference and age at puberty in female progeny. Smith et al. (1989b) also reported a favorable relationship between age of puberty in female offspring and scrotal circumference in the sire. Brinks et al. (1978)

reported a genetic correlation of -0.71 between scrotal circumference and age at puberty for bulls and heifers out of the same sire. This substantial negative correlation suggests that as scrotal circumference of bulls increased, age of puberty of paternal half-sib females will decrease. Based on simulation, Bourdon and Brinks (1987) concluded that heifers that reached puberty at 425 days instead of 365 days had lower pregnancy rates, later calving dates, and weaned lighter calves. Heifers that reached puberty at 425 days also had lower pregnancy rates as cows (Bourdon and Brinks, 1987).

Genetic correlations have also been reported between scrotal circumference of the sire and pregnancy rate, age at first calving, and calving interval of the female progeny. Evans et al. (1999) reported the very weak relationship (0.002) between scrotal circumference and heifer pregnancy rate; whereas Toelle and Robison (1985) reported a very strong correlation (0.56 to 0.93). The study by Toelle and Robison (1985) included both half-sib analysis and sire-daughter analysis. Results from the two analyses differed, the half-sib analysis yielded a genetic correlation of 0.56 and the sire-daughter analysis produced a genetic correlation of 0.93. Both of these correlations are strong and positive, thus as scrotal circumference increases, pregnancy rate was expected to increase.

Toelle and Robison (1985) also reported genetic correlations between scrotal circumference and age at first calving, age at first breeding, and calving interval from the two analyses. The signs of the estimates changed between analyses. In the half-sib analysis, scrotal circumference was negatively correlated with the various traits. This result would benefit producers because heifers being younger the first time they are bred and calve and a shorter calving interval are all desirable. Conversely, the correlations estimated from the sire-daughter analysis were positive and not desirable. Toelle and

Robison (1985) attributed the differences in the sign of the correlations to environmental effects, such as age of dam.

Correlations between scrotal circumference and seminal characteristics have been reported. Coulter et al. (1976) found a correlation of 0.81 between scrotal circumference and output of spermatozoa. Wiemer and Ruttle (1987) reported correlations between scrotal circumference and volume, motility, and percent abnormal cells in rams to be 0.143, 0.112, and -0.083, respectively. Brinks et al. (1978) reported positive correlations of scrotal circumference with percent normal spermatozoa and motility and negative correlations of scrotal circumference with percentages of primary and secondary abnormalities. A bull's risk of producing more than 30% abnormal spermatozoa decreases as scrotal circumference increases (Coe, 1999).

Inbreeding

Use of an inbred population for this research warrants some consideration of effects of inbreeding on the phenotypes being investigated. Inbreeding effects on reproduction have routinely been thought of as negative. McPhee et al (1931) reported a decrease in litter size in the second generation of brother-sister matings of Poland China swine when compared to a non-inbred control line. In a herd of Holstein cows where sire-daughter matings were carried out for three years, 69.5% of the cows were considered sterile and had abnormal reproductive tracts (Fincher and Williams, 1926). The abnormalities of the reproductive tract appeared in the sections deriving from the mullerian ducts, no abnormalities were found in the ovaries or vulva. In most of the cows the mullerian ducts developed into hard, dense cords that had a faint lumen. The cords

were considerably longer than normal cords because along with the oviducts, they also represented the uterus, cervix and sometimes the vagina (Fincher and Williams, 1926). Other studies contradict these findings. King (1916) compared two lines of rats, a control line and a line that had been inbred for 22 generations. No significant difference was reported between the two lines in average litter size and the inbred line actually had 0.4 more pups/litter than the control line.

No definite conclusions can be reached when considering effects of inbreeding on fertility of bulls. Harris et al. (1960) compared inbred, linecross, and outbred Hereford yearling bulls to determine if there was a difference in their ability to mate. All of the bulls were identified as being either satisfactory, questionable, or unsatisfactory breeders. There was a significant difference between the percentage of unsatisfactory bulls in the inbred and linecross groups, but not between the outcross group and either of the other groups. Harris et al. (1960) concluded there was not a close association between increasing levels of inbreeding and decreased fertility. Hultnäs (1959) agreed with Harris et al. (1960) that no concrete conclusion can be drawn between inbreeding and fertility, even though Hultnäs (1959) reported negative relationships of level of inbreeding with libido index and with total number of spermatozoa with abnormal heads.

Inbreeding appears to have a substantial influence on morphology of spermatozoa (Gregory et al., 1951; Donald and Hancock, 1953; Hultnäs, 1959; Harris et al., 1960). Five bulls used by Gregory et al. (1951) were all closely related and had high percentages of abnormal sperm. Another bull in the study by Gregory et al. (1951) that was produced from a sire-daughter mating was considered sterile after collection over several months and contained a large portion of abnormal spermatozoa in all collections. The fact that

the bull was collected over several months implies that sterility was permanent and not caused by a temporary environmental effect. Donald and Hancock (1953) studied 16 bulls that were inbred and were considered sterile due to the majority of spermatozoa having misformed acrosomes. A negative relationship between inbreeding and the number of spermatozoa with abnormal heads was reported by Hultnäs (1959).

Inbred bulls might be expected to experience similar abnormalities of the reproductive tract that were reported by Fincher and Williams (1926) in inbred cows. The cows experienced abnormalities in the region of the reproductive tract that originated from the mullerian duct. However, in bulls the mullerian duct regresses to allow the Wolffian duct to develop, therefore the internal reproductive tracts of the male and female to not develop from the same embryonic structure. The ovaries and vulva of the inbred cows were free of any abnormalities (Fincher and Williams, 1926). These two structures are homologous to the testes and penis in the bull, which were also void of abnormalities. The lack of abnormalities in the reproductive structures that originate from the same embryonic structure supports the conclusion of Hultnäs (1959) and Harris et al. (1960) that no close association can be found between inbreeding and decreased fertility.

Mating plans used in the Line 1 Hereford population result in the intra-contemporary group variance of inbreeding to be low (MacNeil et al., 1992). This lack of variance results in estimation of inbreeding effects being imprecise in this population.

CHAPTER 2

OBJECTIVES

Heritability estimates for traits that effect fertility are important because the estimates will determine if genetic selection is possible and the speed at which progress can be made through selection. Genetic correlations between traits are also important because they provide information as to how one trait will respond when selection is for another trait. Many heritability estimates and correlations among birth weight, scrotal circumference, and semen characteristics are unknown. Knowledge of these estimates and relationships will benefit the producer because they will provide producers with the ability to predict the results of selection.

Therefore, objectives of this study were to:

1) estimate heritability for scrotal circumference, ejaculate color, volume of ejaculate, swirl, concentration of ejaculate, spermatozoa motility, percent live, percent normal spermatozoa, percent primary abnormalities, percent secondary abnormalities, percent abnormal heads, percent abnormal mid-pieces, percent proximal cytoplasmic droplets, percent distal cytoplasmic droplets, percent coiled tails, and percent bent tails;

2) estimate genetic and phenotypic correlations among scrotal circumference, ejaculate color, volume of ejaculate, swirl, concentration of ejaculate, spermatozoa motility, percent live, percent normal spermatozoa, percent primary abnormalities, percent secondary abnormalities, percent abnormal

heads, percent abnormal mid-pieces, percent proximal cytoplasmic droplets, percent distal cytoplasmic droplets, percent coiled tails, and percent bent tails;

3) estimate genetic and phenotypic correlations of birth weight with scrotal circumference, ejaculate color, volume of ejaculate, swirl, concentration of ejaculate, spermatozoa motility, percent live, percent normal spermatozoa, percent primary abnormalities, percent secondary abnormalities, percent abnormal heads, percent abnormal mid-pieces, percent proximal cytoplasmic droplets, percent distal cytoplasmic droplets, percent coiled tails, and percent bent tails; and

4) predict correlated responses in ejaculate color, volume of ejaculate, swirl, concentration of ejaculate, spermatozoa motility, percent live, percent normal spermatozoa, percent primary abnormalities, percent secondary abnormalities, percent abnormal heads, percent abnormal mid-pieces, percent proximal cytoplasmic droplets, percent distal cytoplasmic droplets, percent coiled tails, and percent bent tails to selection for reduced birth weight and for increased scrotal circumference.

CHAPTER 3

MATERIALS AND METHODS

Line 1 Hereford Population

The 841 bulls used in this research were from the Line 1 Hereford population maintained at the USDA, ARS, Fort Keogh Livestock and Range Research Laboratory, Miles City, MT. This population serves as an excellent resource for animal breeders because pedigree information and management histories are available for the population from its establishment.

The initial matings of two half-sib sons of Advance Domino 13 (Advance Domino 20 and Advance Domino 54) to 50 registered Hereford females occurred in 1934. Inbreeding accumulated quickly in the first few generations as sons of Advance Domino 20 were mated to daughters of Advance Domino 54 and vice versa (Knapp et al., 1951). In more recent generations, inbreeding has been avoided. MacNeil et al. (1992) reported a pedigree inbreeding level of approximately 30% with a 2% increase per generation.

From the late 1950's to present all bull calves were left intact until after being evaluated for postweaning growth. After weaning the bulls were acclimatized to feedlot conditions for a period of approximately 4 weeks and evaluated for postweaning growth for a period of 140, 168 or 196 days. At approximately 14 months of age, the first semen collection was conducted on the bulls.

Semen Evaluations

During the years of 1963 and 1967 to 2000, at a mean age of 446 days, semen from selected bulls was collected and evaluated, and scrotal circumference was measured. The same scientist (R. A. Bellows, USDA-ARS, Miles City, MT) performed all of the semen evaluations. The semen collection nearest to one year of age was used for all analyses. For most bulls it was the first collection and took place in the spring for pre-breeding or in the fall prior to sale.

Phenotypic evaluation of each bull included measuring scrotal circumference and an examination of his semen. Scrotal circumference was measured at the greatest distance around the scrotum with a flexible measuring tape after the testis had been pulled into the bottom of the scrotum. Semen samples were collected by electroejaculation. During collection the collection tube was maintained at 36˚- 40˚C using an insulated water jacket. A waterbath was used to maintain the sample at 37˚C throughout the evaluation.

Total volume, color, and any contaminations were recorded within 5 minutes of collection. Color was scored on a scale of 0 to 5, 0 being clear and water-like and 5 being thick, creamy with measurable pearl.

Vitality of the semen sample was assessed through ratings of gross swirl and progressive motility and by determining the percentage of motile sperm. Gross swirl rating (**GSR**) of undiluted semen was performed within 1 minute of collection. Two 10 µl of undiluted semen was placed on two warmed slides and scored on a scale of 0-5 using 10x objective lens. The scale of 0-5 represents the following:

0) no movement present

1) very sluggish swirls and spermatozoa show weak-labored movement

2) slow swirls, but many motile spermatozoa

3) swirls of intermediate speed

4) swirls of rapid speed

5) many swirls showing rapid and vigorous speed

The average of the two scores was recorded. Progressive motility or motility strength rating (**SMR**) and percentage motile spermatozoa, were determined by placing 100 µl of undiluted semen into prewarmed tubes containing 400 µl of Dulbecco's Phosphate-Buffer Saline, pH 7.4, and mixing. Twenty microliters of diluted semen was placed on a warmed glass slide and allowed to spread uniformly under the coverslip. Strength of motility rating was scored on a scale of 0 – 5 and represents the following:

0) none – no spermatozoa showing straight-line movement

1) very weak – some spermatozoa show slow, straight-line movement (>5 seconds to cross a 40X field of view)

2) weak – most spermatozoa show slow, straight-line movement (>5 seconds to cross a 40X field of view)

3) intermediate – most spermatozoa show good, straight-line movement (2-5 seconds to cross a 40X field of view)

4) strong – most spermatozoa show rapid, straight-line movement (1-2 seconds to cross a 40X field of view)

5) very strong – most spermatozoa show very rapid and vigorous, straight-line movement (<1 second to cross a 40X field of view)

Percent progressive motility (0 – 100%) and SMR were measured on at least 3 representative areas of the slide. The average of the three scores for each category was recorded.

Numbers of live and dead spermatozoa and numbers of cells in various morphological classifications (Figure 1) were evaluated by staining 10 µl of semen with 400 µl of eosin-saline solution and counting 100 spermatozoa with a hemocytometer. Morphological abnormalities included abnormal heads, abnormal mid-pieces, proximal cytoplasmic droplets, distal cytoplasmic droplets, coiled tails, and bent tails. Percents primary and secondary abnormalities were calculated according to the Society of Theriogenology (Chenoweth et al., 1992). Primary abnormalities included abnormal heads, abnormal mid-pieces, and proximal cytoplasmic droplets were considered primary abnormalities. Distal cytoplasmic droplets, bent tails, and coiled tails were considered secondary abnormalities.

Of the 842 bulls with recorded phenotypes that used in this study, only 622 bulls had observations for scrotal circumference, spermatozoa motility, and percentage of normal spermatozoa, which are major components of breeding soundness evaluations. Of the 622 bulls, 87.3% met or exceeded the minimum requirements for scrotal circumference (30cm), spermatozoa motility (30% or 1.5 on the scale used in this study), and percentage of normal spermatozoa (70%), therefore 12.7% of the bulls did not meet the requirements in at least one of the three categories. Not meeting the minimum requirement for percentage of normal spermatozoa caused majority of bulls to fail, 75.9% of failing bulls. Spermatozoa motility and scrotal circumference were responsible for 8.9% and 2.5% of the failures, respectively. Bulls failing the breeding soundness

evaluation due to failing to the met the minimum requirements in two of the three areas were 11.49% and 1.3% for spermatozoa motility with percentage of normal spermatozoa and scrotal circumference, respectively. Also, 6.4% of the 622 bulls were either at 70% normal spermatozoa or were within 2% on either side of the 70% threshold. Only 0.3% of bulls were had a 30cm scrotal circumference or were within 0.5cm on either side of the 30cm minimum. These two groups of bulls would probably be the bulls at the greatest risk of being deferred for a later test.

Statistical Analyses

Phenotypic means and standard deviations of the traits studied are presented in Table 3. Normality of the data was determined using the GLM and UNIVARIATE procedures of SAS (SAS, 1989). A linear model with the fixed effects of contemporary group and age of dam and the covariates of age of bull at evaluation, inbreeding level of the bull, and his dam was fitted to the data for each trait. Contemporary group was defined as year of evaluation and season of evaluation because the evaluations predominately took place in the spring and fall. Age of dam was classified as two, three, four, and five or more years of age. Residuals from the model were tested for normality using the Kolmogorov-Smirnov test ($p \leq 0.05$). For all semen characteristics, the residuals were not normally distributed ($p \leq 0.05$). Thus, transformations were performed on the data and residuals from analysis similar to those described above were retested for normality. Transformations recommended by Sokal and Rohlf (1969) were square root, natural log, and arcsine, with each transformation being best suited to correct non-normality in a certain type of data. A square root transformation works best on count

data. Data that is in percentages or proportions, such as percent live, may be transformed using the arcsine transformation. The natural log transformation can be used on data with a frequency distribution skewed to the right or when the mean is positively correlated with the variance. All three transformations were used in attempting to make the distributions of the residuals normal. If the data set contained a zero as a legitimate entry, then one-half was added to all the data points because some transformations, such as the square root, are undefined for a value of zero.

Table 3. Means, standard deviations, and Kolmogorov-Smirnov test-statistic (D) for scrotal circumference and semen characteristics

Trait	μ	SD	D-statistic
Scrotal circumference, cm	35.042	2.096	0.015[a]
Color	2.207	0.869	0.057[b]
Volume, Ml	3.335	1.798	0.082[b]
Concentration	3.234	1.030	0.042[b]
Swirl	2.061	1.443	0.059[b]
Motility	3.256	1.229	0.059[b]
Live, %	78.207	16.544	0.065[b]
Normal spermatozoa, %	81.734	12.558	0.107[b]
Primary abnormalities, %	11.027	10.879	N/A
Abnormal heads, %	3.248	5.716	0.111[b]
Abnormal mid-pieces, %	6.883	8.583	0.175[b]
Proximal cytoplasmic droplets, %	0.896	3.854	0.314[b]
Secondary abnormalities, %	7.278	7.195	N/A
Bent tails, %	1.405	3.352	0.254[b]
Coiled tails, %	5.820	6.788	0.143[b]
Distal cytoplasmic droplets, %	0.048	0.576	0.404[b]

N/A - not available

a $P > 0.05$

b $P < 0.01$

Figures 2 and 4 illustrate the swirl and percent proximal cytoplasmic droplets phenotypes whose residuals were not normally distributed. Figure 3 illustrates the square root transformation of swirl that resulted in the distribution of the residuals being approximately normal. Figures 5, 6, and 7 illustrate the residual values for proximal cytoplasmic droplets whose distributions remained significantly non-normal after transformation. After transformation, only swirl became normally distributed. Therefore, the original data was used for all analyses for ease of interpretation.

Figure 2. Residuals for swirl from a linear model that included the fixed effects of contemporary group (year of birth and season of evaluation), age of dam, age of bull at evaluation, inbreeding level of the bull and his dam ($P < 0.01$)

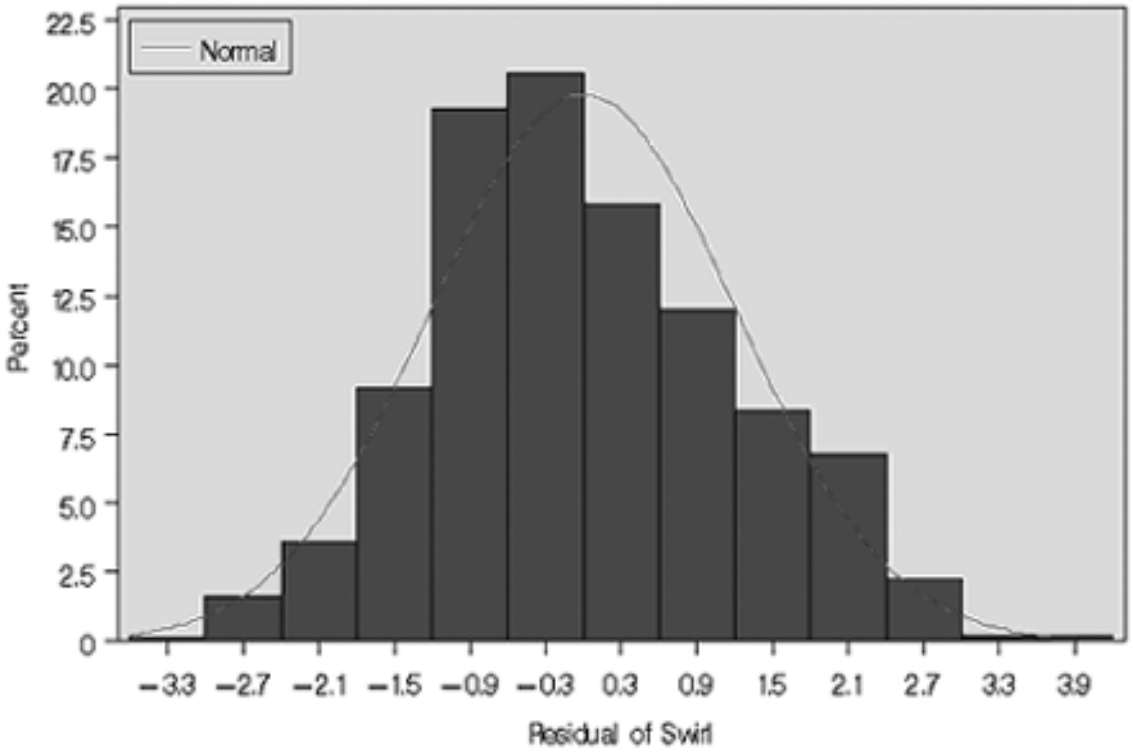


Figure 3. Residuals values after adjustment of square root transformed swirl for the fixed effects of contemporary group (year of birth and season of evaluation), age of dam, age of bull at evaluation, inbreeding level of the bull and his dam ($P > 0.05$)

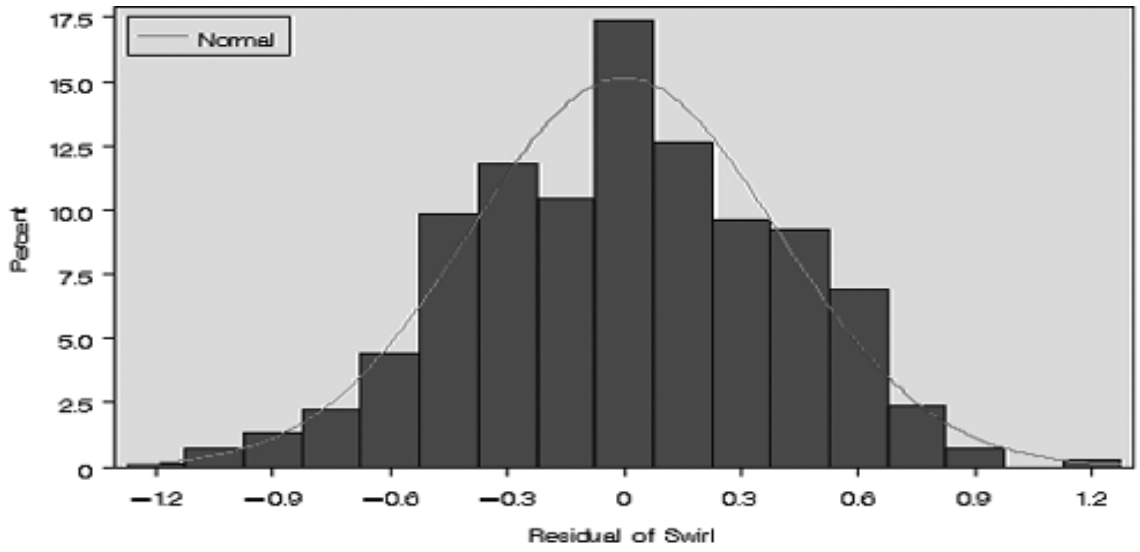


Figure 4. Residuals for proximal cytoplasmic droplets from a linear model that included the fixed effects of contemporary group (year of birth and season of evaluation), age of dam, age of bull at evaluation, inbreeding level of the bull and his dam ($P < 0.01$)

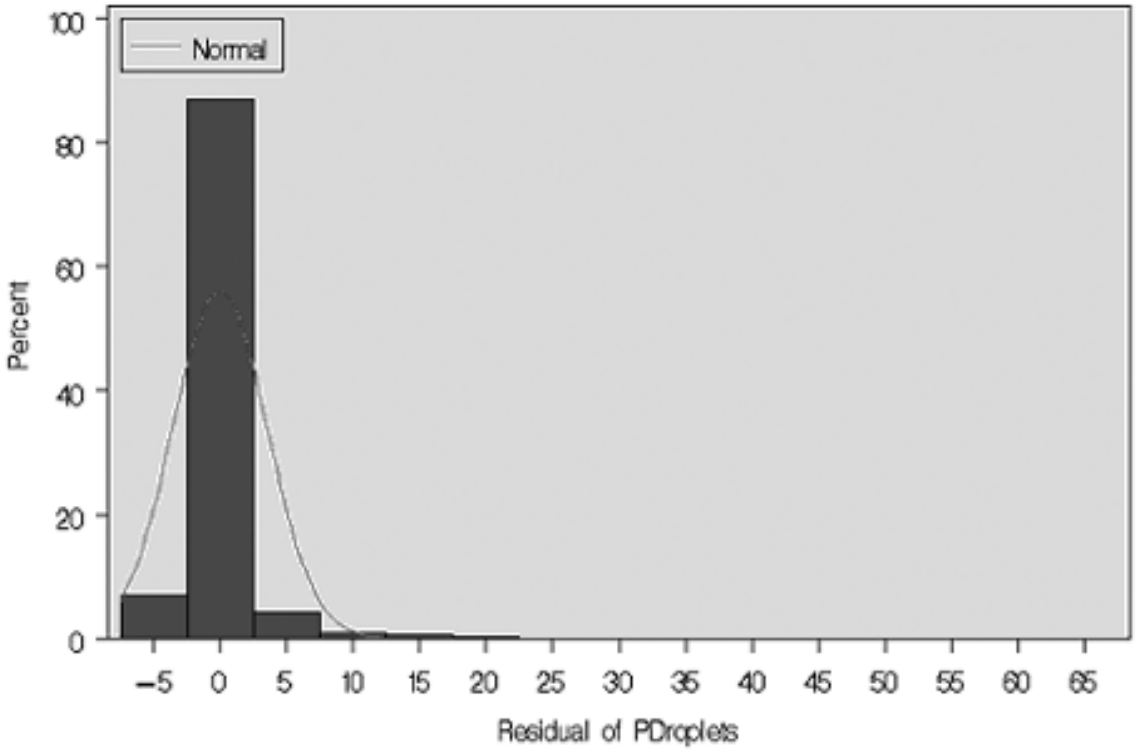


Figure 5. Residuals values after adjustment of arcsine transformed proximal cytoplasmic droplets for the fixed effects of contemporary group (year of birth and season of evaluation), age of dam, age of bull at evaluation, inbreeding level of the bull and his dam ($P < 0.05$)

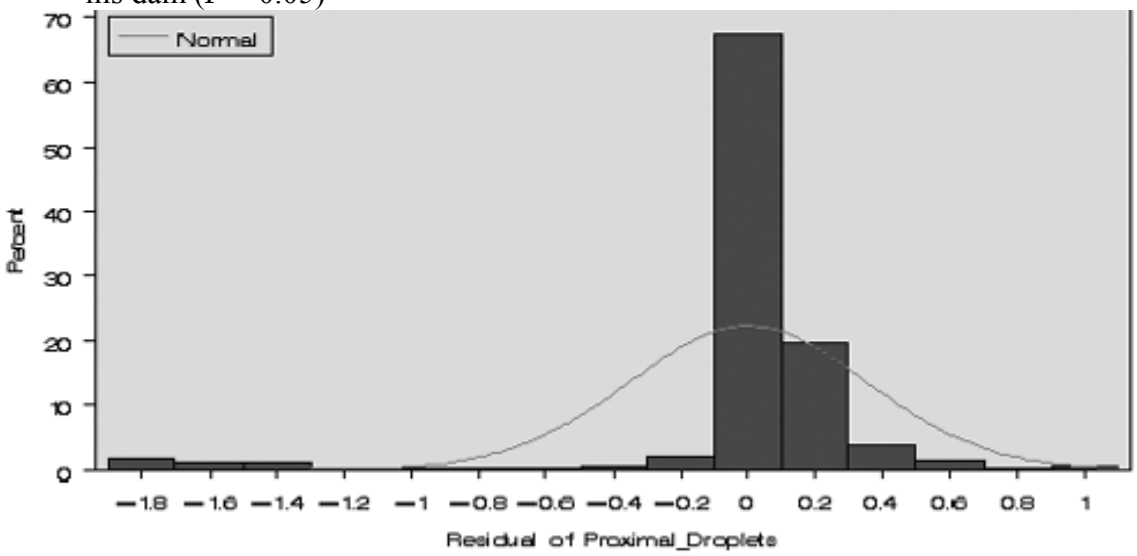


Figure 6. Residuals values after adjustment of natural log transformed proximal cytoplasmic droplets for the fixed effects of contemporary group (year of birth and season of evaluation), age of dam, age of bull at evaluation, inbreeding level of the bull and his dam ($P < 0.05$)

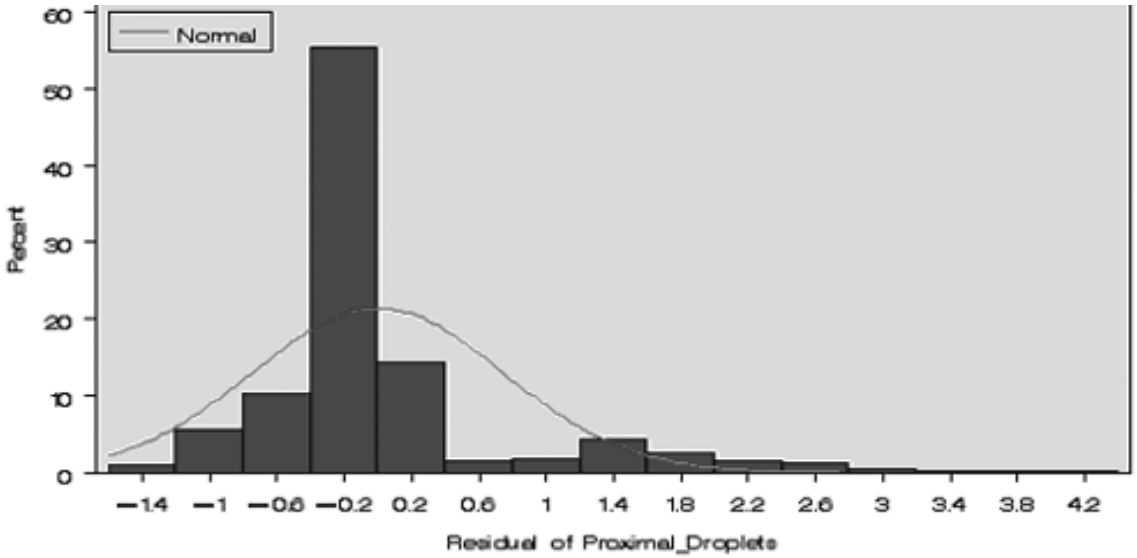
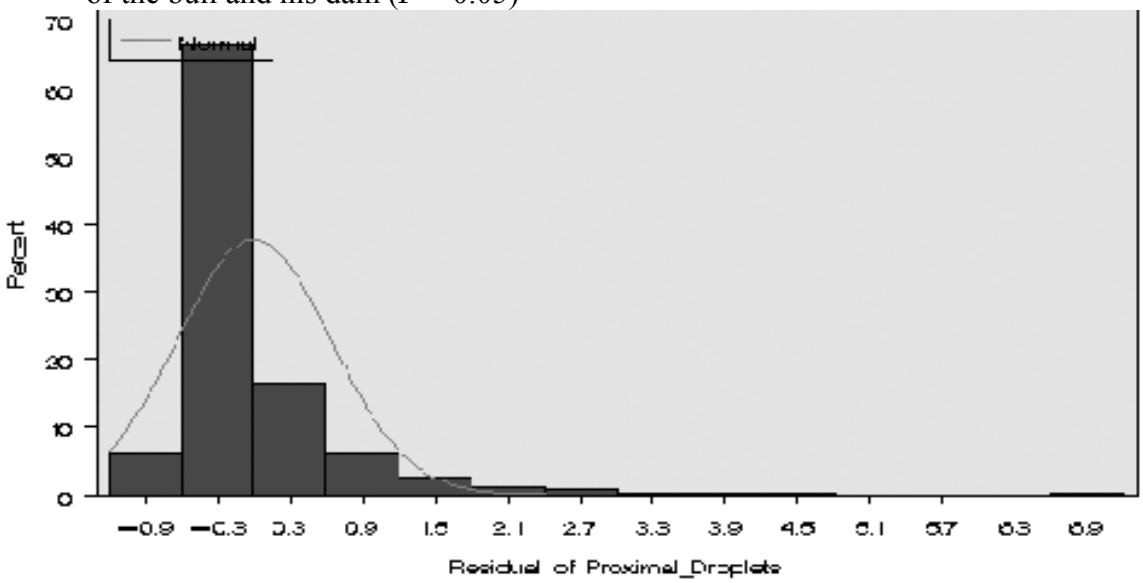


Figure 7. Residuals values after adjustment of square root transformed proximal cytoplasmic droplets for the fixed effects of contemporary group (year of birth and season of evaluation), age of dam, age of bull at evaluation, inbreeding level of the bull and his dam ($P < 0.05$)



Estimation of Parameters

Heritability estimates and correlations among traits were obtained using three different models. All models included the same fixed effects of contemporary group, age of bull at evaluation, and age of dam, and covariates of level of inbreeding of the bull and his dam, and the random effects of direct additive genetics, maternal additive genetics, and permanent maternal environment of the dam.

A single trait model was used to estimate heritability of birth weight, scrotal circumference, and semen characteristics. The equation for the single trait model was:

$$\mathbf{y} = \mathbf{X\beta} + \mathbf{Z_g u} + \mathbf{Z_m m} + \mathbf{Z_c c} + \mathbf{e}$$

where,

y is the vector of observations;

β is the vector of fixed effects (contemporary group, age of bull at evaluation, age

of dam, level of inbreeding of the bull and his dam);

u is the vector of direct additive genetic effects;

m is the vector of maternal additive genetic effects;

c is the vector of permanent maternal environmental effects;

e is the vector of random residual effects; and

X, $\mathbf{Z_g}$, $\mathbf{Z_m}$, and **$\mathbf{Z_c}$** are known incidence matrices connecting the observations to the corresponding fixed and random effects.

Correlations between birth weight and scrotal circumference and semen traits were calculated with a two trait model that was:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \beta + \begin{bmatrix} Z_{g1} & Z_{g12} \\ Z_{g21} & Z_{g2} \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} Z_{m1} & Z_{m12} \\ Z_{m21} & Z_2 \end{bmatrix} \begin{bmatrix} m_1 \\ m_2 \end{bmatrix} + \begin{bmatrix} Z_{c1} & 0 \\ 0 & Z_{c2} \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where subscript,

1 corresponds to birth weight; and

2 corresponds to scrotal circumference or a semen trait.

Correlations among semen characteristics and scrotal circumference were estimated via three-trait analyses. The model used included the same fixed effects, the two traits of interest, and birth weight. Birth weight was included in the model because it was measured on every animal and would account for any nonrandom selection of the bulls. The three trait model used was:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix} = \begin{bmatrix} X_1 & 0 & 0 \\ 0 & X_2 & 0 \\ 0 & 0 & X_3 \end{bmatrix} \beta + \begin{bmatrix} Z_{g1} & Z_{g12} & Z_{g13} \\ Z_{g21} & Z_{g2} & Z_{g23} \\ Z_{g31} & Z_{g32} & Z_{g3} \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \\ u_3 \end{bmatrix} + \begin{bmatrix} Z_{m1} & Z_{m12} & Z_{m13} \\ Z_{m21} & Z_{m2} & Z_{m23} \\ Z_{m31} & Z_{m32} & Z_{m3} \end{bmatrix} \begin{bmatrix} m_1 \\ m_2 \\ m_3 \end{bmatrix} + \begin{bmatrix} Z_{c1} & 0 & 0 \\ 0 & Z_{c2} & 0 \\ 0 & 0 & Z_{c3} \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \\ c_3 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \end{bmatrix}$$

where subscript,

1 corresponds to birth weight;

2 corresponds to scrotal circumference or a semen trait; and

3 corresponds to a semen trait other than the trait represented by 2.

Expectations of all random effects were zero. The (co)variance structures for the random effects for each model are as follows:

Single trait

$$\text{var}\begin{bmatrix} u \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} A\sigma^2_g & A\sigma_{gm} & 0 & 0 \\ A\sigma_{mg} & A\sigma^2_m & 0 & 0 \\ 0 & 0 & I\sigma^2_c & 0 \\ 0 & 0 & 0 & I\sigma^2_e \end{bmatrix}$$

two-trait

$$\text{var}\begin{bmatrix} u_1 \\ u_2 \\ m_1 \\ m_2 \\ c_1 \\ c_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma^2_{g1} & A\sigma_{g12} & A\sigma_{g1m1} & A\sigma_{g1m2} & 0 & 0 & 0 & 0 \\ A\sigma_{g2g1} & A\sigma^2_{g2} & A\sigma_{g2m1} & A\sigma_{g2m2} & 0 & 0 & 0 & 0 \\ A\sigma_{m1g1} & A\sigma_{m1g2} & A\sigma^2_{m1} & A\sigma_{m1m2} & 0 & 0 & 0 & 0 \\ A\sigma_{m2g1} & A\sigma_{m2g2} & A\sigma_{m1m2} & A\sigma^2_{m2} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & I\sigma^2_{c1} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & I\sigma^2_{c2} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & I\sigma^2_{e1} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & I\sigma^2_{e2} \end{bmatrix}$$

three-trait

$$\text{var}\begin{bmatrix} u_1 \\ u_2 \\ u_3 \\ m_1 \\ m_2 \\ m_3 \\ c_1 \\ c_2 \\ c_3 \\ e_1 \\ e_2 \\ e_3 \end{bmatrix} = \begin{bmatrix} A\sigma^2_{g1} & A\sigma_{g12} & A\sigma_{g13} & A\sigma_{g1m1} & A\sigma_{g1m2} & A\sigma_{g1m3} & 0 & 0 & 0 & 0 & 0 & 0 \\ A\sigma_{g21} & A\sigma^2_{g2} & A\sigma_{g23} & A\sigma_{g2m1} & A\sigma_{g2m2} & A\sigma_{g2m3} & 0 & 0 & 0 & 0 & 0 & 0 \\ A\sigma_{g31} & A\sigma_{g32} & A\sigma^2_{g3} & A\sigma_{g3m1} & A\sigma_{g3m1} & A\sigma_{g3m3} & 0 & 0 & 0 & 0 & 0 & 0 \\ A\sigma_{m1g1} & A\sigma_{m1g2} & A\sigma_{m1g3} & A\sigma^2_{m1} & A\sigma_{m12} & A\sigma_{m13} & 0 & 0 & 0 & 0 & 0 & 0 \\ A\sigma_{m2g1} & A\sigma_{m1g2} & A\sigma_{m2g3} & A\sigma_{m21} & A\sigma_{2m2} & A\sigma_{m23} & 0 & 0 & 0 & 0 & 0 & 0 \\ A\sigma_{m3g1} & A\sigma_{m3g2} & A\sigma_{m3g3} & A\sigma_{m31} & A\sigma_{m32} & A\sigma^2_{m3} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & I\sigma^2_{c1} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & I\sigma^2_{c2} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & I\sigma^2_{c3} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & I\sigma^2_{e1} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & I\sigma^2_{e2} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & I\sigma^2_{e3} \end{bmatrix}$$

where,

σ^2_g is the direct additive genetic variance

σ^2_m is the maternal additive genetic variance

σ^2_c is the permanent maternal environmental variance

σ^2_e is the residual variance

σ_{gij} is the covariance between additive direct genetic effects of trait i and trait j

σ_{gimk} is the covariance between additive direct and additive maternal genetic effects for trait i and k

σ_{mkml} is the covariance between additive maternal genetic effects for trait k and l

A is the relationship matrix

I is an identity matrix of dimension equal to the corresponding variance

All analyses were completed using the multiple-trait derivative-free restricted maximum likelihood (**MTDFREML**) package of programs of Boldman et al. (1995). Programs were restarted until the convergence criterion (variance of the simplex) was less than 1 x 10-9 when iterations were stopped. Once the convergence criterion was reached, the analysis was done again with different starting values. This process continued until the minimum -2 log likelihood obtained was confirmed by a second analysis with the convergence criteria differing by less than 0.001. The (co)variance components attained from the last restart were used as final results and estimates of direct heritability and proportion of variance due to permanent maternal environment were obtained.

Correlated Responses

Correlated responses in scrotal circumference and the semen characteristics to single-trait selection for reduced birth weight were predicted. Likewise, correlated responses in the semen characteristics were also calculated when selection for increased scrotal circumference was practiced.

The equations used are as follows:

Decreased birth weight

$$CR = -\sqrt{h^2}_{BW} r_{BW,i} \sigma_i$$

Increased scrotal circumference

$$CR = -\sqrt{h^2}_{SC} r_{SC,j} \sigma_j$$

Where,

h^2 is the estimated heritability of birth weight or scrotal circumference,

BW is birth weight,

SC is scrotal circumference,

r is the genetic correlation between the trait of interest and either birth weight or scrotal circumference, and

σ is the genetic standard deviation of the trait of interest.

Selection intensity was one standard deviation of either birth weight or scrotal circumference.

CHAPTER 4

RESULTS AND DISCUSSION

Heritability Estimates

Scrotal circumference and semen characteristics

Genetic, environmental, and phenotypic variances and heritability estimates are listed in table 4. Estimates were successfully obtained for all traits except percentages of spermatozoa with abnormal heads, bent tails, and distal cytoplasmic droplets. Heritability estimates ranged from low to high. Volume had the lowest estimate (0.09); whereas scrotal circumference had the highest estimate (0.57). The majority of heritability estimates were in the moderate range, 0.20 to 0.39. Heritability estimates were also calculated from the transformed data that had a distribution closest to normal to test whether or not there was a difference between estimates for the original data and the transformed data (Appendix Table 1). No differences were detected between the original and transformed data, supporting the decision to use the original data for the analyses. Scrotal circumference had the highest heritability estimate of all the traits (0.57), but it falls within the range of values reported in the literature, 0.32 to 0.71 (Table 1) (Morris et al., 1992; Evans et al., 1999). Bourdon and Brinks (1986) and Kriese et al. (1991) estimated the heritability of scrotal circumference to be 0.53, similar to the estimate reported here. In a review paper, Koots et al. (1994a) reported an average heritability estimate of 0.45. All of the estimates place scrotal circumference as a moderate to highly heritable trait, which is unusual for a reproductive trait. Most often reproductive traits have low heritability estimates (Koots et al., 1994a). One possible reason the heritability

estimate for scrotal circumference is high is that scrotal circumference may also be considered a growth trait and on average growth traits are of moderate to high heritability (Koots et al., 1994a). The heritability estimate of 0.57 implies that 57% of the variance of circumference of the scrotum is determined by the additive effects of genes that animal received from its parents and response to genetic selection is probable. The remaining 43% of the variance of the circumference measurement results from the non-additive genetic and environmental effects.

Table 4. Estimates of genetic variance (σ^2_g), environmental variance(σ^2_e), phenotypic variance(σ^2_p), and heritability(h^2) of scrotal circumference and semen characteristics

Trait	σ^2_g	σ^2_e	σ^2_p	h^2
Scrotal circumference	1.96	1.49	3.45	0.57
Color	0.10	0.54	0.64	0.15
Volume	0.25	2.65	2.90	0.09
Concentration	0.15	0.78	0.93	0.16
Swirl	0.35	1.35	1.70	0.21
Motility	0.28	1.02	1.31	0.22
Live, %	30.51	104.64	135.16	0.23
Normal spermatozoa, %	53.02	104.12	157.14	0.34
Primary abnormalities, %	53.94	104.23	155.69	0.34
Abnormal heads, %	NP	NP	NP	NP
Abnormal mid-pieces, %	12.46	58.86	71.31	0.17
Proximal cytoplasmic droplets, %	5.52	10.55	16.07	0.34
Secondary abnormalities, %	29.37	71.40	100.10	0.29
Bent tails, %	NP	NP	NP	NP
Coiled tails, %	13.32	31.35	44.67	0.30
Distal cytoplasmic droplets, %	NP	NP	NP	NP

NP - estimates were not obtained

Ejaculate color had a heritability estimate of 0.15, which is considered low and implies that additive gene effects have a minor effect on the color of the ejaculate. There are no other heritability estimates for color in the literature for comparison. Color of the ejaculate was visually measured on a scale of 0 (clear, water-like) to 5 (thick, creamy, measurable pearl). Even though the same evaluator scored all ejaculates used in this study, there is a possibility that the scale changed over the years. This change would introduce some environmental error, which would have reduced the heritability estimate.

The lowest heritability estimate of 0.09 was for semen volume. This value falls close to the heritability estimate reported by Rege et al. (2000) of 0.11 for 12-month-old rams. Concentration also had a low heritability estimate of 0.16. The range of values within the literature, 0.13 to 0.17, support the estimate reported here (Knights et al., 1984; Rege et al., 2000). The low estimates for both traits indicate that environment has a great influence on these traits. A possible source of environmental variation for both traits is the use of an electro-ejaculator to obtain the semen samples. Over the 40 years during which the study took place, numerous people operated the electro-ejaculator. Bulls also react differently to electro-ejaculators, which may have increased environmental variation.

Percent motile spermatozoa and swirl both had moderate heritability estimates, 0.22 and 0.21, respectively. Percent motile spermatozoa can be considered motility of individual spermatozoa, for which Rege et al. (2000) reported a heritability estimate of 0.16 in 12-month-old rams. The estimate for percent motile spermatozoa of 0.22 reported here and the estimate reported by Rege et al. (2000) are similar. A heritability estimate for mass motility, which is comparable to swirl, was reported by Rege et al. (2000). The

value given by Rege et al. (2000) of 0.27 is slightly higher than the estimate for swirl stated here (0.21), but the two values are supportive of a moderate heritability for this indicator of vitality of the spermatozoa. Heritability estimates for overall motility (individual or mass was not identified) have been reported in the literature by Knights et al. (1984) and Smith et al. (1989a), as 0.13 and 0.04 respectively. These two estimates are much lower then either estimate from this study. Differences between the values reported here and those in the literature could be due to different measurements of motility being analyzed in each study.

Estimated heritability for percentage of live spermatozoa in an ejaculate was 0.23. There is a void in the literature for other estimates of percent live spermatozoa. However, Rege et al. (2000) reported a value for percentage of dead spermatozoa in an ejaculate of 0.01, which implies environment plays a large role in the proportion of dead and conversely live spermatozoa. The estimate reported here implies that additive genetics does have an influence on percent live spermatozoa, contradictory to the estimate reported by Rege et al. (2000).

Percent normal spermatozoa had a moderate heritability estimate of 0.34. Smith et al. (1989a) reported an estimate of 0.07, which is substantially less than the estimate calculated in this study. The difference between the two estimates could be from different types of analysis. Smith et al. (1989a) used least squares, while maximum likelihood methods were used in this study. Differences in populations used could have also contributed to the differences in the heritability estimates between studies.

Percent spermatozoa with primary abnormalities had a heritability estimate of 0.34 and the traits that compose primary abnormalities had similar heritability estimates,

with the exception of percent spermatozoa with abnormal heads because an estimate was not attained. Percents of spermatozoa with abnormal mid-pieces and proximal cytoplasmic droplets had heritability estimates of 0.17 and 0.34, respectively. The estimate for percent primary abnormal spermatozoa from this study is supported by the value of 0.31 reported by Smith et al. (1989a). This supports the common belief that primary abnormalities are of genetic origin and as a result permanent.

Heritability of percent spermatozoa with secondary abnormalities was estimated to be 0.29. Heritability estimates were unattainable for percent spermatozoa with bent tails and distal cytoplasmic droplets, which are two of the three traits that make up secondary abnormalities. The remaining trait of percent spermatozoa with coiled tails had an estimated heritability of 0.30, which is very close to the estimate for percent secondary abnormalities. The only value in the literature for either percent secondary abnormalities or percent of spermatozoa with coiled tails was reported by Smith et al. (1989a) for percent secondary abnormalities, 0.02. The two values differ considerably from one another. The estimate from this study suggests that environment does not influence secondary abnormalities as much as the estimate by Smith et al. (1989a) suggests it does.

Secondary abnormalities are commonly thought to be influenced predominantly by the environment, which results from the study by Smith et al. (1989a) support. However, the result from this study suggests otherwise. The present heritability estimate of 0.29 indicates that a sizeable additive genetic influence on secondary abnormalities exists. Differences between the estimates may be a result of different methods of analysis and the use of different populations. Another reason for the difference could be

the lack of variation in both percent of spermatozoa with distal cytoplasmic droplets and percent spermatozoa with bent tails within the present data set. The mean values for distal cytoplasmic droplets and bent tails were 0.048% and 1.405%, respectively. Heritability estimates depend on variation and the lack of variation in distal cytoplasmic droplets and bent tails resulted in heritability estimates not being obtained for these traits. A further consequence of this lack of variation was that the heritability estimate for percentage of secondary abnormalities was almost completely dependent upon the variation in percent spermatozoa with coiled tails. Because the heritability estimate for secondary abnormalities was predominantly based upon percent coiled tails, the heritability estimate for secondary abnormalities and percent coiled tails were similar, 0.29 and 0.30, respectively. If heritability estimates for the other two traits had been obtained, perhaps the estimate presented here for secondary abnormalities would have been similar to the estimate by Smith et al. (1989a) and supported the belief that secondary abnormalities were mainly influenced by the environment.

Birth weight

Direct, maternal, and total (Willham, 1972) heritability estimates for birth weight were, 0.46, 0.23, and 0.24, respectively. In a review paper by Koots et al. (1994a) heritability estimates for direct and maternal birth weight were reported, 0.35 and 0.18, respectively. Differences between estimates could be due to the mixture of breeds used in the review paper. Koots et al. (1994a) also included heritability estimates for direct birth weight heritability by breed. Direct heritability for birth weight in the Hereford populations included by Koots et al. (1994a) was 0.40, which is supportive of the estimate reported here for direct heritability.

Genetic Correlations.

Estimates of genetic correlations and covariances between semen characteristics are listed in table 5. If a heritability estimate was not obtained for a trait, then it was excluded from farther analyses and no correlations were calculated. Relationships ranged from weak to strong in both positive and negative directions.

The majority of the semen characteristics had favorable genetic correlations with each other. Traits where high or low values were desirable in both traits usually had a positive relationship, such as motility and percentage of normal spermatozoa (0.51). Negative relationships were reported between traits where a high value in one trait and a low value in the other trait were desirable. Usually the negative correlations were between spermatozoa abnormalities and the other traits, such as ejaculate volume. All of the favorable genetic correlations are promising because they indicate that positive selection in a bull for one semen characteristics could benefit majority of the other semen characteristics in his male progeny.

There were a few unfavorable genetic correlations between semen characteristics. Ejaculate volume was negatively correlated with percent live and motility, -0.09 and -0.38, respectively. Additional undesirable correlations involved proximal cytoplasmic droplets. Motility, percentage of spermatozoa with coiled tails, and percentage of live spermatozoa had unfavorable genetic correlations with proximal cytoplasmic droplets, 0.32, -0.18, and 0.53, respectively.

Table 5. Genetic correlations (above diagonal) and covariances (below diagonal) for semen characteristics

	COL	VOL	SW	CN	MOT	NORM	CT	ABM	PD	LIVE	1° AB	2° AB
COL		-0.59	0.39	NP	0.42	0.18	0.12	0.01	-0.36	0.13	0.16	-0.35
VOL	-0.10		NP	NP	-0.38	0.32	-0.05	-0.38	-0.15	-0.09	0.33	-0.34
SW	0.07	NP		0.85	NP	0.44	-0.07	-0.56	-0.07	0.82	0.48	-0.47
CN	NP	NP	0.18		0.81	0.36	NP	-0.31	-0.27	NP	0.36	-0.58
MOT	0.06	-0.09	NP	0.15		0.51	-0.12	-0.74	0.32	NP	0.57	-0.54
NORM	0.37	1.13	1.79	0.96	1.79		-0.78	NP	-0.49	0.32	NP	NP
CT	0.13	-0.08	-0.14	NP	-0.21	-18.13		NP	-0.18	-0.05	NP	NP
ABM	0.01	-0.66	-1.12	-0.41	-1.29	NP	NP		0.37	-0.76	NP	NP
PD	-0.25	-0.18	-0.09	-0.22	0.36	-7.40	-1.45	2.64		0.53	NP	NP
LIVE	0.22	-0.24	2.50	NP	NP	12.16	-0.98	5.17	6.96		0.33	-0.43
1° AB	4.41	3.21	2.10	0.01	2.23	NP	NP	NP	NP	13.20		-0.87
2° AB	-2.94	-2.42	-1.44	-1.20	-1.54	NP	NP	NP	NP	-12.91	-32.27	

BW - birth weight, SC - scrotal circumference, COL - ejaculate color, VOL - ejaculate volume, SW - swirl, CN - concentration, MOT - motility, NORM - percent normal spermatozoa, CT - percent coiled tails, ABM - percent abnormal mid-pieces, PD - percent proximal cytoplasmic droplets, LIVE - percent live spermatozoa, 1° AB - percent primary abnormalities, 2° AB - percent secondary abnormalities; NP - estimates were not obtained

Birth weight and scrotal circumference (Table 6) were found to have a moderate and positive genetic correlation of 0.36. This estimate is much higher than the range of 0.02 to 0.10 reported in the literature (Knights et al., 1984; Kriese et al., 1991; Koots et al., 1994b). In a review paper by Koots et al. (1994b) an average genetic correlation between birth weight and scrotal circumference of 0.10 was reported. The results presented here indicate a much stronger genetic relationship between birth weight and scrotal circumference than was previously reported. Differences could be attributed to the number of bulls in the data sets. The majority of the data in the literature came from breed associations and data for this study was from the Line 1 Hereford research herd. Data sets from the breed associations were much larger than the data set for this research. Larger data sets usually result in an estimate closer to the true population parameter because it is a larger sample of the population in question. The data set in this study is relatively small and the estimate presented here may be subject to greater sampling variance due to the fewer numbers of observations. However, data from research stations may have less environmental variance owing to standardized collection, recording, and editing procedures.

Ejaculate color, concentration, and swirl had strong, positive genetic correlations with birth weight, 0.60, 0.58, and 0.44, respectively. Birth weight was also moderately and positively correlated with spermatozoa motility and percentages of normal and live spermatozoa, 0.21, 0.20, and 0.34, respectively. Percent spermatozoa with proximal cytoplasmic droplets, bent tails, abnormal mid-pieces, and secondary abnormalities were all negatively correlated with birth weight, -0.52, -0.20, -0.03, and -0.16, respectively.

Table 6. Genetic correlations between birth weight, scrotal circumference, and semen characteristics and prediction of correlated responses to selection for decreased birth weight (h^2= 0.46) and increased scrotal circumference (h^2 = 0.57)

Trait	$r_{gBW,j}$	$CR_{BW,j}$	$r_{gSC,j}$	$CR_{SC,j}$
Scrotal circumference	0.36	0.34		
Color	0.6	0.13	0.73	0.17
Volume	0.07	0.02	0.2	0.08
Concentration	0.58	0.15	NP	NP
Swirl	0.44	0.18	0.4	0.18
Motility	0.21	0.08	0.34	0.14
Live, %	0.34	1.27	NP	NP
Normal spermatozoa, %	0.2	0.99	NP	NP
Primary abnormalities, %	0.16	0.80	0.36	2.00
Abnormal mid-pieces, %	-0.03	-0.07	-0.36	-0.96
Proximal cytoplasmic droplets, %	-0.52	-0.83	-0.37	-0.66
Secondary abnormalities, %	-0.16	-0.59	-0.45	-1.84
Coiled tails, %	-0.2	-0.50	-0.12	-0.33

NP - estimates were not obtained

These relationships indicate that male progeny sired by bulls with low breeding values for birth weight may be at risk of poor fertility. The positive correlations reported between birth weight and majority of the semen characteristics result in male progeny having low values for semen traits where high values are desired if bulls with low breeding values for birth weight are used as herd sires. Low values in traits, such as percentage of live spermatozoa and motility, put bulls at risk of failing a breeding soundness evaluation. Male progeny of bulls with low breeding values for birth weight are also at risk of failing a breeding soundness evaluation because of the negative relationship between birth weight and many of the spermatozoa abnormalities. The negative relationship indicates that with selection for decreased birth weight of a bull, spermatozoa abnormalities in his progeny will increase. Breeding soundness evaluations

require a minimum of 70% normal spermatozoa, which a bull may be at greater risk of not meeting if percentage of abnormalities increases.

Positive genetic correlations were calculated between scrotal circumference and color of ejaculate, swirl, ejaculate volume, and spermatozoa motility, 0.73, 0.40, 0.20, and 0.34, respectively (Table 6). From the positive relationship between scrotal circumference and ejaculate volume the inference can be made that bulls with large scrotums will sire progeny that could produce greater amounts of semen than if bulls with smaller scrotums were used as sires. Negative genetic correlations exist between scrotal circumference and percents of spermatozoa with abnormal mid-pieces, proximal cytoplasmic droplets, secondary abnormalities, and coiled tails, -0.36, -0.37, -0.43, and -0.12, respectively. These correlations suggest that abnormalities of the spermatozoa that cause a bull to fail a breeding soundness evaluation decrease as the scrotal circumference of the bull's sire increases. Likewise, traits that negatively impact bull fertility will decrease in the male progeny with selection for increased scrotal circumference of the sire. Overall these relationships indicate an increased chance of a bull passing a breeding soundness evaluation if his sire had a large scrotal circumference. However, the positive genetic correlation between scrotal circumference and percent primary abnormalities (0.36) could be problematic if herd sires were selected for increased scrotal circumference. Bulls produced by these sires could experience an increase in primary abnormalities, which would reduce their chances of passing a breeding soundness evaluation. Therefore, some consideration should be taken when selecting herd sires with large scrotal circumference.

Correlated Responses

Predicted correlated responses to selection for decreased birth weight in scrotal circumference and semen traits are listed in table 6. Selection for low birth weight could cause negative effects on a majority of the traits. Given the preceding results and selection intensity equal to 1.0, the direct response to selection for decreased birth weight would be -2.12 kg. Percent live and normal spermatozoa were positively correlated with birth weight and would decrease along with birth weight when selection for decreased birth weight was practiced, -1.27% and -0.99% per unit of selection intensity applied to birth weight, respectively. Unfortunately, greater values of these traits are desirable and increase the probability of a bull passing a breeding soundness evaluation. With selection for a 2 standard deviation decrease in birth weight 21 more bulls would be expected to fail the breeding soundness evaluation because the minimum requirements for scrotal circumference or percentage of normal spermatozoa would no longer be met. Also, majority of the abnormalities are negatively correlated with birth weight and would thus increase if low birth weight selection was practiced. The percent decrease in percent normal spermatozoa and greater numbers in abnormal spermatozoa place bulls at risk of not meeting the 70% normal spermatozoa requirement of the breeding soundness evaluation. The possibility of negatively effecting semen characteristics in bulls being retained should be considered when selection for low birth weight is practiced.

The only favorable outcome in a semen trait if selection for decreased birth weight was practiced would be in percent primary abnormalities. A positive relationship exists between birth weight and percent primary abnormalities. If birth weight was decreased by one standard deviation or -2.12kg, then percent primary abnormalities

would be expected to decrease in the male progeny by 0.80%. Reducing primary abnormalities increases a bull's chance of passing the breeding soundness evaluation and being classified as a satisfactory breeder.

Selection for increased scrotal circumference would have a positive effect on majority of semen characteristics (Table 6). The direct response to selection for increased scrotal circumference was 1.06cm. The largest positive impact would be on spermatozoa abnormalities. Percent abnormal mid-pieces and secondary abnormalities would be expected to decrease by 0.96% and 1.84%, respectively, as scrotal circumference increased. Unfortunately the response to selection in percentage of normal spermatozoa was unattainable; therefore the effect of selection on the additional numbers of bulls passing a breeding soundness evaluation as a result of selection for increased scrotal circumference can not be determined. However, the relationships between scrotal circumference and many of the spermatozoa abnormalities could result in more bulls exceeding the threshold for normal morphology of spermatozoa in breeding soundness evaluations.

The only relationship that warrants concern is between scrotal circumference and percent primary abnormalities. Percent primary abnormalities are expected to increase by 2% per unit of selection intensity applied to scrotal circumference. Compared to the changes in the rest of the semen traits, this change is considerable. A bull must meet a minimum scrotal circumference to pass a breeding soundness evaluation, however selection for increased scrotal circumference in order to reach the minimum scrotal circumference may have adverse effects on his male progeny. If the male progeny

remained intact and were used as breeding stock, then their fertility may be reduced due to an increased percentage of primary abnormalities.

Phenotypic Correlations

Phenotypic correlations between birth weight and all other traits were weak and ranged from -0.02 to 0.18 (Table 7). The weak correlations between birth weight and all traits suggest that birth weight would not be a reliable indicator for yearling scrotal circumference and semen quality.

Weak phenotypic correlations were calculated between scrotal circumference and semen characteristics (Table 7). The directions of the phenotypic correlations were consistent with those for the genetic correlations for all traits. Relationships between scrotal circumference and semen characteristics suggest that scrotal circumference may be a helpful indicator of semen quality, especially for swirl (0.18) and percent abnormal mid-pieces (-0.20). These findings are in agreement with Coe (1999), who reported a positive relationship between scrotal circumference and semen quality. Because these correlations are not strong, scrotal circumference should be used in combination with other measures in determining semen quality.

Most phenotypic correlations among semen traits were weak, but favorable (Table 7). Stronger correlations were between traits that are logically connected, such as percent normal spermatozoa and percent coiled tails (-0.55). Swirl and percent live were also strongly correlated, 0.47, which makes sense because a spermatozoa must be alive to move.

Table 7. Phenotypic correlations (above diagonal) and covariances (below diagonal) for semen characteristics

	BW	SC	COL	VOL	SW	CN	MOT	NORM	CT	ABM	PD	LIVE	1° AB	2° AB
BW		0.18	0.04	-0.02	0.06	0.07	0.04	0.02	-0.04	-0.01	-0.01	0.08	0.01	-0.01
SC	1.51		0.16	0.08	0.18	NP	0.13	NP	-0.03	-0.20	-0.17	NP	0.02	0.00
COL	0.14	0.24		0.09	0.45	NP	0.27	0.18	-0.01	-0.12	-0.20	0.15	0.19	-0.21
VOL	-0.16	0.26	0.12		NP	NP	0.00	0.09	-0.06	-0.02	-0.08	0.13	0.09	-0.06
SW	0.34	0.45	0.47	NP		0.64	NP	0.38	-0.17	-0.31	-0.12	0.47	0.39	-0.33
CN	0.32	NP	NP	NP	0.81		0.40	0.25	NP	-0.19	-0.21	NP	0.00	-0.27
MOT	0.23	0.28	0.25	-0.01	NP	0.44		0.40	-0.21	-0.36	0.00	NP	0.42	-0.35
NORM	0.87	NP	1.85	1.84	6.22	3.00	5.79		-0.55	NP	-0.33	0.40	NP	NP
CT	-1.24	-0.32	-0.06	-0.71	-1.45	NP	-1.61	-46.18		NP	-0.07	-0.14	NP	NP
ABM	-0.44	-3.08	-0.83	-0.32	-3.46	-1.52	-3.49	NP	NP		0.06	0.00	NP	NP
PD	-0.10	-1.23	-0.64	-0.52	-0.61	-0.80	-0.01	-16.79	-1.95	2.05		0.07	NP	NP
LIVE	4.16	NP	1.40	2.50	7.05	NP	NP	57.80	-10.99	-38.61	3.12		0.40	-0.36
1° AB	0.70	0.36	1.89	1.87	6.35	0.01	5.97	NP	NP	NP	NP	58.23		-0.81
2° AB	-0.32	-0.043	-1.68	-1.08	-4.32	-2.62	-3.97	NP	NP	NP	NP	-42.22	-100.62	

BW - birth weight, SC - scrotal circumference, COL - ejaculate color, VOL - ejaculate volume, SW - swirl, CN - concentration, MOT - motility, NORM - percent normal spermatozoa, CT - percent coiled tails, ABM - percent abnormal mid-pieces, PD - percent proximal cytoplasmic droplets, LIVE - percent live, 1° AB - percent primary abnormalities, 2° AB - percent secondary abnormalities

NP - estimates not obtained

Three phenotypic correlations were unfavorable: percent proximal cytoplasmic droplets and percent live; and percent primary abnormalities with color and volume, 0.07, 0.19, and 0.09, respectively. High numbers of percent live are desirable, however, this relationship indicates that high numbers of percent live will result in high numbers of percent proximal cytoplasmic droplets. Bulls are at risk of failing a breeding soundness evaluation if percent proximal cytoplasmic droplets surpasses the 29% of abnormalities allowed by the breeding soundness evaluation (Chenoweth et al., 1992). Fortunately, these phenotypic correlations indicate only weak associations between these traits.

CHAPTER 5

CONCLUSIONS

Heritability estimates were obtained for scrotal circumference and the majority of the semen characteristics indicating that these traits are at least partly influenced by additive genetic effects. The influence of additive genetics is greater for some traits, such as scrotal circumference, where heritability estimates are higher. Because these traits are heritable, selection is expected to be effective. Response to selection will vary depending on phenotypic variability, the heritability, and the intensity of selection. Traits with high heritability estimates will respond to selection faster than traits with low heritability estimates because a larger proportion of the phenotype is passed on to the next generation and environment has less of an influence.

Birth weight and scrotal circumference in a bull may be indicators of semen traits in their male progeny because the majority of the genetic correlations between birth weight or scrotal circumference and the semen characteristics are moderate to strong. Scrotal circumference of a sire may be indicative of swirl and spermatozoa motility in male progeny. Both of these traits are important in breeding soundness evaluations. Therefore, scrotal circumference of a bull may provide some insight into the outcome of breeding soundness evaluations of his progeny.

Selection of sires for decreased birth weight may result in negative impacts on scrotal circumference and semen characteristics in their progeny. Decreased birth weight could cause traits where high values are desirable to decrease, while spermatozoa abnormalities increased. Both of these effects are detrimental to a bull's fertility.

However, selection for increased scrotal circumference could have positive effects on semen characteristics. Selection for increased scrotal circumference would result in spermatozoa abnormalities decreasing and the other traits increasing, which is beneficial to fertility and passing a breeding soundness evaluation.

Phenotypic correlations of scrotal circumference and semen traits with birth weight were weak and thus largely uninformative. Thus, birth weight would not be a reliable predictor of yearling scrotal circumference and semen characteristics. However, phenotypic correlations between scrotal circumference and semen characteristics were moderate and indicated that scrotal circumference would be a reliable indicator of yearling semen traits as long as it was used with other methods to predict bull fertility. Phenotypic correlations among semen traits were moderate and the strongest correlations were between traits that have a part-whole relationship with each other.

CHAPTER 6

IMPLICATIONS

Improvements in traits important to bull fertility and those stressed by breeding soundness evaluations are possible through genetic selection. However, not all correlations among traits were favorable. Therefore, caution should be taken when selecting for only one trait at a time to avoid negative impacts on components of bull fertility. Consideration should be taken when retaining bulls sired by bulls with low birth weights because of the unfavorable genetic correlations of scrotal circumference and semen characteristics with birth weight. Selection for decreased birth weight should be practiced with caution because of the negative impacts on semen characteristics that may jeopardize a bull's chance of passing a breeding soundness evaluation. Also birth weight should not be used as an indicator of yearling scrotal circumference and semen traits based in the phenotypic correlations between scrotal circumference and semen characteristics with birth weight.

Semen characteristics may be positively impacted by selection for increased scrotal circumference. Favorable relationships existed between scrotal circumference and majority of semen characteristics important to bull fertility. Selection for increased scrotal circumference should not hinder the ability of a bull's progeny to pass a breeding soundness evaluation. However, scrotal circumference should be used in combination with other methods to form a reliable predictor of bull fertility.

CHAPTER 7

INFORMATION NEEDS

More knowledge is needed to understand the relationships between growth traits and bull fertility. Correlations, both genetic and phenotypic, of weaning weight and yearling weight with semen characteristics would be beneficial. These correlations may provide further insight in to bull fertility and a new method in prediction of fertility.

More studies of primary and secondary abnormalities are needed to determine the biological basis of these traits. Studies report contradicting results as to which factor, either genetic or environmental, influences secondary abnormalities. With more studies estimating heritability of these characteristics, a firmer conclusion could be drawn.

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APPENDIX A

HERITABILITY AND CORRELATION ESTIMATES

Table A-1. Heritability estimates (h^2) for semen characteristics[a] after transformation that resulted in the distribution of residuals after fitting effects of contemporary group and age of dam and the covariates of age of bull at evaluation, inbreeding level of the bull and his dam closest to normal

Trait	h^2
Volume[1]	0.06
Swirl[1]	0.18
Normal spermatozoa, %[3]	NP
Abnormal heads, %[1]	NP
Abnormal mid-pieces, %[2]	0.16
Proximal cytoplasmic droplets, %[2]	0.12
Bent tails, %[2]	0.08
Coiled tails, %[2]	0.09
Distal cytoplasmic droplets, %[2]	NP

[a] traits where original values resulted in residual distributions closest to normal were not included in the table; [1] square root transformation; [2] natural log transformation; [3] arcsine transformation; NP - estimates were not obtained

Table A-2. Environmental correlations (above diagonal) and covariances (below diagonal) among semen characteristics

	COL	VOL	SW	CN	MOT	NORM	CT	ABM	PD	LIVE	1° AB	2° AB
COL		0.18	0.47	NP	0.25	0.20	-0.05	-0.15	-0.16	0.16	0.2	-0.17
VOL	0.22		NP	NP	0.05	0.04	-0.07	0.03	-0.06	0.16	0.04	-0.01
SW	0.40	NP		0.61	NP	0.37	-0.20	-0.26	-0.13	0.38	0.36	-0.29
CN	NP	NP	0.63		0.32	0.22	NP	-0.16	-0.20	NP	0.22	-0.19
MOT	0.19	0.08	NP	0.29		-0.38	-0.24	-0.28	-0.11	NP	0.36	-0.28
NORM	1.48	0.71	4.43	2.04	4.00		-0.48	NP	-0.27	0.43	NP	NP
CT	-0.19	-0.63	-1.31	NP	-1.40	-28.05		NP	-0.03	-0.17	NP	NP
ABM	-0.85	0.34	-2.34	-1.12	-2.20	NP	NP		-0.02	-0.30	NP	NP
PD	-0.39	-0.33	-0.51	-0.57	-0.36	-9.39	-0.50	-0.59		-0.12	NP	NP
LIVE	1.18	2.74	4.55	NP	NP	45.64	-10.01	-23.78	-3.86		0.43	-0.34
1° AB	1.55	0.73	4.26	2.04	3.75	NP	NP	NP	NP	45.03		-0.78
2° AB	-1.08	-0.19	-2.88	-1.48	-2.43	NP	NP	NP	NP	-29.31	-68.38	

COL - ejaculate color, VOL - ejaculate volume, SW - swirl, CN - concentration, MOT - motility, NORM - percent normal spermatozoa, CT - percent coiled tails,

ABM - percent abnormal mid-pieces, PD - percent proximal cytoplasmic droplets, LIVE - percent live,1° AB - percent primary abnormalities,

2° AB - percent secondary abnormalities; NP- estimates were not obtained