

ABSTRACT

OH, SANG HYON. Estimation of Genetic Parameters for Boar Semen Traits. (Under the direction of Miles Todd See.)

During the last half of the 20th century, the world pork industry has achieved astonishing developments in pig breeding. Now swine farms are larger, ownership more concentrated, and farms have become more industrialized. Artificial insemination (AI) plays an important role in animal breeding increasing utilization of genetically superior sires. Currently boars selected for commercial use as AI sires are evaluated on grow-finish performance and carcass characteristics. The objectives of this study were to (A) estimate genetic correlations between production and semen traits in the boar; average daily gain (ADG), back fat thickness (BF) and muscle depth (MD) as production traits, and total sperm cells (TSC), total concentration (TC), volume collected (SV), number of extended doses (ND), and acceptance rate of ejaculates (AR) as semen traits; (B) to model the variances and covariances of total sperm cells ($\times 10^9$) over the active lifetime of AI boars; and (C) to compare multiple traits and random regression analyses applied to total sperm cells (TSC). Average heritability estimates were 0.39 for ADG, 0.32 for BF, 0.15 for MD, and repeatability estimates were 0.38 for SV, 0.37 for TSC, 0.09 for TC, 0.39 for ND, and 0.16 for AR. Semen traits showed negative genetic correlations with MD. Genetic correlations would indicate that current selection objectives are having a negative effect on semen traits. Therefore, current AI boar selection practices may be having a detrimental effect on semen production. In random regression analysis for total

sperm cells, maximum log likelihood value was observed for sixth, fifth, and seventh order polynomials for fixed, additive genetic and permanent environmental effects, respectively. Best fit as determined by Akaike's Information Criterion was based on a model with sixth, fourth, and seventh order polynomials for fixed, additive genetic and permanent environmental effects, respectively. Best fit as determined by Schwarz Criterion was by fitting fourth, second, and seventh order polynomials for fixed, additive genetic and permanent environmental effects, respectively. Heritability estimates for total sperm cells ranged from 0.27 to 0.61 across age of boar classifications. Heritability for total sperm cells tended to increase with age of boar classification. The cyclic nature of heritability for total sperm cells that was observed over the active lifetime of boars may be due in part to number of observations across seasons limiting our ability to correct for seasonal effects on sperm production. In MTDFREML analysis, heritability estimates of 9, 12, 15, 18, 21, 24, and 27 months of age were, respectively, 0.28, 0.29, 0.26, 0.27, 0.30, 0.79, and 0.41. The results from MTDFREML seemed to be overestimated when compared to random regression. Therefore, random regression methods are the most appropriate to analyze semen traits as they are longitudinal data measured over the boars lifetime.

ESTIMATION OF GENETIC PARAMETERS FOR BOAR SEMEN TRAITS

by

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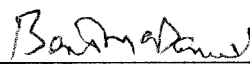
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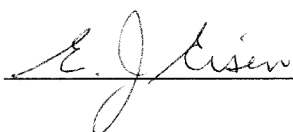
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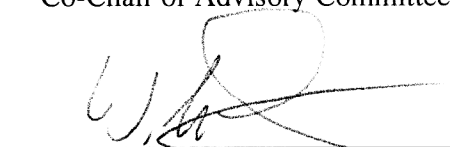


Co-Chair of Advisory Committee



Co-Chair of Advisory Committee





This work is dedicated to
My parents
Chang-Soo Oh and Bok-Soon Lee

BIOGRAPHY

Sang Hyon Oh, son of Chang-Soo Oh and Bok-Soon Lee was born on January 14, 1973, in Seoul, South Korea. He resided with his parents and his four sisters Hee-Jung Oh, Hee-Kyung Oh, Kyung-June Oh, and Sang-Hwan Oh in Seoul, and graduated from Chung-am high school in 1991. He graduated in 1995 from Seoul National University, with a Bachelor of Science degree in Animal Science. He then completed a Master of Science degree in Animal Science from Seoul National University in 1997. He worked as a research assistant in Institute of Animal Science and Technology at Seoul National University from March, 1997 to February, 1998. He entered the PhD program in Animal Science at Seoul National University in March, 1998, however, He began the PhD program at North Carolina State University under the direction of Dr. Todd See in August, 1998. During the PhD program, he married Song-Yee Han on December 26, 1999, his son and daughter, Hans Jin-Young Oh and Hannah Min-Young Oh, were born on July 29, 2001 and February 4, 2003, respectively.

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LIST OF ABBREVIATIONS

- ADG,** average daily gain
- AR,** Acceptance rate of ejaculates
- BF,** back fat
- MD,** muscle depth
- ND,** Number of extended doses
- SV,** semen volume
- TC,** total concentration
- TSC,** total sperm cells

CHAPTER I

LITERATURE REVIEW

1.1 Introduction

Estimating genetic parameters for various livestock traits has been a main topic of animal breeding during the past half century. Now, in addition to statistical animal breeding, molecular genetics is receiving great emphasis. In a sense, studying statistical breeding at this moment, while epoch-making events in animal genetics are researched from finding QTL to cloning, might look a little outdated. However, advances in statistical animal breeding and broadening its range of application and traits of interest also provide great opportunities for animal agriculture.

During the last half century, the world pork industry has achieved astonishing developments in pig breeding. Now, the industry is larger and more concentrated, and farms have become more industrialized (Singleton, 2001). Therefore, the reality is that selection by existing statistical breeding methods have not yet been fully exploited. An example of industrialization in livestock is the introduction of artificial insemination (AI), which plays an important role in animal breeding, allowing the utilization of genetically superior sires. The objectives of AI are to use desirable genes widely, to control disease, and to increase economic profits. The possibility of AI was first suggested by Spallazani in 1780 using dogs (Robertson, 1954). In livestock, AI with horses was successful in the 1890's, and its usage became widespread before and after World War I. Studies were performed mainly in Russia before the war, and in the early 1900's, AI was first used in Denmark (1936) and in England (1942) (Rendel, 1950). In the U.S., Artificial Breeding Association, an AI organization was established in 1938. AI in pigs first began around 1956 in Western Europe, primarily in Norway and Great Britain. In the beginning AI was rapidly adopted to prevent diseases; however, usage reduced gradually because the

technicians and farmers didn't have enough information and experience, and it was expensive (Willems, 1978). However, many farmers paid attention to AI because of the advantage of lower costs compared to natural service (Robertson, 1954).

AI in the US has been increased dramatically during the past 10 years. It has been recently reported that AI now accounts for more than 60 percent of the total swine mating in the United States (Singleton, 2001). The adoption of AI has already had a significant impact on the structure of the swine genetics industry. As new reproductive technologies and techniques continue to be developed even more rapid changes can be anticipated. Because most farms keep trying to minimize the amount of semen used, the reliance on fewer total boars in the pork industry also requires that these boars be more accurately selected. However, the genetic control of male fertility traits in pigs has not been extensively studied, although there may be opportunities for genetic selection. Currently, boars selected as "AI quality" are indexed and selected strictly on performance and carcass characteristics. The measures of reproductive fitness, semen quality and semen quantities that a boar can provide are not considered. However, the amount and quality of semen that a boar can produce is a function of his genotype for male fertility and will determine his potential for producing progeny. With increasing AI in pigs, data describing both semen quality and quantity are now available. Therefore, influence on reproductive performance and relation to growth and carcass traits can be analyzed in large data sets. This information, when combined with relative economic values, can in turn be used to more accurately select "AI boars" on a function of their total performance. By improving the accuracy of selection of AI sires for amount and quality of semen, it may be possible to further reduce the numbers of boars required to service sows and

thereby improve overall productivity and profitability.

In these studies, semen traits of pigs with longitudinal data, processed by alternative methods due to computational limits, will be illuminated. After the significance of these traits is made clear, more correct genetic parameters from a new statistical method, random regression (Meyer, 1998b) will be discussed and computed to an alternative method.

1.2 Current strategies used to estimate boar semen quality

The semen quality of other species of livestock has been extensively studied in the past (Goerke et al., 1970; Nestor, 1976; Ansah et al., 1985; Humblot and Ducrocq, 1996). However, selection for reproductive traits of pigs has been focused mainly on the sow. The evaluation of boar semen quality has been done primarily with visual evaluations.

Appearance such as color and odor are the simplest strategies for scoring semen quality, but should not be ignored. In general, four basic parameters are measured to evaluate boar semen quality: concentration, motility, morphology and acrosome integrity. Concentration and motility are related to farrowing rate and litter size and are the main characteristics of the ejaculate. Morphology and acrosome integrity are also effective methods to distinguish semen viability. The rationale of acrosome integrity is that sperm with poor morphology can fertilize eggs, but sperm without intact acrosome integrity cannot fertilize eggs (Rozeboom, 2000). These methods and tools have been developed by many physiologists (Flowers, 1998). Extensive studies have also been conducted about how boar semen can be preserved and quality maintained even with long

transportation time. To accomplish this focus has been on the development of improved extenders (Rozeboom, 1999). Objective methods have also been developed that are able to reduce the need for subjective evaluations. For example, critical velocity, average path velocity, straight line velocity, amplitude of linear head displacement, beat cross frequency, straightness and linearity, etc. using computer assisted sperm analysis (CASA) are being used to assess semen quality. (Farrell et al., 1998; Hirano et al., 2001).

1.3 Average performance

Means for average daily gain (ADG) in literature range from 0.5 to 0.9 kg/day (from 0.5 to 0.7 kg/d; Hetzer and Miller, 1972; Hutchens et al., 1981; Kaplon et al., 1991; from 0.7 to 1.0 kg/d; Johnson et al., 1973; Bereskin et al, 1976; Drewry, 1980; Christian et al., 1980). Means over 1 kg/d were reported by Van Alst and Robison (1992). In general, crossbreds have better performance than purebreds, and male better than female (Bullock et al, 1991). Hetzer and Miller (1972) found that a low-fat line had greater ADG than a high-fat line in Duroc pigs, while the opposite was found in Yorkshire pigs.

For Backfat (BF), means in the literature range from 12 to 50 mm. Hetzer and Miller (1972) reported BF means of approximately 40-50 mm. Swiger et al (1979) also found comparatively high BF thickness (37 ± 3.8 mm) using data from 5,925 pigs tested at the Ohio Swine Evaluation Station. Intermediate average (29.3 ± 1 mm; selected line, 27.3 ± 1 mm; control line) BF was reported by Kuhlert and Jungst (1992), from a selection experiment for increased weight at 70-day of age over six generations in Landrace pigs. Van Diepen and Kennedy (1989) reported relatively thin BF means in Yorkshire pigs, which were respectively 13.20 mm in On-farm boars, and 12.38 mm in

test station boars. These results show that selection for leaner pigs has had a dramatic response.

Muscle depth has not been as well researched. Gresham et al. (1994) reported a study of live and carcass characteristics of market hogs. Means and standard deviations of muscle depth were 53.4 ± 7.1 mm and 53.9 ± 7.9 mm in live barrows and gilts, respectively, while, carcass measurements for barrows and gilts were 59.2 ± 7.2 mm and 59.2 ± 6.9 mm, respectively. Sather et al. (1998) reported that QM Hamline pigs had muscle depth of 44.5 mm, while Landrace and Large White had less muscle depth (41.1 and 38.7 mm). On the other hand, Hermesch et al. (2000) obtained similar values, but found different results using different measuring instruments.

Strzeżek et al. (2000) reported means and standard deviations of total volume (mL), number of sperm per ejaculate ($\times 10^9$), and sperm concentration ($\times 10^6$ /mL) as 127.36 ± 6.98 , 11.44 ± 1.82 , and 122.50 ± 15.30 in summer, and 133.73 ± 5.70 , 13.68 ± 2.01 , and 152.93 ± 21.42 in winter, respectively. This implies that boars have better semen in winter than in summer. Xu et al. (1996) reported that volume (mL) per ejaculate, total number of sperm ($\times 10^9$) per ejaculate, and concentration ($\times 10^6$ cell/mL) of ejaculate were, on the average, 133.3, 61.40, and 453.75, respectively. Xu et al. (1998) also reported from six boars that ejaculate volume ranged (mL) from 181.3 to 384.9, and total sperm ($\times 10^9$) per ejaculate ranged from 311.0 to 482.8.

Huang and Johnson (1996) compared a line selected for testis size to a control line, and reported least squares means for semen volume, number of sperm, and sperm concentration of 170.7 (mL), 42.9 ($\times 10^9$), and 264.5 ($\times 10^6$ cell/mL) when collected three times per week, and 142.9 (mL), 19.3 ($\times 10^9$), and 141.5 ($\times 10^6$ cell/mL) for daily

collection.

Statistics have not been reported for number of doses or acceptance rate of ejaculates.

1.4 Environmental effects

1.4.1 Breed effect

It has been reported that the Duroc breed has greater growth rate than Yorkshire (Quijandria et al., 1970; Johnson et al., 1973; Bereskin et al., 1975; Miller et al., 1979; Bereskin and Frobish, 1982; Van Alst and Robison, 1992), while Hetzer and Miller (1972) obtained the opposite result. Large White breed had a higher ADG than Landrace (Ferraz and Johnson, 1993). However, some studies found that breed did not affect ADG (Hacker et al., 1969; Bereskin et al., 1976; Drewry, 1980).

Yorkshire has been reported as the leanest breed (Noffsinger et al., 1959; Drewry, 1980; Kennedy, 1984; Li and Kennedy, 1994). Ferraz and Johnson (1993) reported that Large White pigs had similar backfat to Landrace pigs, with mean backfat thickness of 16.6 ± 3.2 mm in Large White, and 16.4 ± 0.3 mm in Landrace. Kuhlert et al (1981), Cox and Smith (1968), and Hacker et al. (1969) found that breed significantly affected backfat thickness.

Koh et al. (1976) reported that Landrace and Duroc semen had higher farrowing rate than Yorkshire semen. In addition, insemination of females by the same breed of boar had lower farrowing rate than inseminations of females by a different breed or insemination of crossbred females. Kuo et al. (1997) presented the effects of breed and season on semen characteristics. They showed that there were significant breed

differences for all semen characteristics, except sperm motility and total sperm number per ejaculation. Their results show that the semen quality of Landrace boars was superior to that in Duroc or Yorkshire boars. On the other hand, Masek et al. (1977) reported that there was no difference between Landrace and White Thoroughbred boars in volume of ejaculate, concentration of spermatozoa, and total number of spermatozoa. Xu et al. (1996) found from 3 different breeds of boars that volumes were significantly different in 3 boars, and total numbers of sperm per ejaculate were similar in two boars; however, concentrations were not significantly different in all boars.

1.4.2 Seasonal effect

Season has an important effect on semen traits. Performance is usually better in winter and spring than in summer (Nestor, 1976; Mathevon et al, 1998). Kuo et al. (1997) reported a significant seasonal effect on boar semen quality; percent of normal sperm and sperm concentration declined during summer while percent of immature sperm increased in summer. The results of interaction analysis between breed and season indicated that the semen characteristics of Landrace and Yorkshire were more influenced by season than Duroc boars. As a result, they recommended that Landrace boars had the best semen quality under subtropical climate. Ciereszko et al. (2000) reported that semen quality varied with season, including high production of spermatozoa in autumn and winter and low production in summer; semen quality also differed across breeds. However, they showed that acrosin activity of boar spermatozoa was not affected by breed, but did exhibit distinct seasonal changes. There were dramatic changes in acrosin activity between July and October. Schnurrbusch et al. (2002) recently presented the effects of

season on the concentrations of gonadotrophins and testicular hormones such as FSH, LH, prolactin, testosterone, estradiol-17 β , ejaculate volume and number of spermatozoa per ejaculate. They reported that ejaculate volume and the number of spermatozoa per ejaculate decreased in August/September and increased from October to December/January.

Various factors like ambient temperature, humidity, and the duration of daylight contribute to seasonal effects (Mathevon et al., 1998). Boar semen production is most affected by temperature (Du Mesnil du Buisson et al., 1978). Taylor et al. (1985a) reported that ejaculate volume and total sperm in the bull were depressed at -24 to -19°C and 27 to 32°C below and above the optimum temperature of 16 to 21°C . They observed no effect of temperature on concentration of the ejaculate. Huhn et al. (1995) found that litter size decreased as the daily temperature increased, but the number of hours of sunlight daily did not affect reproductive traits.

1.4.3 Nutritional factors

Research has shown that chronic malnutrition and heat stress inhibit spermatogenesis, and decrease libido. Marin-Guzman et al. (1997) reported that dietary Se and vitamin E positively affect boar semen quality. Protein intake influenced semen quantity but had little effect on the semen quality or libido of the boar (Kemp and Hartog, 1990). Therefore, various nutritional schemes have been suggested (Bearden and Fuquay, 1992).

1.4.4 Others

Research has shown that sexual preparation increases semen quality in the bull (Foster et al., 1970; Almquist, 1973), which implies that the semen collector may affect semen quality traits such as volume and number of spermatozoa (Mathevon et al., 1998). Also, it was reported that higher semen quality was obtained with specific intervals, especially 4 to 5 days between collections (Mathevon et al, 1998; Huang and Johnson, 1996). On the other hand, Du Mesnil du Buisson et al. (1978) reported in his review paper that the age of boar, day of week of collection, collection frequency, and genetic variability affect sperm production. For example, in the bull there were pronounced age differences for semen production, and trends in total sperm per ejaculate peaked at midweek (Taylor et al. 1985a).

1.5 Estimates of heritability or repeatability

Heritability estimates in the literature ranged from 0.05 to 0.75 for ADG. Merks and Van Kemenade (1989) obtained 0.05 ± 0.03 from crossbred data. Bereskin (1987) reported from data collected over 9 years that heritability using sire component of variance in Duroc and Yorkshire pigs was 0.11 ± 0.13 . Heritability estimated by restricted maximum likelihood (REML) methods was 0.27 in Polish Large White (Kaplon et al., 1991). Bryner et al. (1992) estimated heritability of ADG as 0.24 using the pseudo-expectation as a REML approximation. Comparing purebred and crossbred populations, heritability estimates were 0.28 ± 0.06 and 0.39 ± 0.10 (Stanislaw et al., 1967), while McLaren et al (1985) obtained similar results that were 0.39 ± 0.15 and 0.42 ± 0.10 , respectively. Reutzel and Sumption (1968), and McPhee et al (1979) estimated

0.34 ± 0.17 and 0.36 ± 0.10, Hetzer and Miller (1972) obtained 0.17 ± 0.04 in Duroc, and 0.33 ± 0.04 in Yorkshire. The results by Ferraz and Johnson (1993) ranged from 0.23 to 0.24. Hutchens et al (1981) reported comparatively high heritability estimates of 0.69 ± 0.18 in paternal half-sib, and of 0.54 ± 0.14 in maternal half-sib.

For backfat, heritability estimates range from 0.10 to 0.70. Keele et al (1988) reported comparatively low estimates from 0.1 to 0.22. Estimates for 2,792 Landrace×Yorkshire crosses was 0.37 ± 0.07 (Van Steenbergen et al., 1990). Ferraz and Johnson (1993) reported estimates ranging from 0.40 to 0.50. Bryner et al. (1992) estimated heritability of backfat as 0.56. Li and Kennedy (1994) obtained 0.51, 0.53, 0.55 and 0.50 in Yorkshire, Landrace, Duroc and Hampshire pigs using DFREML. Hetzer and Miller (1972), and Bereskin (1987) reported high heritability estimates of approximately 0.60.

Hermesch et al. (2000) reported heritability estimates of ADG from two different time periods, from three to 18 weeks, and 18 to 22 weeks, which were 0.27 and 0.13, respectively. Backfat and muscle depth (MD) were measured with real time ultrasound and Hennesy Chong grading machine. The results were on average 0.61 for BF and 0.21 for MD with real time ultrasound, and 0.46 for BF and 0.02 for MD with Hennesy Chong grading machine. They concluded that carcass traits such as BF and MD were highly heritable with higher estimates for real time ultrasound measurements recorded on the live animal than Hennesy Chong measurements on the carcass.

A limited number of heritability estimates have been calculated for muscle depth. Nsoso et al. (1999) reported an average heritability estimate of 0.20 in sheep.

Little appears to be known of heritability estimates for boar semen traits. Masek

et al. (1977) obtained repeatability estimates of 0.58, 0.24, and 0.42 for semen volume, total sperm cells, and total concentration, respectively, using two-factorial hierarchical analysis of variance. Du Mesnil du Buisson et al. (1978) reported that the heritability for the number of spermatozoa produced per ejaculate under comparable collection rate conditions was 0.35 even though the standard errors were too high to affirm interpreting the results. Huang and Johnson (1996) estimated repeatability of semen volume, sperm concentration (million/mL), and total number of sperm (billion) as 0.53, 0.40, 0.26 for three collections per week, and 0.57, 0.37, 0.16 for daily collections. On the other hand, Brandt and Grandjot (1998) reported that heritability of volume, number of sperm, and density were 0.16, 0.24, and 0.24 on the average of two lines, and repeatabilities were 0.29, 0.46, and 0.42, respectively. Fixed effects were considered as boar line, AI station, season, and boar age (Grandjot et al. 1997).

A wide range of genetic parameters has been reported in the literature for various species. In poultry, Nestor (1976) obtained a heritability estimate of 0.35 for semen yield by response to selection in artificially lighted turkey males after five generations of selection. The heritability estimates for average value of the semen traits throughout the reproductive season in turkey were 0.54 for yield, 0.70 for sperm concentration, and 0.48 for total sperm per collection (Nestor et al., 1979). For Medium White turkeys divergently selected for low and high semen ejaculate volumes over 13 generations. Hales et al. (1989) reported that heritability estimates determined by full-sib correlations averaged 0.61 and 0.54 for low and high lines, respectively.

In chickens, Ansah et al. (1985) reported through selection experiment that the heritability estimates of ejaculate volume, sperm concentration, and sperm number per

ejaculate from maximum likelihood were 0.34, 0.37, 0.54 for selected, and 0.64, 0.65, 0.73 for control line, respectively. Also, the repeatability estimates of these were 0.35, 0.33, 0.42 for selected, and 0.48, 0.50, 0.51 for control line, respectively.

In Holstein bulls, heritabilities of total sperm, volume, and concentration of all ejaculates were 0.03, 0.18, and 0.10 for all ejaculates and 0.05, 0.16, and 0.16 for first ejaculates. Repeatabilities were 0.26, 0.23, and 0.37 for all ejaculates and 0.31, 0.23, and 0.42 for first ejaculates (Taylor et al., 1985a). Genetic and phenotypic correlations were -0.72 and -0.47 for the correlations between volume and concentration, respectively (Diarra et al., 1977). On the other hand, heritability estimates of 198 Canadian Holstein bulls for volume of the ejaculate, sperm concentration, and number of sperm were, respectively, 0.24, 0.52, 0.31 for young bulls and 0.44, 0.36, 0.54 for mature bulls. Heritability and repeatability estimates using the expectation-maximization (EM) REML algorithm were 0.12, 0.00, 0.02 and 0.24, 0.45, 0.44 for volume, concentration, and total sperm, respectively in 200 young bulls (Taylor et al., 1985b). Gipson et al. (1987) estimated the heritability of sperm concentration as 0.20 in young beef bulls. In a study of the relationships between semen production and semen quality of Normande bulls, Humblot and Ducrocq (1996) obtained the heritability of the average volume of the ejaculate, and concentration as 0.65 ± 0.09 and 0.37 ± 0.09 , respectively. Ducrocq and Humblot (1995) reported genetic parameters for average volume of the ejaculate, spermatozoa concentration, motility score and percentage of motile spermatozoa after thawing from 1,957 young Normande bulls. Heritabilities were 0.65 for the average volume of the ejaculate, 0.23 for motility score, 0.37 for concentration, and 0.24 for motile spermatozoa after thawing. Total percentage of abnormal spermatozoa was less

heritable (0.19).

In sheep, Goerke et al. (1970) reported estimates of heritability for sperm cell concentration and semen volume of 0.07 and 0.43 by paternal half-sib analysis of variance, and -0.04 and 0.43 by regression of offspring on sire. The genetic, phenotypic and environmental correlations between sperm cell concentration and semen volume were 0.21, 0.09, and 0.07, respectively.

Heritability or even repeatability estimates of number of doses or acceptance rate of ejaculates has not been reported.

1.6 Genetic and phenotypic correlations

Genetic and phenotypic correlations between ADG and BF are generally negative or very low; Stanislaw et al. (1967; -0.07, -0.39), Reutzel and Sumption (1968; -0.98, -0.34), and Li and Kennedy (1994; -0.13, -0.08). However, Bereskin and Davey (1978) estimated phenotypic correlation of ADG and BF as 0.59, and McPhee et al. (1979) reported that genetic and phenotypic correlations as 0.55 and 0.10, respectively.

Genetic and phenotypic correlations between muscle depth, and average daily gain or backfat have not been reported.

Correlations between semen traits in pigs have not been reported. However, Taylor et al (1985a) estimated genetic correlations in bulls between semen volume and total sperm cells, semen volume and total concentration, and total sperm cells and total concentration as 0.55, -0.07, and 0.67, respectively. Ducrocq and Humblot (1995) also reported the genetic correlation between semen volume and total concentration was on average -0.13. On the other hand, Gipson et al. (1987) obtained a phenotypic correlation

between total sperm cells and total concentration as 0.84 from paternal half-sib analysis.

The only report of genetic correlation between production and semen traits was made by Brandt and Grandjot (1998). They investigated the relationship between semen volume and ADG, volume and BF, density and ADG, and density and BF in the boar. Estimates were -0.21 ± 0.12 , -0.19 ± 0.13 , 0.30 ± 0.11 , and -0.21 ± 0.10 , respectively.

Relationships between number of doses or acceptance rate of ejaculates have not been reported.

1.7 Statistical methods of genetic parameters.

Breeding value estimation has evolved from selection index to BLUP methodology by Henderson (1953). Multiple traits BLUP analysis was made possible by Henderson and Quass (1976). However, practical use was difficult due to calculating the inverse of the numerator relationship matrix until Henderson (1976) suggested the solution. Therefore, multiple trait animal model BLUP methodology has been widely implemented as the most accurate method to estimate breeding value. Iterative methods which enable breeding value estimation were developed to manage the large amount of data composing mixed model equations (Misztal and Gianola, 1987).

Genetic parameters can be estimated by Henderson's Methods (Henderson, 1953), Maximum Likelihood (Hartley and Rao, 1967), MIVQUE (Rao, 1971), REML (Patterson and Thompson, 1971), and DFREML (Smith and Graser, 1986; Graser et al., 1987). DFREML was suggested to utilize the sparseness of the inverse numerator relationship matrix to reduce the computing requirements. Gibbs sampling (Jensen et al., 1994; Wang et al., 1994) and Method R (Reverter et al., 1994) have been developed more recently.

REML and DFREML are now broadly used, and Gibbs sampling methods are being actively researched.

1.7.1 REML

Harville (1977) reviewed the field of Maximum likelihood for the estimation of variance components. Even though Maximum likelihood estimators have good properties, they have limitations in that the distribution of the data is assumed to be known, and that estimators are biased when fixed effects are managed as if they were known.

Patterson and Thompson (1971) showed that these limitations could be removed by "Restricted Maximum Likelihood (REML)". At first, the fact that REML calculates estimates less affected by bias than ANOVA methods was good enough to stimulate people in animal breeding. However, in the case of REML, it is computationally difficult due to the inverse of coefficient matrix. Therefore, Graser et al. (1987) considered a derivative-free (DF) REML algorithm for the univariate analysis under an animal model. Estimation methods like MTDFREML, Gibbs sampling method and Method R have been developed to make up for the limitations of Maximum Likelihood and the computational requirements of REML.

1.7.2 Derivative free REML

Smith and Graser (1986), and Graser et al. (1987) developed a new method that did not require derivations or expectations. DFREML (Graser et al., 1987) uses different values until log likelihood, λ , is maximized. Meyer (1993) incorporated the methods of Smith and Graser (1986) in excellent programs and wrote user notes:

"...The approach is suitable for models including additional random effects and multivariate analyses."

MTDFREML is an extension of this method for multiple traits by Boldman et al. (1995). Through MTDFREML the estimation of genetic parameters for multiple trait models was accelerated. DFREML utilize Gaussian elimination, tridiagonalization, and sparse matrix methodology to deal with large amounts of data.

1.7.3 Method R

Even with REML and DFREML, there are still problems with data analysis due to the inverse of coefficient matrix. Therefore, more effective methods in view of computing time were developed. Method R estimates variance components by using the linear regression coefficient, that is, "R", of more accurate recent data on less accurate previous individual genetic predictions (Reverter et al., 1994). Misztal (1997) wrote about Method R as:

"...Computing disk space and central processing unit time can be lowered when the mixed model equations are solved by iteration on the data using the method of modified second-order Jacobi. Estimation of the dominance variance for very large animal models is feasible with method R....

...Computations with dominance models are now feasible for large data files."

Therefore, method R is more effective than any other method in terms of the computing time and the data size. However, careful consideration of the confidence interval of parameters is needed. Especially, the confidence interval of heritability is rarely reported. Mallinckrodt et al. (1997) developed and implemented a procedure for

obtaining approximate confidence interval for heritability from Method R estimates.

In multivariate animal models, it is hard to estimate genetic parameters having a sampling correlation. However, if we ignore this, it may result in wrong estimates. Confidence regions for heritability and variance portion by permanent environmental effects using Method R estimates were studied to solve problems by a bootstrap approach (Reverter et al., 1998).

On the other hand, Snelling et al. (1995) studied the comparison of several methods like animal model marginal maximum likelihood, sire model marginal maximum likelihood, and animal model Method R. However, the differences among these methods did not substantially influence the rank of individual predictions.

As a result, Method R is an efficient method in processing time even though not affecting the rank of predictions. However, it can give very biased estimates of variances when relationship matrices are not complete and selection has been practiced.

1.7.4 Analysis of repeated measurements

1.7.4.1 Longitudinal data analysis

Growth and performance of all biological organisms change as time goes on. Traits measured at different times and traits that are measured at various times during life are known as *longitudinal* data. These traits can be observed infinitely as year, month, week, and so on. Therefore, they have also called *infinitely dimensional* characters (Kirkpatrick et al., 1989). These kinds of data can be analyzed using an animal model with repeated records (Henderson, 1984), or using a multiple-trait model that treats records from different measurements as different traits (Nestor et al., 1979; Reents et al.,

1995). Multiple regression model or spline functions might be fit to longitudinal data; however, it is important that linear models with parameters be fitted (Schaeffer, 2000).

In addition, random regression models allow researchers to analyze traits with extremely large data sets considered as one trait (Meyer, 1998b). Meyer and Hill (1997) presented a covariance functions to analyze animal breeding data by restricted maximum likelihood. Actually, covariance functions are the method of modeling ‘infinite-dimensional’ variances and covariances of observations that are repeated potentially infinitely over continuous units such as time or age, i.e., longitudinal data (Kirkpatrick et al. 1990). This allows one to calculate covariances between any time points, and to select individuals at any specific point. If covariance functions are applied to mixed linear model as random effects of time functions, the solutions of covariance functions can be estimated by calculating regression coefficient of random effects (Meyer, 1998b). The coefficients of covariance functions are estimated as covariances between random regression coefficients of the random regression model (Meyer, 1998a).

1.7.4.2 Covariance function to random regression model

Random regression models basically consist of two functions in one model.

$$y = Xb + Z\alpha + Z_D\gamma + \varepsilon \quad (1)$$

where, y is the vector of N observations measured on N_D animals, b includes the vector of fixed effects, α is the vector of $k_A \times N_A$ additive genetic random regression coefficients, γ is the vector of $k_R \times N_D$ permanent environmental random regression coefficients, and ε is the vector of N measurement errors. N_A denotes the total number of animals in the analysis including parents without records, and is equal to or

greater than N_D . Z and Z_D are the corresponding genetic and permanent environmental covariance functions A and R .

Generally, the model for repeated records with w as age (week) would be considered as below.

$$y_w = Xb_w + a_w + e_w \quad (2)$$

where, a_w is the random animal effect for each age. If a_w would be separated in to polynomial vectors at each time point and regression coefficients of these, then a_w would be changed to:

$$\begin{aligned} a_{ji} &= m_i' r_j \\ &= \begin{pmatrix} 1 & q_i & q_i^2 & \dots & q_i^{k-1} \end{pmatrix} \begin{pmatrix} r_{j1} \\ r_{j2} \\ r_{j3} \\ \vdots \\ r_{jk} \end{pmatrix} \end{aligned}$$

where, m_i is the polynomial vector at standardized age i , and r_j is the random regression coefficient vector of individual j . Separating e_w in (2) to permanent (p_{ji}) and temporary(te) environmental effects, the model would be equal to equation (1). Permanent (p_{ji}) environmental effects have different covariance functions than a_{ji} . If variances of r_j are assumed to be $\text{Var}(r_j) = T$, then variances of a_{ji} become

$$\begin{aligned} \text{Var}(a_{ji}) &= \text{Var}(m_i' r_j) \\ &= m_i' T m_i \end{aligned} \quad (4)$$

The equation of the covariance function is as follows (Kirkpatrick et al., 1989; Meyer and Hill, 1997; Schaeffer, 2000):

$$\begin{aligned}
\text{Cov}(y_1, y_m) &= f(t_1, t_m) \\
&= \sum_{i=0}^{k-1} \sum_{j=0}^{k-1} \phi_i(t_1) \phi_j(t_m) h_{ij} \\
&= \sum_{i=0}^{k-1} \sum_{j=0}^{k-1} q_1^i q_m^j \tau_{ij}
\end{aligned}$$

where, k is the order of covariance structure, G , and q_l and q_m are the standardized time between -1 and 1 . q_l can be calculated by t_l using the equation as below.

$$q_l = -1 + 2 \left(\frac{t_l - t_{\min}}{t_{\max} - t_{\min}} \right)$$

h_{ij} are the elements of matrix H , τ_{ij} are the elements of another matrix T . Function $\phi(t_l)$ are Legendre polynomials. A matrix, Λ can be made using the coefficients of Legendre Polynomials. A matrix, which includes polynomials about standardized time, is defined as another matrix, M :

$$\Phi = M\Lambda$$

$$\begin{aligned}
G &= \Phi H \Phi' \\
&= M(\Lambda H \Lambda')M' \\
&= M T M'
\end{aligned}$$

This is the same result as equation (4), which means we can get the covariance structure for a random regression model.

From equation (1), the mixed model matrix is as below (Meyer, 1998b):

$$\begin{pmatrix}
X'R^{-1}X & X'R^{-1}Z & X'R^{-1}Z_D & X'R^{-1}y \\
Z'R^{-1}X & Z'R^{-1}Z + K_A^{-1} \otimes A^{-1} & Z'R^{-1}Z_D & Z'R^{-1}y \\
Z_D'R^{-1}X & Z_D'R^{-1}Z & Z_D'R^{-1}Z_D + K_R^{-1} \otimes I_{N_D} & Z_D'R^{-1}y \\
y'R^{-1}X & y'R^{-1}Z & y'R^{-1}Z_D & y'R^{-1}y
\end{pmatrix}$$

Meyer (1998b) derived REML estimation as

$$\log L = -\frac{1}{2}(N_A \log|K_A| + k_A \log|A| + N_D \log|K_R| + \log|C^*| + \log|R| + y'P^*y)$$

where, $\log|C^*|$ is the log determinant of the coefficient matrix, and $y'P^*y$ is the residual sums of squares.

Covariance functions including covariances of genetic and permanent environmental effects in animal model can be estimated by REML. REML can be applied by derivative-free procedure, Average Information algorithm (AI-REML), or Expectation-Maximization (EM) algorithm. Derivative-free procedures to maximize log likelihood are the widely used simplex method (Nelder and Mead, 1965), Powell method (Powell, 1964), or Newton-Raphson type algorithm (Lindstrom and Bates, 1988). Currently available programs for estimating covariance functions are DXMRR procedure (Meyer, 1998a) and ASREML (Gilmour et al., 2002).

1.7.4.3 Application of random regression models (RRM)

RRM for longitudinal data have been mainly applied in cattle. Jamrozik and Schaeffer (1997a), Van der Werf et al. (1998), Olori et al. (1999), and Strabel and Misztal (1999) reported the RRM analysis of test day records of dairy cows, and Meyer (2000) evaluated weights of mature beef cows. Anderson and Pederson (1996) analyzed growth and feed intake in pigs. In addition, adjustments due to heterogeneous variance in measurement errors have been studied actively. Meyer (2001) reported that heterogeneous covariance could be adjusted by imposing covariance function (CF) or variance function (VF). When adjustments are not made for heterogeneity, BLUP estimates would be biased, and the accuracy of EBVs reduced. Lidauer and Mäntysaari (2001) suggested a “multiplicative method” which adjusts observations by multiplying by

the function of heteroskedasticity. Jamrozik et al. (1997b) applied quadratic orders of polynomial functions to measurement errors for removing heterogeneity.

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CHAPTER II

ESTIMATES OF GENETIC CORRELATIONS BETWEEN PRODUCTION AND SEMEN TRAITS IN BOAR

Estimates of genetic correlations between production and semen traits in boar

Abstract

Currently, boars selected for commercial use as AI sires are evaluated on grow-finish performance and carcass characteristics. If AI sires were also evaluated and selected on semen production, it may be possible to reduce the number of boars required to service sows, thereby improving the productivity and profitability of the boar stud. The objective of this study was to estimate genetic correlations between production and semen traits in the boar: average daily gain (ADG), back fat thickness (BF) and muscle depth (MD) as production traits, and total sperm cells (TSC), total concentration (TC), volume collected (SV), number of extended doses (ND), and acceptance rate of ejaculates (AR) as semen traits. Semen collection records and performance data for 843 boars and two generations of pedigree data were provided by NPD USA. Back fat thickness and MD were measured by real-time ultrasound. Genetic parameters were estimated from five four-trait and one five-trait animal models using MTDFREML. Average heritability estimates were 0.39 for ADG, 0.32 for BF, 0.15 for MD, and repeatability estimates were 0.38 for SV, 0.37 for TSC, 0.09 for TC, 0.39 for ND, and 0.16 for AR. Semen traits showed a strong negative genetic correlation with MD and positive genetic correlation with BF. Genetic correlations between semen traits and ADG were low. Therefore, current AI boar selection practices may be having a detrimental effect on semen production.

Introduction

The production of a large quantity of high quality semen is important to pork producers since most sows are artificially inseminated (Singleton, 2001). The adoption of artificial insemination (AI) has had a significant impact on the structure of the swine genetics industry. It has been reported that AI now accounts for more than 60 percent of the total swine mating in the United States (Singleton, 2001). This effectively reduces the number of boars required in the U.S. swine breeding herd and at the same time increases the importance of high fertility and genetic merit for each boar. While genetic evaluation procedures (BLUP) to select the top boars for AI are commonplace, the genetic control of semen traits has not been extensively studied. Currently, boars selected for commercial use as AI sires are evaluated on grow-finish performance and carcass characteristics. If AI sires were also evaluated and selected on semen production, it may be possible to reduce the number of boars required to service sows, thereby improving the productivity and profitability of the boar stud. In the past, male fertility traits were not analyzed due to loss of data during natural mating (Brandt and Grandjot, 1998). However, a larger data set can be obtained due to adoption of artificial insemination techniques. Correlation analysis between semen traits and grow-finish performance can be based on these data.

The objective of this study was to estimate genetic correlations between production traits such as average daily gain (ADG), back fat thickness (BF) and muscle depth (MD), and boar reproductive traits such as semen volume collected (SV), total sperm cells ($\times 10^9$) (TSC), total concentration of sperm per mL ($\times 10^6$) (TC), number of extended doses (ND), and acceptance rate of ejaculates (AR).

Materials and Methods

Data Source

Semen collection records and performance data for 843 boars selected for artificial insemination were provided by NPD USA (Roanoke Rapids, NC). A total of 1,736 individuals were included in the pedigree file. Boars represented three breeds and were housed in two farms. Each farm was similar in numbers of boars of each breed.

Traits were ADG, BF, MD, SV, TSC, TC, ND, and AR. Backfat thickness and MD were measured longitudinally by real-time ultrasound using Aloka 500 (Corometrics; Ithaca, NY). Semen traits were recorded as repeated records. Semen volume was measured as the weight of the ejaculate volume. Total concentration was measured using a self-calibrating photometer. Total sperm cells were determined by multiplying SV and TC. Acceptance rate of ejaculates is based on the subjective evaluation of technicians and for an individual collection is binomial. Acceptance rate was calculated over the lifetime of the boar as the number of accepted collections divided by the total collections placing this data on a more normal scale. Technicians discarded ejaculates when blood or urine was present in the collection, when an evaluation of semen morphology presented a large number of abnormal sperm cells or when motility of sperm cells was low. Number of extended doses was calculated using total sperm cells divided by desired number of sperm cells per dose. For these data, each dose averaged 2.7 billion sperm with 100 ml fluid.

For these analyses the arithmetic mean of each semen trait for each individual was calculated to perform the multiple trait analyses with production traits. Therefore, our estimates for semen production traits are repeatabilities since permanent

environmental effects were not separated in the model. This also resulted in averaging out the effects of collector, year-season and age of boar.

Genetic parameters were estimated from five four-trait and one five-trait animal models. Five different combinations of four multiple traits were (1) ADG, BF, MD and SV (2) ADG, BF, MD and TSC (3) ADG, BF, MD and TC (4) ADG, BF, MD and ND (5) ADG, BF, MD and AR, respectively. The five-trait analysis consisted of all semen traits, SV, TSC, TC, ND, and AR.

Statistical Analysis

Least square means were estimated for fixed effects such as breed and farm, and the differences within fixed effects were compared using least significant differences with PDIFF option in SAS 8.01. The analysis model included fixed effects of farm, test batch, and breed.

Models for single and multiple trait evaluations were as follows:

$$Y_{ijklm} = \mu + A_i + F_j + T_k + B_l + e_{ijklm}$$

where, μ is overall mean, A_i is the random additive genetic effect of i^{th} animal, F_j is the fixed effect of j^{th} farm, T_k is the fixed effect of k^{th} test batch, B_l is the fixed effect of l^{th} breed and e_{ijklm} is measurement error. Initial analyses of each trait were conducted using a single trait, animal model. The vector presentation of this model is: $\mathbf{Y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e}$ where, \mathbf{Y} is the vector of observations for all traits, \mathbf{b} is a vector of common fixed effects due to farm, test batch and breed, \mathbf{u} is a vector of random genetic effects and \mathbf{e} is a vector of residuals and \mathbf{X} and \mathbf{Z} are incidence matrices relating observations to the fixed and animal effects, and $\mathbf{E} [\mathbf{y}' \mathbf{u}' \mathbf{e}']' = [\mathbf{b}'\mathbf{X}' \mathbf{0}' \mathbf{0}']'$. Variances of the random variables were:

$$\mathbf{V} \begin{bmatrix} \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G}_o \otimes \mathbf{A} & \mathbf{0} \\ \mathbf{0} & \mathbf{R}_o \otimes \mathbf{I} \end{bmatrix}$$

where \otimes denotes a direct product operation, \mathbf{G}_o and \mathbf{R}_o are genetic and residual covariance matrices, with order equal to the number of traits in the analysis, and \mathbf{A} is the numerator relationship matrix.

Variance and covariance components were estimated by a derivative-free REML algorithm (Graser et al., 1987) using the MTDFREML computer programs developed by Boldman et al. (1995). This set of programs minimizes -2 times the restricted log likelihood function (Λ), that is, $-2\Lambda = \text{constant} + \log|\mathbf{R}| + \log|\mathbf{G}| + \log|\mathbf{C}| + \mathbf{y}'\mathbf{P}\mathbf{y}$ where \mathbf{C} is a full-rank coefficient matrix for the mixed model equations and $\mathbf{y}'\mathbf{P}\mathbf{y}$ is the weighted sum of squares for the residuals, with \mathbf{P} a projection matrix. Stopping criterion was set as 10^{-10} for the simplex variance. Convergence was achieved after stopping criterion was obtained at the same or larger -2Λ , after a minimum of two cold restarts with the parameter estimates as new starting values.

Using information acquired from univariate analyses of each trait as starting values the multi-trait models were applied to estimate the (co)variance structure. To aid convergence and complete this analysis with available computing resources, the (co)variance structure was estimated from separate four-trait and five-trait analyses. For a four-trait model

$$\mathbf{G}_o = \begin{bmatrix} \sigma_{a_{11}}^2 & \sigma_{a_{12}} & \sigma_{a_{13}} & \sigma_{a_{14}} \\ \sigma_{a_{21}} & \sigma_{a_{22}}^2 & \sigma_{a_{23}} & \sigma_{a_{24}} \\ \sigma_{a_{31}} & \sigma_{a_{32}} & \sigma_{a_{33}}^2 & \sigma_{a_{34}} \\ \sigma_{a_{41}} & \sigma_{a_{42}} & \sigma_{a_{43}} & \sigma_{a_{44}}^2 \end{bmatrix}$$

where $\sigma_{a_{ii}}^2 =$ additive genetic variance of trait i , $\sigma_{a_{ii}}^2$ is the genetic covariance between

two. Estimation of the genetic and environmental correlations (ρ_{ij}) from the REML (co)variance estimates is straightforward.

Analysis of rank correlations

Correlations between individual breeding values for each trait were obtained from the different multiple traits analyses. Pearson correlation coefficients using SAS 8.01 were calculated and tests of significance were performed under $H_0: \rho = 0$.

Results and Discussion

Sample means are presented in Table 1 for production traits and Table 2 for semen traits. These values were higher for ADG and lower for BF than those obtained by Smith et al. (1965) and Johnson et al. (2002), but standard deviations were similar. Hermesch et al. (2000) reported that the mean of MD was 37.8 mm recorded with real time ultrasound equipment and 46.6 mm with Hennesy Chong machine. The average MD in this study was greater (57.26 mm). Table 2 shows arithmetic sample means for semen traits. Ejaculate volume in this study was slightly lower than the results of Xu et al. (1998). However, TSC were higher. The distribution of each trait (Table 3) allowed for the assumption of normality, however, AR showed the greatest departure from normality but we considered the distribution to be close enough to normal for the assumptions of the BLUP procedure.

Breed 1 had more desirable BF, MD and TC than breeds 2 and 3 (Table 4). Breed 2 had the highest ADG and SV, and Breed 3 had the highest TSC and ND. Breeds 1 and 2 produced more acceptable ejaculates than breed 3. These results indicate that breeds have

different roles in breeding programs. Farms 1 and 2 differed only in ADG, ND and AR ($P < 0.05$), which implies that farm location and/or personnel at that location differ in ability to perform and evaluate boar collection.

Tables 5 through 10 present heritability, repeatability, genetic and phenotypic correlation estimates of production and semen traits from the different multiple traits analyses. Table 11 presents the pooled results across all analyses. Estimates of heritability were, on average, 0.39, 0.32, and 0.15 for ADG, BF, and MD, and repeatability estimates were 0.38, 0.37, 0.09, 0.39, and 0.16 for SV, TSC, TC, ND and AR, respectively. Genetic parameters were very consistent across the four trait combinations (Table 5 through 9). Heritabilities of production traits have been well documented, and the estimates found for ADG and BF in this study are similar to literature averages (McPhee et al., 1979; Lutaaya et al., 2001), but lower than that reported by Smith et al. (1962) and Mrode et al. (1993).

Muscle depth has not generally been considered in the past, with loin eye area more often reported as a measure of quantity of muscle. However, Hermesch et al. (2000) reported the heritability of MD to be 0.21 when measured by real time ultrasound, which is slightly higher than the heritability (0.15) in this study. Nsoso et al. (1999) also reported that heritability estimates of MD averaged 0.20 in sheep.

Heritability and repeatability estimates for ejaculate volume have been reported in Europe, as low as 0.10 (Buisson et al., 1974) to medium range of 0.26 to 0.35 heritability (Du Mesnil du Buisson et al., 1978; Steen et al., 1983; Grandjot et al., 1997). Brandt and Grandjot (1998) found in a study of two selected lines that the mean heritability estimates were 0.16, 0.24, and 0.25 for volume, density, and number of sperm cells, respectively. In this study, the repeatability estimate of SV (.38) was higher than

Brandt and Grandjot (1998), but may be influenced by permanent environmental effects.

Genetic correlations between production traits were 0.59 between ADG and BF, 0.20 between ADG and MD, and 0.02 between BF and MD. The genetic correlation between ADG and BF was higher than that reported by Mrode et al. (1993; 0.32) and Johnson et al. (1999; 0.37). Genetic correlations between MD and ADG, and MD and BF were low or not significantly correlated.

Genetic correlations between semen traits were comparatively high. However, genetic correlations between acceptance rate of ejaculates (AR) and TSC, TC and ND were negative which implies that good quantitative semen values don't necessarily result in good qualitative aspects. This negative correlation indicates that boars producing ejaculates with a higher concentration would also be more likely to produce fewer acceptable ejaculates. The high genetic correlations observed between many of the quantitative semen traits are to be expected as these traits are very highly related and often derived from each other. Increased TSC is genetically associated with increased SV, and agrees with Taylor et al. (1985). Genetic correlation between SV and TC was 0.02, which is in contrast with the previously reported estimate of -0.49 (Brandt and Grandjot, 1998).

Genetic correlations between ADG and semen traits were generally low and not different from zero. Genetic correlations may be biased downward due to the inability to properly account for permanent environmental effects associated with semen traits. Genetic correlations between BF and semen traits were positive in sign and therefore selection for BF would have an adverse effect on semen traits. Conversely, genetic correlations between ADG, BF, SV, and TC reported by Brandt and Grandjot (1998) were

negative. Strong negative genetic correlations were observed between MD and semen traits, excluding AR. Genetic correlations between BF and MD and semen traits in this study would indicate that current selection objectives would be expected to result in reduced male fertility. There was a consistent negative genetic relationship between lean content (MD and BF) and semen traits. Nestor (1976) reported in turkeys that body weight of a genetic line selected for semen yield at sexual maturity tended to be lower than the control line after six generations of selection. He proposed that this result may be due to loose linkage of the genes involved in growth and semen production, which may have broken up in a few generations of selection.

Statistics of breeding value for each reproductive trait from the five-multiple traits analysis are in Table 12. Breeding value estimates for the various semen traits would indicate that there is an opportunity to select for genetically superior boars that would produce ejaculates that are more acceptable and would yield more extended doses. The range in breeding values shows that from best to worst there is an 18% difference in acceptance rate and nearly 22 more extended doses per ejaculate.

Table 13 shows correlations between breeding values from different multiple traits analysis for each semen trait. Pearson correlations for SV, TSC, TC, ND, and AR were .76, .75, .60, .77, and .45, respectively. All were significantly different from zero ($P < .0001$), but not approaching one. This result is expected due to the genetic correlations between BF and MD and the semen traits and genetic correlations among semen traits. Therefore to implement genetic selection for semen traits the most efficient evaluation procedure needs to be determined. This may be a separate genetic evaluation of semen traits and then appropriate weightings with BF and MD in the development of breeding

objectives.

Implications

Genetic selection for semen traits is possible. However, selection for increased muscle depth and reduced backfat may result in reduced boar fertility as measured by semen volume, total sperm cells, and total concentration of sperm per mL. Therefore, current swine industry selection practices would be expected to result in reduced male fertility. Additional work is needed to understand the relative economic importance of semen traits in the development of breeding objectives.

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Table 1. Sample means of production traits

Traits measured	n	Mean	SD	Min.	Max.
Average daily gain (kg/day)	843	0.695	0.07	0.474	0.920
Breed					
1	331	0.690	0.07	0.503	0.892
2	161	0.700	0.07	0.539	0.910
3	351	0.699	0.07	0.474	0.920
Farm					
1	621	0.704	0.07	0.539	0.920
2	222	0.672	0.07	0.474	0.833
Back fat (mm)	827	13.39	3.05	6.00	26.00
Breed					
1	325	11.85	2.38	6.00	20.00
2	160	14.37	2.94	9.00	26.00
3	342	14.39	3.06	8.00	25.00
Farm					
1	612	13.64	2.99	7.00	26.00
2	215	12.68	3.09	6.00	23.00
Muscle depth (mm)	827	57.26	6.28	41.00	77.00
Breed					
1	325	59.18	5.98	43.00	75.50
2	160	55.35	5.41	42.00	69.00
3	342	56.33	6.47	41.00	77.00
Farm					
1	612	57.65	6.24	41.00	77.00
2	215	56.14	6.27	41.00	76.00

Table 2. Sample means for semen traits

Traits measured	n	Mean	SD	Min.	Max.
Semen volume collected (ml)	843	206.8	58.87	28.00	410.66
Breed					
1	331	175.1	44.30	28.00	314.76
2	161	238.9	58.56	118.15	410.66
3	351	222.1	57.08	92.00	409.61
Farm					
1	621	210.0	62.04	28.00	410.66
2	222	197.9	47.93	77.75	409.61
Total sperm cells ($\times 10^9$)	839	104.5	27.93	2.30	188.15
Breed					
1	331	100.9	25.45	13.13	173.23
2	160	99.9	31.35	2.30	170.62
3	348	110.1	27.66	20.60	188.15
Farm					
1	617	104.4	29.12	2.30	188.15
2	222	104.9	24.40	13.13	182.28
Total concentration of sperm/mL ($\times 10^7$/mL)	839	52.59	15.97	0.25	126.07
Breed					
1	331	59.37	15.22	3.62	126.07
2	160	42.46	13.35	0.25	81.96
3	348	50.79	14.82	6	98.35
Farm					
1	617	51.69	16.16	0.25	126.07
2	222	55.08	15.19	3.62	111.69
Number of extended doses	839	35.22	9.58	1.00	65.46
Breed					
1	331	34.96	9.24	4.00	57.10
2	160	32.36	9.69	1.00	54.90
3	348	36.77	9.55	6.00	65.46
Farm					
1	617	34.27	9.65	1.00	58.33
2	222	37.86	8.88	4.00	65.46
Acceptance rate of ejaculates (%)	712	90.02	14.36	7.69	100.00
Breed					
1	288	91.60	12.35	35.71	100.00
2	125	93.03	12.79	20.00	100.00
3	299	87.24	16.23	7.69	100.00
Farm					
1	513	91.42	13.20	7.69	100.00
2	199	86.42	16.49	16.67	100.00

Table 3. Coefficient of variation (CV), skewness and kurtosis for each trait

Traits	CV	Skewness	Kurtosis
Average daily gain	10.42	0.160	-0.121
Backfat	22.77	0.736	0.921
Muscle depth	10.97	0.100	-0.178
Semen volume	28.46	0.478	0.402
Total sperm cells	26.73	-0.139	0.504
Total concentration	30.36	0.204	1.000
Number of extended doses	27.20	-0.212	0.298
Acceptance rate of ejaculates	15.96	-2.397	6.713

Table 4. Least squares means for production and semen traits¹ by breed and farm

	ADG	BF	MD	SV	TSC	TC	ND	AR
Breed 1	0.686 ^a	11.88 ^a	59.97 ^a	176.3 ^a	98.83 ^a	57.68 ^a	33.86 ^a	91.78 ^a
Breed 2	0.700 ^b	14.45 ^b	56.64 ^b	245.8 ^b	100.1 ^a	40.35 ^b	32.89 ^a	90.30 ^a
Breed 3	0.695 ^{ab}	14.25 ^b	56.55 ^b	226.0 ^c	110.1 ^b	49.64 ^c	36.79 ^b	86.13 ^b
Farm 1	0.702 ^a	13.68 ^a	58.15 ^a	212.4 ^a	101.1 ^a	49.31 ^a	33.07 ^a	91.94 ^a
Farm 2	0.686 ^b	13.37 ^a	57.29 ^a	219.6 ^a	104.9 ^a	49.14 ^a	35.96 ^b	86.86 ^b

H0: LSMean(i)=LSMean(j) (Significant level = 0.05)

¹ADG = Average daily gain; BF = Backfat; MD = Muscle depth; SV = Semen volume; TSC = Total sperm cells; TC = Total concentration; ND = number of extended doses; AR = acceptance rate of ejaculates

Table 5. Four-trait analysis (1); heritabilities, and repeatability (diagonals), and genetic and phenotypic correlations below and above diagonal, respectively, between production traits (ADG, BF and MD) and Semen Volume (SV) ^{1,2,3}

	ADG	BF	MD	SV
ADG	.39	.36	.39	-.02 ^{ns}
BF	.59	.32	.16	.19
MD	.23	.06	.14	-.12
SV	.12	.16	-.94	<u>.38</u>

¹Phenotypic correlations were tested under $H_0: \rho = 0$ (Significant level = 0.05)

²ns: not significant

³Repeatability is underlined.

Table 6. Four-trait analysis (2); heritabilities, and repeatability (diagonals), and genetic and phenotypic correlations below and above diagonal, respectively, between production traits (ADG, BF and MD) and Total Sperm Cells (TSC) ^{1,2,3}

	ADG	BF	MD	TSC
ADG	.39	.36	.39	.14
BF	.58	.31	.16	.11
MD	.21	.01	.15	.06 ^{ns}
TSC	.00	.35	-.93	<u>.40</u>

¹Phenotypic correlations were tested under $H_0: \rho = 0$ (Significant level = 0.05)

²ns: not significant

³Repeatability is underlined.

Table 7. Four-trait analysis (3); heritabilities, and repeatability (diagonals), and genetic and phenotypic correlations below and above diagonal, respectively, between production traits (ADG, BF and MD) and total concentration of sperm per mL (TC) ^{1,2,3}

	ADG	BF	MD	TC
ADG	.39	.36	.39	.11
BF	.58	.32	.16	-.09
MD	.20	.01	.16	.16
TC	-.18	.41	-.49	<u>.11</u>

¹Phenotypic correlations were tested under $H_0: \rho = 0$ (Significant level = 0.05)

²ns: not significant

³Repeatability is underlined.

Table 8. Four-trait analysis (4); heritabilities, and repeatability (diagonals), and genetic and phenotypic correlations below and above diagonal, respectively, between production traits (ADG, BF and MD) and number of extended doses (ND) ^{1,2,3}

	ADG	BF	MD	ND
ADG	.38	.36	.39	-.01 ^{ns}
BF	.58	.30	.16	.06 ^{ns}
MD	.19	.01	.15	-.01 ^{ns}
ND	.00	.39	-.91	<u>.42</u>

¹Phenotypic correlations were tested under $H_0: \rho = 0$ (Significant level = 0.05)

²ns: not significant

³Repeatability is underlined.

Table 9. Four-trait analysis (5); heritabilities, and repeatability (diagonals), and genetic and phenotypic correlations below and above diagonal, respectively, between production traits (ADG, BF and MD) and acceptance rate of ejaculates (AR) ^{1,2,3}

	ADG	BF	MD	AR
ADG	.38	.36	.39	-.08
BF	.60	.34	.16	.03 ^{ns}
MD	.17	.00	.15	.03 ^{ns}
AR	-.22	.62	.09	<u>.18</u>

¹Phenotypic correlations were tested under $H_0: \rho = 0$ (Significant level = 0.05)

²ns: not significant

³Repeatability is underlined.

Table 10. Repeatabilities (diagonals), genetic and phenotypic correlations below and above diagonal between semen traits (SV, TSC, TC, ND, and AR)

	SV	TSC	TC	ND	AR
SV	<u>.37</u>	.46	-.48	.40	.09
TSC	.74	<u>.33</u>	.41	.91	.06
TC	.02	.58	<u>.07</u>	.41	.18 ^{ns}
ND	.67	.96	.52	<u>.35</u>	.02 ^{ns}
AR	.22	-.12	-.51	-.14	<u>.14</u>

¹Phenotypic correlations were tested under $H_0: \rho = 0$ (Significant level = 0.05)

²ns: not significant

³Repeatability is underlined.

⁴SV = Semen volume; TSC = Total sperm cells; TC = Total concentration; ND = number of extended doses; AR = acceptance rate of ejaculates

Table 11. Heritabilities, Repeatabilities (diagonal), genetic and phenotypic correlations below and above diagonal between production (ADG, BF, and MD) and semen (SV, TSC, TC, ND, and AR) traits⁵

	ADG	BF	MD	SV	TSC	TC	ND	AR
ADG	.39*	.36	.39	-.02 ^{ns}	.14	.11	-.01 ^{ns}	-.08
BF	.59*	.32*	.16	.19	.11	-.09	.06 ^{ns}	.03 ^{ns}
MD	.20*	.02*	.15*	-.12	.06 ^{ns}	.16	-.01 ^{ns}	.03 ^{ns}
SV	.12	.16	-.94	.38*	.46	-.48	.40	.09
TSC	.00	.35	-.93	.74	.37*	.41	.91	.06
TC	-.18	.41	-.49	.02	.58	.09*	.41	.18 ^{ns}
ND	.00	.39	-.91	.67	.96	.52	.39*	.02 ^{ns}
AR	-.22	.62	.09	.22	-.12	-.51	-.14	.16*

¹* Arithmetic means calculated from parameters of different multiple traits analysis.

²Phenotypic correlations were tested under $H_0: \rho = 0$ (Significant level = 0.05).

³ns: not significant.

⁴Repeatabilities are underlined.

⁵ADG = Average daily gain; BF = Backfat; MD = Muscle depth; SV = Semen volume; TSC = Total sperm cells; TC = Total concentration; ND = number of extended doses; AR = acceptance rate of ejaculates

Table 12. Statistics of breeding value estimates for each semen trait (SV, TSC, TC, ND, and AR)¹

	SV	TSC	TC	ND	AR
Mean	0.371	0.186	0.008	0.066	0.017
SD	15.40	7.225	1.297	2.497	1.781
Skewness	0.444	0.117	0.165	0.109	-0.807
Kurtosis	3.046	1.565	1.493	1.409	3.502
Percentile					
Max.	95.56	31.52	5.736	11.54	6.885
Upper 1%	44.11	19.36	3.726	6.955	4.185
Upper 5%	26.77	12.52	2.255	4.337	2.715
Upper 10%	18.04	8.909	1.534	3.137	2.012
Upper 25%	8.019	4.044	0.692	1.379	0.967
Median	-0.066	0.000	0.000	0.000	0.077
Lower 25%	-7.908	-3.733	-0.727	-1.315	-0.744
Lower 10%	-16.838	-8.321	-1.540	-2.900	-1.994
Lower 5%	-23.23	-11.68	-2.181	-4.035	-2.912
Lower 1%	-40.43	-18.15	-3.232	-6.270	-5.900
Min.	-63.85	-29.29	-5.431	-10.13	-10.87

¹SV = Semen volume; TSC = Total sperm cells; TC = Total concentration; ND = number of extended doses; AR = acceptance rate of ejaculates

Table 13. Pearson correlations between breeding values estimated from multiple trait analyses with different combinations of traits

Comparison ¹	Pearson Correlation Coefficients
ABM_SV vs SV	.76
ABM_TSC vs TSC	.75
ABM_TC vs TC	.60
ABM_ND vs ND	.77
ABM_AR vs AR	.45

¹Comparison of breeding values for semen traits estimated from a four-trait model including ADG, BF, MD, and one semen trait, and a five-trait model including all semen traits.

²A = Average daily gain; B = Backfat; M = Muscle depth; SV = Semen volume; TSC = Total sperm cells; TC = Total concentration; ND = number of extended doses; AR = acceptance rate of ejaculates

CHAPTER III

GENETIC VARIATION IN TOTAL SPERM CELLS PER EJACULATE OVER THE ACTIVE LIFETIME OF AI BOARS

Genetic variation in total sperm cells per ejaculate over the active lifetime of AI boars

Abstract

The objective of this study was to model the (co) variance of total sperm cells ($\times 10^9$) over the active lifetime of AI boars. Data from boars selected for AI were provided by NPD USA. Records ($n=19,629$) from 834 boars were edited to include only records produced at 9, 12, 15, 18, 21, 24, and 27 months of age. Variance components were estimated for total sperm cells at each age using multiple trait, derivative free REML (MTDFREML). Fixed effects in the model were year-season, breed, collector, and farm. A permanent environmental effect for boar was included to account for the repeated measures. Twenty-one combinations of five trait analyses were conducted. Means are reported for each parameter estimate, and standard deviations were considered as standard errors. Genetic variance increased gradually over time, peaked at 24 months of age, and decreased after that. Heritability estimates of total sperm cells were 0.28, 0.29, 0.26, 0.27, 0.30, 0.79, and 0.41 for 9, 12, 15, 18, 21, 24, and 27 months of age, respectively. Estimates of genetic correlations were higher between adjacent ages. Genetic correlations between measures of total sperm cells at different ages averaged 0.64. A negative genetic correlation was observed between 9 and 24 months of age. This might be due to the limited amount of data between age observations and the selection of records to defined age ranges. These results indicate that measures of total sperm cells at different ages are genetically different traits.

Introduction

Evidence has been reported that changes in animal performance with increasing age are influenced by genetic factors. Animal breeders are interested in genetic parameters that describe the change of traits over time. Analysis of these changes can be undertaken using repeatability (Henderson, 1984), multiple trait (Reents et al., 1995) and random regression models (RRM). Random regression (Meyer, 1998) allows for the calculation of (co) variances at every age. Multiple trait animal models have traditionally been used for traits measured over time by defining observations at distinct ages as different traits. However, computational requirements need to explain the number of traits equal to the number of ages (Meyer and Hill, 1997). Therefore, records collected over ages are often analyzed as repeated measurements or as different traits that are separated by specific intervals. The objective of this study is to analyze records of total sperm cells per ejaculate over seven age classifications by multiple traits animal models using MTDFREML program.

Materials and Methods

Data Source

Semen collection records and performance data for 843 boars selected for artificial insemination were provided by NPD USA (Roanoke Rapids, NC). A total of 1,736 individuals were included in the pedigree file. Boars represented three breeds and were housed in two farms. Each farm was similar in numbers of boars of each breed. Thirty-four collectors collected these data over 5 year 4 seasons.

Total sperm cells were determined by multiplying semen volume, measured as the weight of the ejaculate volume by total concentration measured using a self-calibrating photometer. Total sperm cell records from seven different ages, 9 to 27 months recorded at three month intervals were used as separate traits. The pedigree file included 1,736 individuals. Number of observations at 9, 12, 15, 18, 21, 24, and 27 months of age were 305, 413, 370, 306, 248, 200 and 109, respectively (Table 1). Number of animals with valid records was 750. Frequency of records was highest at 12 months of age, decreasing gradually over time.

Statistical Analysis

Least square means were estimated for fixed effects such as breed and farm, and the differences within fixed effects were compared by least significant differences using PDIFF option in SAS 8.01. The statistical model included fixed effects of year-season, breed, collector, and farm.

Variance components for the multiple trait analysis were estimated by derivative free REML using MTDFREML (Boldman et al., 1995). Fixed effects for the model were year-season, breed, collector, and farm. A permanent environmental effect for boar was included to account for repeated measures. Convergence was considered to have been reached when the variance of the -2 log likelihood in the simplex was less than 1×10^{-9} . Twenty-one combinations of five trait analyses were conducted resulting in means for each parameter estimate, and standard deviations were considered as standard errors.

The multiple trait model was as follows:

$$Y_{ijklmn} = \mu + A_i + YS_j + B_k + C_l + F_m + PE_i + e_{ijklmn}$$

where, μ is overall mean, A_i is the random additive genetic effect of i^{th} animal, YS_j is the fixed effect of j^{th} year-season, B_k is the fixed effect of k^{th} breed, C_l is the fixed effect of l^{th} collector, F_m is the fixed effect of m^{th} farm, PE_i is the random permanent environmental effect of i^{th} animal, and e_{ijklmn} is measurement error. The vector presentation of this model is: $\mathbf{Y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{Z}\mathbf{pe} + \mathbf{e}$ where, \mathbf{Y} is the vector of observations for all traits, \mathbf{b} is a vector of common fixed effects due to year-season, breed, collector, and farm, \mathbf{u} is a vector of random genetic effects and \mathbf{e} is a vector of residuals and \mathbf{X} and \mathbf{Z} are incidence matrices relating observations to the fixed and animal effects, and $\mathbf{E} [\mathbf{y}' \mathbf{u}' \mathbf{pe}' \mathbf{e}']' = [\mathbf{b}'\mathbf{X}' \mathbf{0}' \mathbf{0}' \mathbf{0}']'$. Variances of the random variables were:

$$\mathbf{V} \begin{bmatrix} \mathbf{u} \\ \mathbf{pe} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G}_o \otimes \mathbf{A} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{PE} \otimes \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{R}_o \otimes \mathbf{I} \end{bmatrix}$$

where \otimes denotes a direct product operation, \mathbf{G}_o , \mathbf{PE} and \mathbf{R}_o are genetic, permanent environmental, and residual covariance matrices, with order equal to the number of traits in the analysis, and \mathbf{A} is the numerator relationship matrix.

Variance and covariance components were estimated by a derivative-free REML algorithm (Graser et al., 1987) using the MTDFREML computer programs developed by Boldman et al. (1995). This set of programs minimizes -2 times the restricted log likelihood function (Λ), that is, $-2\Lambda = \text{constant} + \log|\mathbf{R}| + \log|\mathbf{G}| + \log|\mathbf{C}| + \mathbf{y}'\mathbf{P}\mathbf{y}$ where \mathbf{C} is a full-rank coefficient matrix for the mixed model equations and $\mathbf{y}'\mathbf{P}\mathbf{y}$ is the weighted sum of squares for the residuals, with \mathbf{P} a projection matrix. Stopping criterion was set as 10^{-10} for the simplex variance. Convergence was achieved after stopping criterion was obtained at the same or larger -2Λ , after a minimum of two cold restarts

with the parameter estimates as new starting values.

The (co)variance structure was estimated from twenty-one separate five-trait analyses. Estimation of the genetic and environmental correlations (ρ_{ij}) from the REML (co)variance estimates is straightforward.

Results and Discussion

Means($\times 10^9$) and standard deviations of total sperm cells at each age were 85.16 ± 36.42 , 106.3 ± 40.21 , 114.3 ± 43.89 , 117.9 ± 44.81 , 115.5 ± 44.83 , 116.4 ± 44.19 , and 125.8 ± 42.06 for 9, 12, 15, 18, 21, 24, and 27 months of age, respectively. Coefficient of variation was the highest at 9 months of age and lowest at 27 months of age, however, there were not much difference among ages (Table 1). Breed 3 had more sperm cells ($P < 0.05$) at each age than breeds 1 and 2 (Table 2). Farms did not differ ($P > 0.05$) except at 15 months of age. There was not a farm by age interaction ($P > 0.05$).

Genetic variance increased gradually over time, peaking at 24 months of age and decreasing at 27 months of age (Table 3). Estimates of genetic covariance were higher between adjacent ages. A negative genetic correlation was observed between 9 and 24 months of age (Table 3). Permanent environmental (co) variance estimates increased over age, and peaked at 24 months of age (Table 4). Estimates of permanent environmental covariance were generally consistent at all ages (Table 6). Phenotypic variances also tended to increase over age (Table 6).

Meyer (2001) reported that heterogeneous covariance could be adjusted by imposing covariance function (CF) or variance function (VF). If those are not adjusted, BLUP estimates would be biased, and then it is impossible to get accurate EBVs. Lidauer

and Mäntysaari (2001) suggested a so called “multiplicative method”, which could adjust observations by multiplying them by a function of heteroskedasticity. Jamrozik et al. (1997) applied quadratic orders of polynomial functions to measurement errors to remove heterogeneity. Temporary environmental variances appear quadratic or cubic (Table 5). Therefore, further studies might model the change in measurement errors for random regression analysis based on these methods.

Heritability estimates were 0.28, 0.29, 0.26, 0.27, 0.30, 0.79, and 0.41 for 9, 12, 15, 18, 21, 24, and 27 months of age, respectively. Heritability of TSC at 24 months of age was high because of high genetic variance at the age and may be due in part to selection of records for specific age points. Genetic correlations between measures of TSC at different ages averaged 0.64. Genetic correlations between adjacent ages were higher than those between more distant ages (Table 7). Decreasing genetic correlations with increasing age may also be due to the limited amount of data and the selection of records to defined age ranges.

Implications

Estimates of genetic parameters would indicate that measures of total sperm cells at different ages are genetically different traits. However, the ability to accurately estimate genetic correlations between different ages is reduced by limiting records to specific ages. Therefore, multiple traits methods may not be most appropriate for analyzing longitudinal data. This method may be appropriate with sufficient numbers of records at each age and availability of computer resources.

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Table 1. Statistic of data analyzed

Age (month)	9	12	15	18	21	24	27
Number of records	305	413	370	306	248	200	109
Mean	85.16	106.3	114.3	117.9	115.5	116.4	125.8
SD	36.42	40.21	43.89	44.81	44.83	44.19	42.06
CV	42.77	37.85	38.41	38.02	38.83	37.98	33.43

Table 2. Least squares means of total sperm cells for breed and farm by age of boar

Age (month) Fixed effect	9	12	15	18	21	24	27
Breed							
1	69.89 ^a	97.22 ^a	99.47 ^a	101.5 ^a	107.8 ^a	123.3 ^a	105.3 ^a
2	76.11 ^{ab}	105.7 ^{ab}	104.2 ^a	110.3 ^{ab}	109.9 ^a	116.7 ^a	112.1 ^a
3	79.36 ^{bc}	108.8 ^{bc}	117.7 ^c	122.8 ^{bc}	130.0 ^c	142.0 ^c	109.8 ^a
Farm							
1	81.80 ^a	109.8 ^a	118.9 ^a	120.2 ^a	120.2 ^a	122.4 ^a	120.0 ^a
2	68.43 ^a	97.97 ^a	95.37 ^b	102.9 ^a	111.6 ^a	132.2 ^a	98.15 ^a

H0: LSMean (i) = LSMean (j) (P<0.05)

Table 3. Estimates of genetic (co) variance for total sperm cells over the active lifetime of AI boars

Age (month)	9	12	15	18	21	24	27
9	319.7 57.12 ^a						
12	275.6 1.117	390.4 59.84					
15	291.2 13.54	354.9 69.19	439.2 47.11				
18	179.0 191.2	324.4 58.97	334.3 98.04	487.4 87.62			
21	40.17 188.9	222.4 174.0	286.4 73.04	291.4 112.3	511.9 95.59		
24	-24.92 95.31	151.1 183.8	224.3 118.6	260.2 77.62	306.8 130.5	1388 163.1	
27	85.51 0.74	211.2 107.7	249.7 68.59	264.7 77.15	315.0 124.0	457.7 0.581	632.9 153.3

^a Standard deviation

Table 4. Estimates of permanent environmental (co) variance for total sperm cells over the active lifetime of AI boars

Age (month)	9	12	15	18	21	24	27
9	3.324 2.410 ^a						
12	0.416 0.748	6.561 7.310					
15	0.677 1.995	0.050 0.408	9.472 9.941				
18	0.726 1.585	0.987 1.133	0.615 1.116	8.388 6.047			
21	0.366 1.593	0.672 1.383	0.973 1.534	3.958 6.989	9.312 10.34		
24	1.016 1.971	0.786 0.701	0.357 2.367	1.236 1.548	-0.692 3.217	18.23 12.85	
27	0.847 1.457	0.495 0.582	0.374 0.726	0.543 1.451	0.562 0.512	0.317 1.409	10.57 8.695

^a Standard deviation

Table 5. Estimates of temporary environmental (co) variance for total sperm cells over the active lifetime of AI boars

Age (month)	9	12	15	18	21	24	27
9	798.6 54.77 ^a						
12	254.6 4.670	970.1 59.54					
15	162.1 19.51	299.7 49.40	1249 44.25				
18	131.9 163.5	61.29 56.83	309.4 94.59	1277 77.17			
21	232.1 145.3	217.2 132.6	372.6 67.38	360.9 93.42	1170 77.23		
24	286.5 68.74	490.0 153.1	229.1 106.4	140.8 60.36	474.7 86.12	340.5 160.4	
27	270.4 65.28	386.3 81.62	178.9 72.81	237.6 78.78	-56.27 121.9	176.7 59.05	905.6 143.9

^a Standard deviation

Table 6. Estimates of phenotypic (co) variance for total sperm cells over the active lifetime of AI boars

Age (month)	9	12	15	18	21	24	27
9	1122 7.558 ^a						
12	530.1 4.100	1369 8.642					
15	453.9 27.35	654.7 26.07	1698 18.18				
18	311.6 30.89	386.7 11.55	644.3 11.54	1773 22.14			
21	272.6 48.06	440.2 43.79	660.0 26.21	654.3 25.73	1692 30.12		
24	262.6 32.79	641.9 62.04	453.7 40.27	402.2 48.14	780.8 62.19	1747 35.50	
27	356.7 65.48	598.0 59.56	428.9 47.16	502.9 55.44	259.3 81.70	634.7 59.29	1549 49.71

^a Standard deviation

Table 7. Estimates of heritability and genetic correlation for total sperm cells over the active lifetime of AI boars

Age (month)	9	12	15	18	21	24	27
9	0.28 0.05 ^a						
12	0.73 0.07	0.29 0.04					
15	0.77 0.07	0.87 0.13	0.26 0.03				
18	0.50 0.49	0.77 0.18	0.71 0.23	0.27 0.05			
21	0.16 0.53	0.52 0.42	0.62 0.22	0.62 0.29	0.30 0.05		
24	-0.05 0.14	0.18 0.26	0.29 0.16	0.32 0.09	0.37 0.11	0.79 0.09	
27	0.21 0.05	0.44 0.22	0.50 0.14	0.49 0.12	0.52 0.12	0.54 0.05	0.41 0.09

^a Standard deviation

Table 8. Estimates of permanent environmental effects proportion of total variance on diagonals, correlations on off diagonals for total sperm cells over the active lifetime of AI boars

Age (month)	9	12	15	18	21	24	27
9	0.003 0.002 ^a						
12	0.179 0.273	0.005 0.005					
15	0.182 0.394	0.056 0.172	0.006 0.006				
18	0.148 0.480	0.250 0.271	0.102 0.130	0.005 0.003			
21	0.174 0.400	0.194 0.448	0.101 0.218	0.258 0.335	0.006 0.006		
24	0.124 0.385	0.173 0.283	0.139 0.233	0.200 0.235	0.054 0.310	0.010 0.007	
27	0.226 0.375	0.235 0.323	0.146 0.193	0.098 0.178	0.132 0.202	0.014 0.244	0.007 0.006

^a Standard deviation

Table 9. Estimates of temporary environmental proportion of total variance and correlations for total sperm cells over the active lifetime of AI boars

Age (month)	9	12	15	18	21	24	27
9	0.71 0.05 ^a						
12	0.30 0.01	0.71 0.05					
15	0.16 0.02	0.27 0.04	0.74 0.03				
18	0.14 0.18	0.06 0.05	0.25 0.08	0.72 0.05			
21	0.25 0.16	0.21 0.13	0.31 0.06	0.30 0.08	0.69 0.05		
24	0.63 0.17	0.82 0.10	0.38 0.16	0.24 0.12	0.71 0.07	0.19 0.09	
27	0.32 0.10	0.41 0.08	0.17 0.07	0.22 0.08	-0.06 0.12	0.31 0.09	0.54 0.18

^a Standard deviation

CHAPTER IV

**GENETIC PARAMETERS FOR VARIOUS RANDOM REGRESSION
MODELS TO DESCRIBE TOTAL SPERM CELLS PER EJACULATE
OVER THE ACTIVE LIFETIME OF BOARS**

Genetic parameters for various random regression models to describe total sperm cells per ejaculate over the active lifetime of boars

Abstract

The objective of this study was to model the variances and covariances of total sperm cells ($\times 10^9$) over the active lifetime of AI boars. Data from boars ($n = 834$) selected for AI were provided by NPD USA. Total number of records and animals were 19,629 and 1,736, respectively. Parameters were estimated for total sperm cells by age of boar classification under a random regression model using the Simplex method and DxMRR procedures. The analysis model included breed, collector and year-season as fixed effects. Random effects included additive genetic effect, permanent environmental effect of boar, and measurement error. All measurement errors were assumed to be equal. Observations were removed when the number of data at a given age of boar classification was less than 10. Preliminary evaluations showed the best fit with fifth order polynomials, indicating that the best model would have fifth order fixed regression and fifth order random regressions for animal and permanent environment effects. In this study, random regression models were fitted to evaluate all combinations of first through seventh order polynomial covariance functions. Goodness of fit for models was tested using Akaike's Information Criterion and Schwarz Criterion. The maximum log likelihood value was observed for sixth, fifth, and seventh order polynomials for fixed, additive genetic and permanent environmental effects, respectively. However, the best fit as determined by Akaike's Information Criterion and Schwarz Criterion was by fitting sixth, fourth, and seventh, and fourth, second, and seventh order polynomials for fixed, additive genetic

and permanent environmental effects, respectively. Heritability estimates for total sperm cells ranged from .27 to .48 across age of boar classifications. In addition, heritability for total sperm cells tended to increase with age of boar classification. Observed heritability for total sperm cells was cyclic over the active lifetime of boars and may be due in part to number of observations across seasons limiting our ability to correct for seasonal effects on sperm production.

Introduction

Artificial insemination plays an important role in animal breeding by allowing greater utilization of genetically superior sires. It has been shown that there is an opportunity for genetic improvement of male fertility traits (Oh et al., 2003; Brandt and Grandjot, 1998). However, the genetic control of semen traits in pigs has not been extensively studied. Moreover, total sperm cells per ejaculate (TSC) are longitudinal data where volume changes over age. In previous studies, this type of data was analyzed by multiple trait methods choosing the most important time points as separate traits. Because of the number of potential observations over a boar's lifetime, it would be difficult to thoroughly analyze this type of data due to computational limits. Semen data have also been analyzed similar to growth curves ignoring genetic effects (Morant and Gnanasakthy, 1989), or were considered simple repeated measurements ignoring time dependency.

In many cases, the assumption of a univariate repeated model is not appropriate while a full multivariate model with the number of traits equal to the number of ages would result in a highly overparameterized analysis. Therefore, a model using the

minimum number of traits is required (Meyer and Hill, 1997). Random regression models (RRM) developed by Meyer (1998) have been extensively applied to the test-day model analysis of milk yield of dairy cattle (Jamrozik and Schaeffer, 1997; Van der Werf et al., 1998; Olori et al., 1999; Strabel and Misztal, 1999; Meyer, 2000). Random regression models have also been fitted to weight data of pigs (Huisman et al., 2002). Random regression models provide a method for analyzing independent components of variation that reveal specific patterns of change over time. The objective of this study was to model the (co) variances of total sperm cells ($\times 10^9$) over the active lifetime of AI boars.

Materials and Methods

Data

Total sperm cell records (n=19,629) for 834 boars were provided by NPD USA (Table 1). One thousand seven hundred and thirty six individuals were included in the pedigree file. Boars represented three breeds and were housed in two farms. Each farm was similar in numbers of boars of each breed. Thirty-four collectors collected these data over 5 year 4 seasons. Total sperm cells were determined by multiplying semen volume, measured as the weight of the ejaculate volume by total concentration measured using a self-calibrating photometer. Observations were removed when the number of data at a given age of boar classification time point was less than 10, or total sperm cells were missing, zero or less than zero (Figure 1). Total sperm cells were measured from 1998 to 2002 with approximately one-half recorded in 2000. Data were distributed evenly across seasons (Table 2). Number of animals with N records is shown in Table 3. Differences between boar collection date and birth date were used to provide each record with a fixed

age of boar classification in weeks. When a boar had two observations during one week of age the record closest to the whole week was utilized.

Statistical Analysis

Parameters were estimated for total sperm cells (TSC) by age of boar classification under a random regression model using DxMRR (Meyer, 1998). In evaluation of boar semen, fixed effects previously considered were boar line, AI station, season, and boar age (Grandjot et al. 1997). The analysis model included breed, collector and year-season as fixed effects; additive genetic effects, permanent environmental effect of boar, and measurement error as random effects. Random regression models were fitted to evaluate all combinations of first through seventh order polynomial covariance functions for fixed effect of age of boar classification, additive genetic, and permanent environmental effects. This resulted in the evaluation of 343 models. Methods to reduce orders of orthogonal polynomials were studied using eigenvalues (Meyer and Hill, 1997; Schaeffer, 2000). However, the absolute standard is ambiguous, and the number of effective eigenvalues was different for every fitted model. Therefore, it is not easy to determine the optimum orders of polynomials. In our study, all combinations from first to seventh orders for fixed, additive genetic, and permanent environmental effects were analyzed. Goodness of fit for models was tested using Akaike's Information Criterion (AIC) and Schwarz Criterion (SC).

$$AIC = -2\log L + 2 \times p$$

$$SC = -2\log L + p \times \log (N - r(X))$$

where p is the number of parameters estimated and $r(X)$ is the rank of the coefficient matrix of fixed effects (Meyer, 2001a).

The general model is

$$y_{ij} = F_{ij} + \sum_{n=0}^{k_F-1} \beta_n \phi_n(w_{ij}) + \sum_{n=0}^{k_A-1} \alpha_{in} \phi_n(w_{ij}) + \sum_{n=0}^{k_P-1} \delta_{in} \phi_n(w_{ij}) + \epsilon_{ij}$$

where y_{ij} is the j -th record from the i -th animal, w_{ij} is the standardized (-1 to 1) age at recording, $\phi_n(w_{ij})$ is the n -th Legendre polynomial of age, F_{ij} is a set of fixed effects, β_n are the fixed regression coefficients to model the population mean, α_{in} are the random regression coefficients for additive genetic effects, and δ_{in} are the random regression coefficients for permanent environmental effects, respectively. k_F , k_A , and k_P denote the corresponding orders of fit.

In matrix notation,

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Cp} + \mathbf{e}$$

where,

\mathbf{y} : vector of N observations measured on N_D animals

\mathbf{b} : vector of fixed effects (including F_{ij} and β_n)

\mathbf{a} : vector of $k_A \times N_A$ additive genetic random regression coefficients

\mathbf{p} : vector of $k_R \times N_D$ permanent environmental random regression coefficients

\mathbf{e} : vector of N measurement errors

\mathbf{X} , \mathbf{Z} and \mathbf{C} : corresponding design matrices

k_A and k_R : the order of fit for \mathbf{a} and \mathbf{p} and corresponding genetic and permanent environmental covariance function A and R .

$$V \begin{bmatrix} a \\ p \\ e \end{bmatrix} = \begin{bmatrix} K_A \otimes A & 0 & 0 \\ 0 & K_p \otimes I & 0 \\ 0 & 0 & R \end{bmatrix}$$

K_A and K_p are the matrices of coefficients of the covariance function for additive genetic and permanent environmental effects. A is the numerator relationship matrix, and I is an identity matrix. It is assumed that all measurement errors are equal.

Results and Discussion

Mean and standard deviation of total sperm cells were 111.69 ($\times 10^9$) and 42.40, respectively. Average total sperm cells increased almost linearly with age (Figure 2). However, fluctuations were observed after approximately 140 week of age due to decreasing numbers of records. Standard deviations of average total sperm cells maintained consistent intervals over time.

The random regression model, fitting $k_F = 6$, $k_A = 5$, and $k_p = 7$ for fixed, additive genetic and permanent environmental effects showed the largest log likelihood value. This model was the 4th best fitting model based on AIC and the 52nd best fitting model based on SC. Generally, log likelihood value will increase as number of parameters in the model increase. Therefore, log likelihood values are less conservative than Akaike's Information Criterion (AIC) and Schwarz Criterion (SC) values, which are weighted by number of parameters (Table 4). Schwarz Criterion is stricter than AIC. AIC showed best fit when $k_F = 6$, $k_A = 4$, $k_p = 7$, and this was the 3rd best fitting model based on log likelihood and 20th best fitting model based on SC. Schwarz Criterion showed the best fit when $k_F = 4$, $k_A = 2$, $k_p = 7$, and this model was ranked 10th best

fitting model by log likelihood and 2nd best fitting model by AIC. Based on the conservative nature of SC and the relative ranking by the other criterion this model may be the best overall fit. Generally, higher order of fit for the orthogonal polynomials on age was found to be beneficial.

Log likelihood values (Figure 3), AIC values (Figure 4) and SC values (Figure 5) for all combinations of k_A and k_p were similar in pattern where values tended to be more desirable as the orders were higher. However, in AIC and SC values, 2nd and 3rd order fits of additive genetic effects had the lowest values, which are the best fit.

Additive genetic and permanent environmental effects and eigenvalues for the three best fit models are shown in Table 5. Based on the number of non-zero eigenvalues(λ) or eigenvalues relatively closer to zero the model of $k_F = 6$, $k_A = 5$, and $k_p = 7$ could be reduced to the order of $k_A = 3$, $k_p = 5$, and the model of $k_F = 6$, $k_A = 4$, $k_p = 7$ could be to $k_A = 2$, $k_p = 4$, and the model of $k_F = 4$, $k_A = 2$, $k_p = 7$ could be to $k_A = 2$, $k_p = 6$, respectively. The methods to reduce orders of orthogonal polynomials were studied using eigenvalues (Meyer and Hill, 1997; Shaeffer, 2000). However, the absolute standard is ambiguous, and the number of effective eigenvalues was different in every result of fitted model. Therefore, it is not easy to determine the optimum orders of polynomials.

Heritability estimates over week of age are presented in Figure 6. These values are the means and standard deviations of heritability at each week from all 343 models combinations of first to seventh order orthogonal polynomials. Heritability estimate for total sperm cells ranged from 0.27 to 0.48. These values strongly agree with the repeatability (0.37) reported in Chapter 1. Standard deviations tended to decrease from 33

weeks of age to about 45 weeks, maintained consistent intervals by 100 weeks of age, and then increased rapidly. This increase in variance closely follows the numbers of total sperm cell records over age as shown in Figure 1. Comparing Figures 1 and 6 it would also appear that heritability tends to increase when there is less information. Huissman et al. (2002) reported a similar observation in an evaluation of pig body weights. The cyclic nature of the heritability estimates may be due in part to number of observations across seasons limiting our ability to correct for season. Heritability estimates also tended to increase with increasing age of boar.

Heritability estimates in this study were similar to those reported in the literature. Masek et al. (1977) estimated 0.24 as repeatability using two-factorial hierarchical analysis of variance. Du Mesnil du Buisson et al. (1978) reported that the heritability for the number of spermatozoa produced per ejaculate in comparable collection rate conditions was 0.35 even though the standard deviations were too high to affirm interpreting the results. Huang and Johnson (1996) estimated repeatability of total number of sperm (billion) as 0.26 for three collections per week, and 0.16 for daily collections. On the other hand, Brandt and Grandjot (1998) reported that heritability and repeatability of number of sperm cells was 0.24 and 0.46 on average, respectively.

Figures 7, 8, and 9 are three-dimensional graphs showing similar trends of additive genetic (co) variances from the models of $k_F = 6$, $k_A = 5$, $k_p = 7$, and $k_F = 6$, $k_A = 4$, $k_p = 7$, and $k_F = 4$, $k_A = 2$, $k_p = 7$, respectively. Genetic variances tended to increase with age for each model. This is in contrast to permanent environmental (Figures 10 through 12) and phenotypic (Figures 13 through 15) variances that were relatively consistent over age, and is linked to the observed increase in heritability. Meyer (2001b)

and Lidauer and Mäntysaari (2001) suggested adjustments be made for heterogeneous variance in measurement errors. In our study, measurement errors were assumed to be homogeneous across age and Figures 13 through 15 would support this assumption. Covariance estimates between ages decreased as the interval between ages increased.

Graphs (Figures 10, 11 and 12) of permanent environmental effects for each model were similar, although the values differ. Sudden increases in permanent environmental variances and covariances after 140 weeks of age may be due to the limited amount of data for those ages. Graphs of phenotypic (co) variances (Figures 13, 14 and 15) were similar to those observed for permanent environmental (co) variances.

Genetic correlations, like genetic covariances, (Figures 16, 17 and 18) were high between adjacent ages and decreased as the interval between ages increased. Figure 17 showed the highest genetic correlations even between distant ages, which might be due to orders of polynomials ($k_F = 6$, $k_A = 4$, $k_p = 7$). Genetic correlations from the model with polynomial orders of $k_F = 4$, $k_A = 2$, $k_p = 7$ decreased as the intervals of ages increased ranging from 0.4 to 0.5. These results indicate that later performance may be harder to predict accurately from records at an early age.

Phenotypic correlations were approximately 0.5 between adjacent ages (Figure 19, 20 and 21). In general phenotypic correlations, like the phenotypic genetic correlations, decreased as the intervals between ages increased. Negative phenotypic correlations between old and young ages are remarkable, which may have been due to the small numbers of records at older ages.

Implications

Genetic variance of total sperm cells increases during the productive life of the boar resulting in heritability estimates increasing from 0.27 to 0.48. Genetic correlations between total sperm cells at different ages were larger for adjacent ages. Random regression models with comparatively high order polynomials for fixed, additive genetic and permanent environmental effects provided the best fit.

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Table 1. Summary of data structure

Number of records	19,629
Number of animals in pedigrees	1,736
Number of animals with records	834
Mean of total sperm cells	111.69
Standard deviation	42.40

Table 2. Frequency of records by year and season for data included in the random regression analysis

Year	Frequency	%	Season	Frequency	%
1998	26	0.13	Spring	5,972	30.42
1999	2,875	14.65	Summer	4,505	22.95
2000	10,733	54.68	Fall	4,080	20.79
2001	5,415	27.59	Winter	5,072	25.84
2002	580	2.95			

Table 3. Number of animals with N records

N records	Number of animals	N records	Number of animals
1	54	38	22
2	16	39	22
3	17	40	6
4	23	41	6
5	26	42	6
6	17	43	4
7	15	44	10
8	13	45	6
9	8	46	5
10	25	47	4
11	12	48	6
12	9	49	3
13	15	51	3
14	16	52	1
15	17	53	1
16	18	54	3
17	24	55	5
18	54	56	4
19	32	57	3
20	7	58	4
21	11	59	3
22	14	60	5
23	19	61	1
24	20	62	3
25	10	63	1
26	10	65	2
27	12	68	1
28	14	69	2
29	14	70	2
30	14	71	1
31	9	72	3
32	16	75	1
33	17	76	2
34	16	78	1
35	23	80	1
36	22	82	1
37	19	97	1

Table 4. Order of fit for fixed (k_F), additive genetic (k_A), and permanent environmental (k_P) effects, number of parameters (p), log likelihood (-77000), AIC (+154300), SC (+154000), and ranks of log likelihood, AIC and SC

Order of fit			p	logL	rank	AIC	rank	SC	rank
k_F	k_A	k_P							
6	5	7	44	24.28	1	39.43	4	86.23	52
7	5	7	44	20.44	2	47.11	6	93.92	63
6	4	7	39	20.32	3	37.36	1	44.75	20
5	5	7	44	20.13	4	47.74	8	94.54	65
7	4	7	39	19.51	5	38.99	3	46.38	21
5	4	7	39	16.77	7	44.47	5	51.86	22
4	2	7	32	13.09	10	37.82	2	-9.96	1
7	7	2	32	2.69	26	58.61	17	10.83	4
6	7	2	32	2.6	27	58.80	18	11.02	5
5	2	6	25	-29.13	46	108.26	34	5.31	2
7	2	6	25	-31.29	49	112.59	36	9.63	3

Table 5. Estimates of variances (diagonal), covariances (below diagonal), and correlations (above diagonal) between random regression coefficients and eigenvalues (λ) of coefficient matrix, for models with order of fit of 6, 5, 7 and 6, 4, 7, and 4, 2, 7 for fixed, additive genetic and permanent environmental effects, respectively

Order of random regression coefficients							
0	1	2	3	4	5	6	λ
Additive genetic effect							
747.06	0.48	-0.39	-0.43	-0.64			790.34
113.51	76.14	-0.18	-0.33	0.37			74.13
-70.57	-10.45	42.85	0.99	0.29			65.62
-75.85	-18.60	41.34	40.96	0.20			0.05
-84.26	15.46	9.23	6.28	23.13			0.00
Permanent environmental effect							
361.50	0.23	-0.27	0.57	0.36	0.22	0.13	1194.38
53.91	150.43	0.09	0.03	-0.27	-0.21	-0.05	25.55
-38.36	8.59	58.02	0.44	0.61	0.77	0.77	0.00
159.76	4.43	48.81	215.71	0.86	0.82	0.58	154.42
131.94	-62.24	88.29	241.18	362.71	0.97	0.64	382.42
94.88	-58.13	131.22	270.79	413.82	501.11	0.78	0.01
33.44	-8.57	77.69	113.49	161.31	229.73	174.91	67.62
Additive genetic effect							
889.06	0.76	0.01	0.00				937.22
202.94	79.33	-0.64	-0.64				115.93
1.01	-31.72	30.94	1.00				0.00
0.29	-42.06	40.82	53.86				0.04
Permanent environmental effect							
314.74	0.15	-0.04	0.71	0.45	0.39	0.30	1381.52
30.38	127.84	0.27	0.28	-0.05	-0.01	0.20	296.03
-7.33	29.92	97.94	0.61	0.72	0.83	0.83	159.65
204.34	51.51	99.02	265.60	0.90	0.87	0.63	0.00
156.03	-12.12	140.64	289.81	389.20	0.97	0.62	0.00
160.85	-2.37	192.17	332.51	448.67	546.20	0.78	0.00
70.14	29.38	107.16	133.47	160.16	237.95	171.30	75.62
Additive genetic effect							
768.06	0.49						795.322
137.47	102.21						74.9486
Permanent environmental effect							
347.64	0.20	-0.61	0.43	0.21	0.13	0.10	857.88
51.66	186.71	0.16	-0.32	-0.44	-0.59	-0.24	98.80
-91.60	17.38	65.33	0.09	0.12	0.00	0.26	0.00
92.60	-51.60	8.58	135.90	0.69	0.58	0.40	12.29
63.62	-97.77	16.13	131.79	266.07	0.88	0.52	394.76
49.75	-163.44	0.03	137.61	293.47	415.91	0.75	145.25
22.50	-39.96	26.24	56.89	103.87	188.48	152.84	61.42

Figure 1. Number of total sperm cell records by age of boar

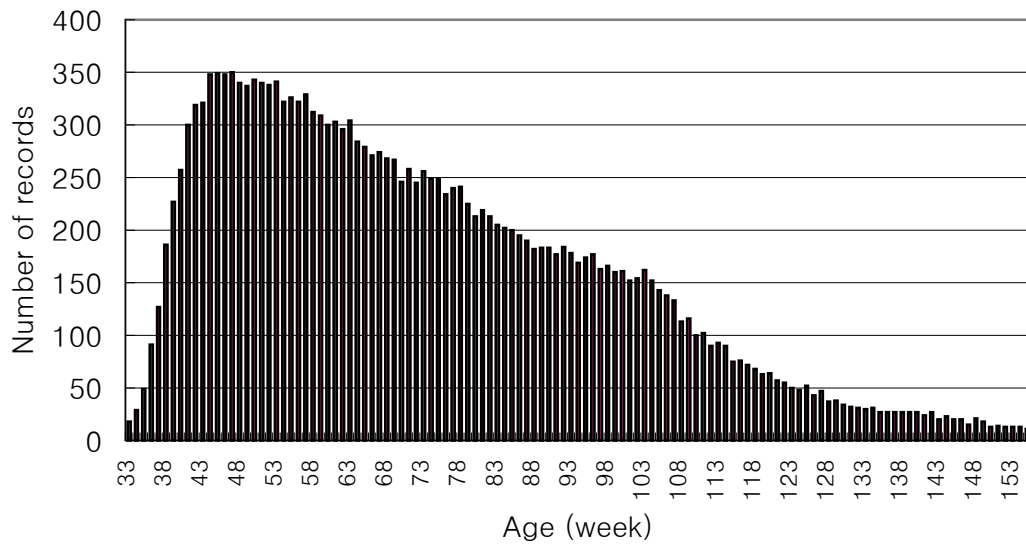


Figure 2. Total sperm cells by age of boar

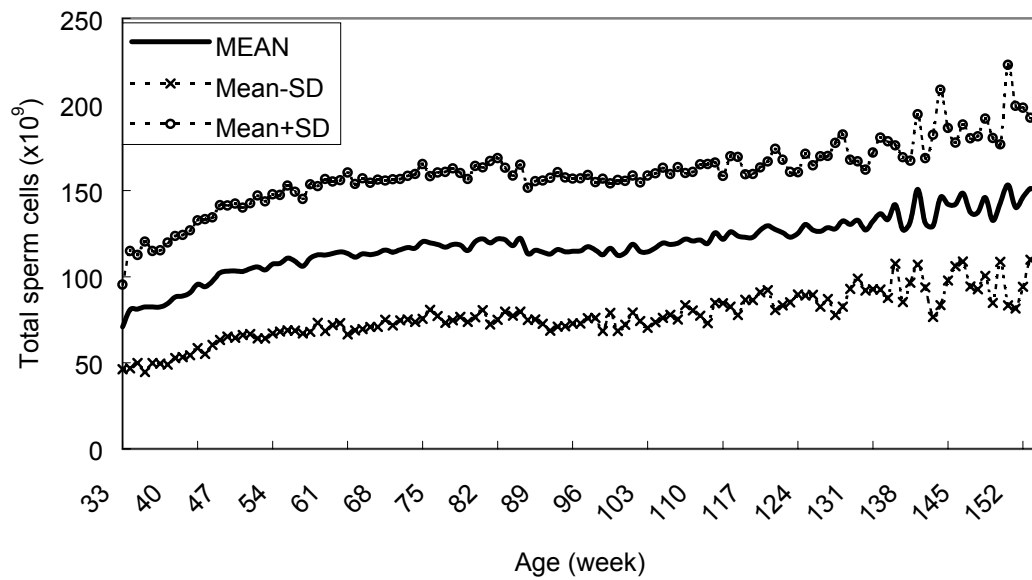


Figure 3. Log likelihood values by polynomial order of additive genetic effects and polynomial order of permanent environmental effects

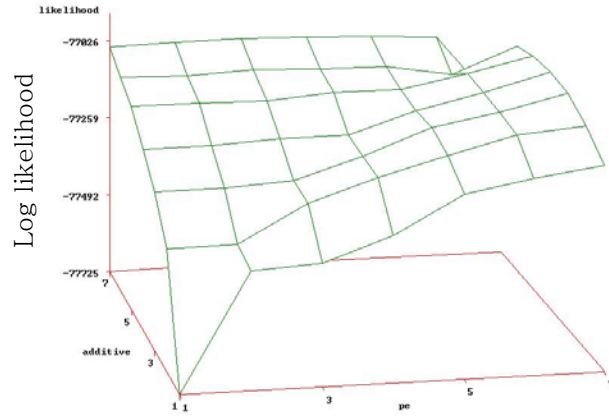


Figure 4. Akaike's Information Criterion values by polynomial order of additive genetic effects and polynomial order of permanent environmental effects

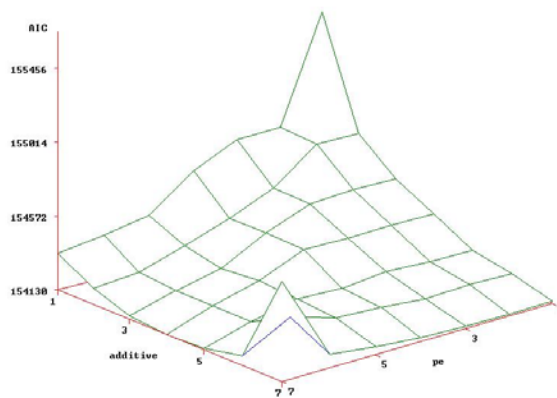


Figure 5. Schwarz Criterion values by polynomial order of additive genetic effects and polynomial order of permanent environmental effects

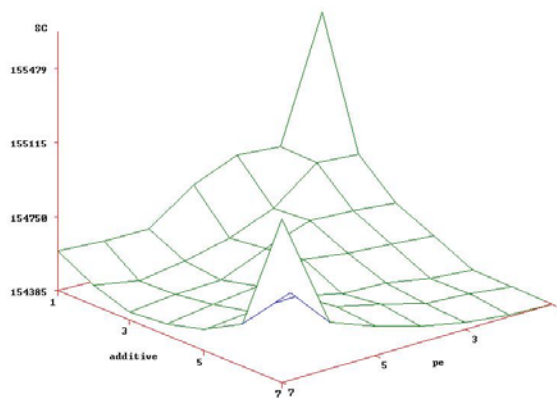


Figure 6. Heritability estimates of total sperm cells by age of boar

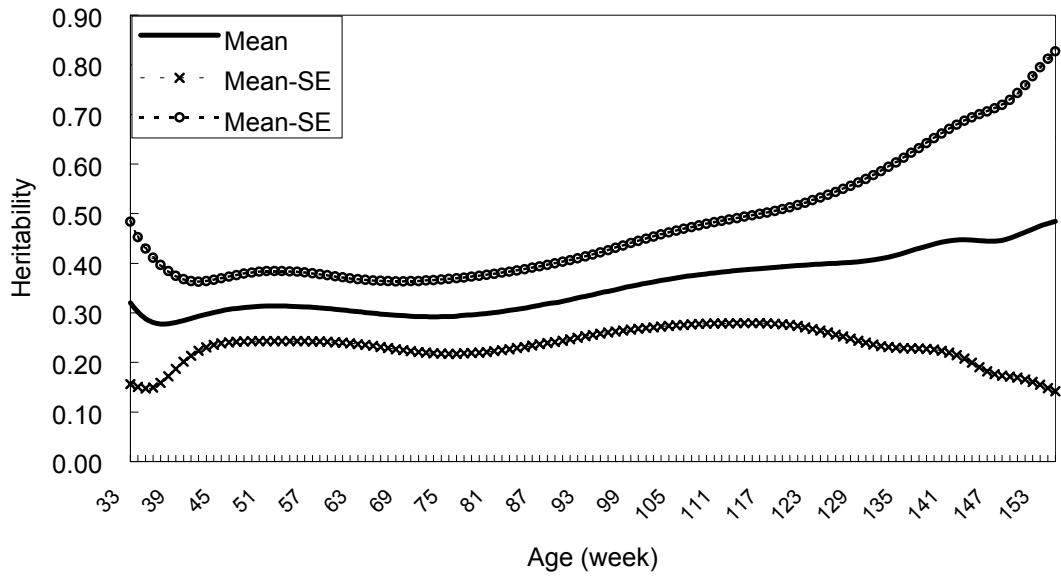


Figure 7. Additive genetic (co) variances between ages with polynomial order of fit of 6, 5 and 7 for fixed, additive genetic, and permanent environmental effects, respectively

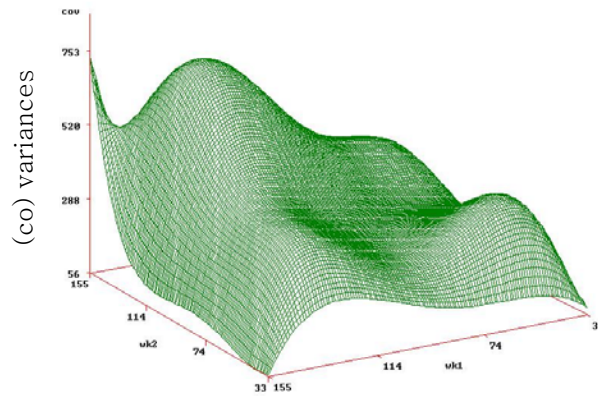


Figure 8. Additive genetic (co) variances between ages with polynomial order of fit of 6, 4 and 7 for fixed, additive genetic, and permanent environmental effects, respectively

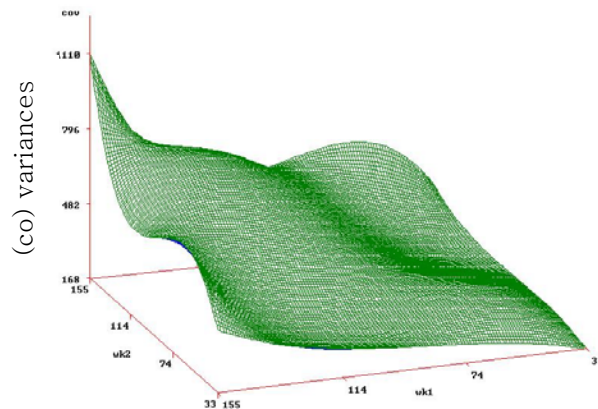


Figure 9. Additive genetic (co) variances between ages with polynomial order of fit of 4, 2 and 7 for fixed, additive genetic, and permanent environmental effect, respectively

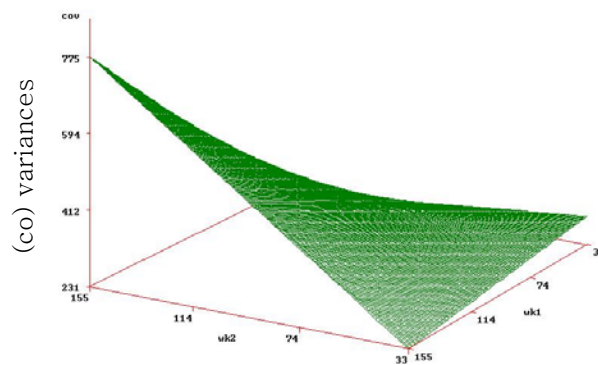


Figure 10. Permanent environmental (co) variances between ages with polynomial order of fit of 6, 5 and 7 for fixed, additive genetic, and permanent environmental effects, respectively

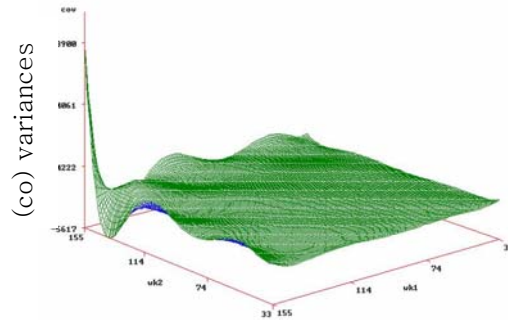


Figure 11. Permanent environmental (co) variances between ages with polynomial order of fit of 6, 4 and 7 for fixed, additive genetic, and permanent environmental effects, respectively

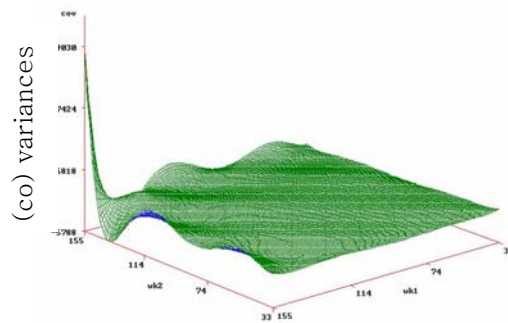


Figure 12. Permanent environmental (co) variances between ages with polynomial order of fit of 4, 2 and 7 for fixed, additive genetic, and permanent environmental effect, respectively

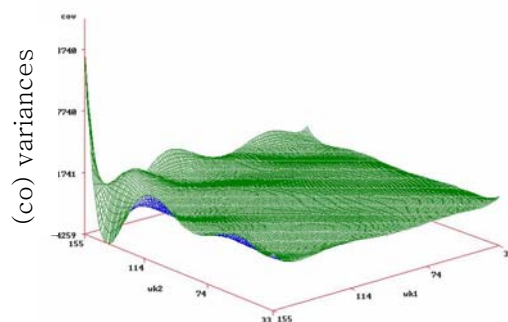


Figure 13. Phenotypic (co) variances between ages with polynomial order of fit of 6, 5 and 7 for fixed, additive genetic, and permanent environmental effects, respectively

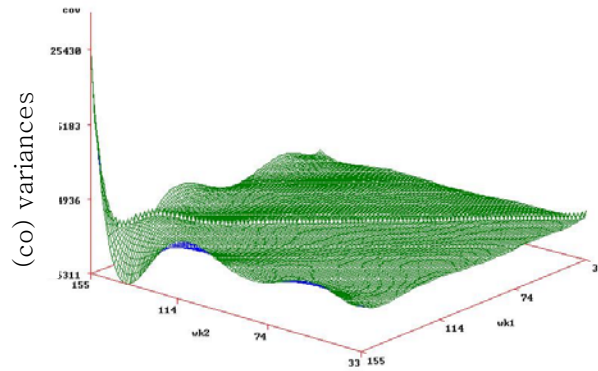


Figure 14. Phenotypic (co) variances between ages with polynomial order of fit of 6, 4 and 7 for fixed, additive genetic, and permanent environmental effects, respectively

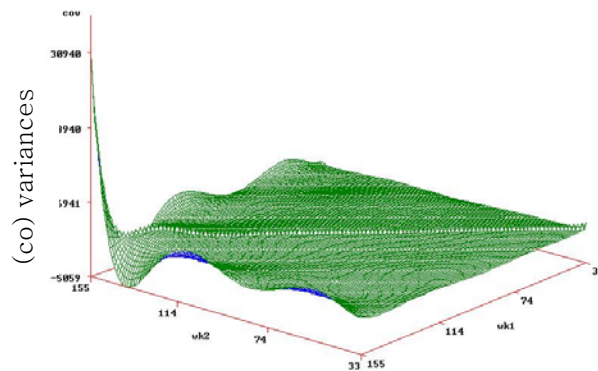


Figure 15. Phenotypic (co) variances between ages with polynomial order of fit of 4, 2 and 7 for fixed, additive genetic, and permanent environmental effects, respectively

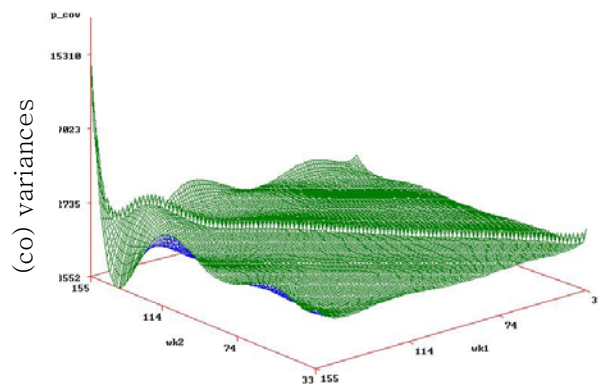


Figure 16. Heritabilities and genetic correlations between ages with polynomial order of fit of 6, 5 and 7 for fixed, additive genetic, and permanent environmental effects, respectively

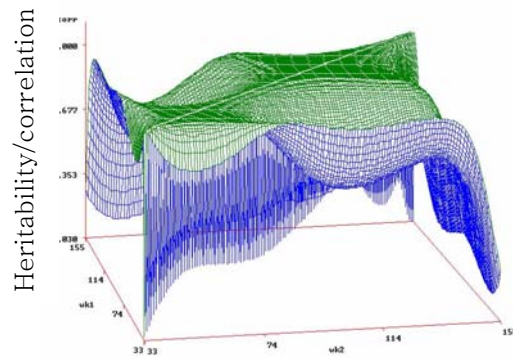


Figure 17. Heritabilities and genetic correlations between ages with polynomial order of fit of 6, 4 and 7 for fixed, additive genetic, and permanent environmental effects, respectively

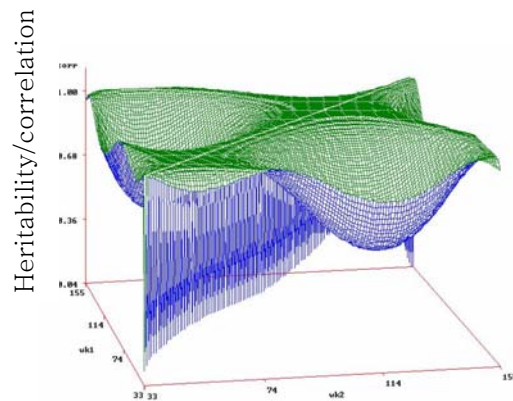


Figure 18. Heritabilities and genetic correlations between ages with polynomial order of fit of 4, 2 and 7 for fixed, additive genetic, and permanent environmental effects, respectively

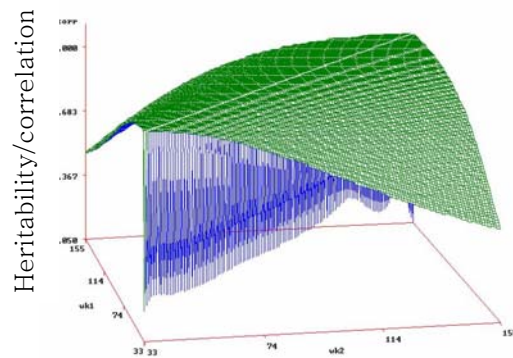


Figure 19. Phenotypic correlations between ages with polynomial order of fit of 6, 5 and 7 for fixed, additive genetic, and permanent environmental effects, respectively

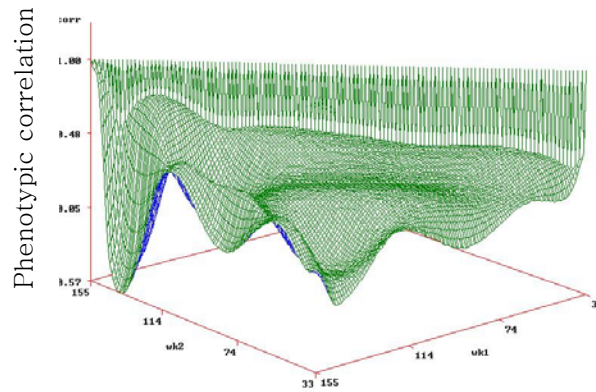


Figure 20. Phenotypic correlations between ages with polynomial order of fit of 6, 4 and 7 for fixed, additive genetic, and permanent environmental effects, respectively

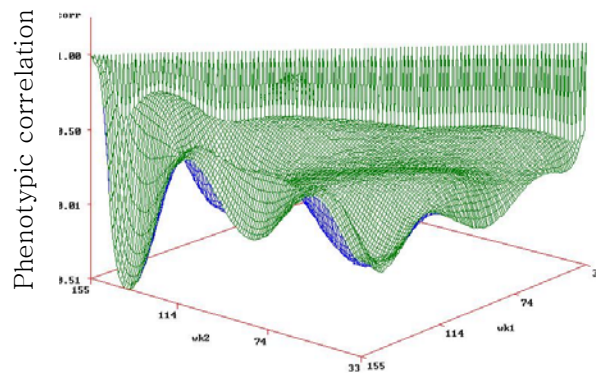
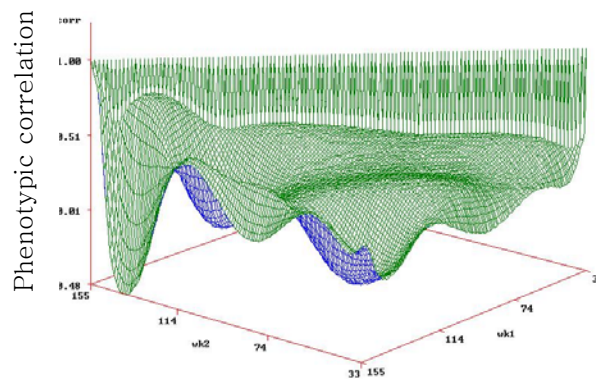


Figure 21. Phenotypic correlations between ages with polynomial order of fit of 4, 2 and 7 for fixed, additive genetic, and permanent environmental effects, respectively



CHAPTER V

CONCLUSIONS

Genetic selection for semen traits is possible. Repeatability estimates were 0.38 for semen volume, 0.37 for total sperm cells, 0.09 for total concentration of sperm per mL, 0.39 for number of extended doses, and 0.16 for acceptance rate of collected ejaculates. Semen traits showed a strong negative genetic correlation with muscle depth and positive genetic correlation with back fat. Genetic correlations between semen traits and average daily gain were low. Therefore, current AI boar selection practices may be having a detrimental effect on semen production as selection for increased muscle depth and reduced backfat may result in reduced boar fertility as measured by semen volume, total sperm cells, and total concentration of sperm per mL. Current swine industry selection practices would be expected to result in reduced male fertility.

Estimates of genetic parameters from both multiple trait and random regression methods would indicate that measures of total sperm cells at different ages are genetically different traits. Genetic variance of total sperm cells increases during the productive life of the boar resulting in heritability estimates increasing from 0.27 to 0.48. Figure 1 shows the comparison of heritability estimates between the three best fit models determined from random regression in Chapter IV and the evaluation of seven ages by multiple trait methods presented in Chapter III. The results are very similar except for the heritability at 24 months of age from MTDFREML that had very high genetic variance. Other than 24 months the results are consistent but it appears that the multiple trait method resulted in an overestimation of heritability of total sperm cells. This overestimation may be due to the reduced amount of data or due to age classifications.

The ability to accurately estimate genetic correlations between different ages is reduced by limiting records to specific ages. Therefore, multiple traits methods may not

be most appropriate for analyzing longitudinal data. This method may be appropriate with sufficient numbers of records at each age and availability of computer resources. Random regression analysis provides much more detail with regard to the changes of the variance components with age. Genetic correlations between total sperm cells at different ages were larger for adjacent ages. Random regression models with comparatively high order polynomials for fixed, additive genetic and permanent environmental effects provided the best fit.

These studies conclusively show there is an opportunity for genetic selection on semen traits. Genetic correlations would indicate that current selection objectives are having a negative effect on semen traits. Random regression methods are the most appropriate to analyze semen traits as they are longitudinal data measured over the boars lifetime. Additional work is needed to understand the relative economic importance of semen traits in the development of breeding objectives.

Figure 1. Comparison of analyses from RRM and MTDFREML for heritability estimates of total sperm cells.

