



Genetic relationships among sperm quality traits of Duroc boars collected during the summer season

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ABSTRACT

The goals of the study were to estimate the heritability and repeatability of boar sperm quality traits during the summer season, estimate phenotypic and genetic correlations between sperm quality traits, and assess the effect of these traits on total number born (TNB). Semen samples were collected and individually processed from Duroc boars ($n = 363$) from May through October 2017. Single sire litter information was available for 121 of the boars. Heritability, repeatability, genetic correlations, and phenotypic correlations were estimated for and among the following traits: total percentage of motile cells (MOT), total percentage of progressively motile cells (PROG), percentage of cells with a distal droplet (DIST), percentage of cells with a proximal droplet (PROX), percentage of cells with a bent tail (BENT), percentage of cells with a distal midpiece reflex (DMR), mean sperm head elongation (ELON), and total sperm cells per ejaculate (TOTSP). Heritability estimates ranged from 0.08 to 0.24 and repeatability estimates ranged from 0.21 to 0.62. The phenotypic and genetic correlations between sperm motility traits and morphological defects indicated a negative relationship. Sperm morphological defects had positive phenotypic and genetic correlations with each other. Total sperm per ejaculate showed positive genetic correlations with the motility traits. Positive phenotypic and genetic correlations existed between ELON and the motility traits. Total sperm motility ($P < 0.001$) positively affected TNB while DIST ($P < 0.001$), PROX ($P < 0.001$), BENT ($P = 0.05$) and DMR ($P = 0.002$) negatively affected TNB. Results indicate genetic selection could enhance sperm quality during the summer season in boars.

1. Introduction

Terminal line boars are typically selected for breeding values for production traits such as growth, efficiency, and carcass quality (Oh et al., 2006; Marques et al., 2017) with no selection emphasis in regards to fertility. A large percentage of high indexing boars that are selected as sires are culled, however, for poor sperm quality, limiting their use for genetic improvement. Results from a study conducted by Schulze et al. (2014) indicated 47.3% of young boars selected for genetic superiority of production traits did not meet boar stud sperm quality thresholds. The most commonly reported issue among these boars was sperm morphological defects (MD) followed by lesser than desirable total motility, with the boars of the Duroc breed most commonly rejected on this basis in

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comparison to Landrace, Pietran, Large White, and Yorkshire boars (Schulze et al., 2014). With the Duroc breed being the most widely used terminal breed in North America (National Swine Registry, 2018), the results of these relatively greater rejection rates than for boars of other breeds could be having substantial economic impacts on breeding companies and producers alike. Knox et al. (2008) reported ejaculate discard rates throughout the year of 1% to 10%, with the majority of semen discards resulting from seasonal and individual boar effects.

Decreased semen quality has been well documented during the summer months due to heat stress (Stone, 1982; Flowers, 1997; Boyer and Almond, 2017). Even a temperature slightly greater than that of the boar's thermoneutral zone (17.7–20 °C) of 22.2 °C can lead to impaired spermatogenesis (Boyer and Almond, 2017), decreased sperm motility and increased MD (Stone, 1982; Flowers, 1997; Boyer and Almond, 2017), cellular degradation of germ cells, decreased libido, and decreased conception rates, with marked effects when temperatures are greater than 28.3 °C (Stone, 1977; Blackshaw, 1977; Boyer and Almond, 2017). Because both sperm motility and MD affect production, i.e.: conception, farrowing rate, and total number of piglets born (Waberski et al., 1994; Rozeboom, 2000; Smital et al., 2005), boar studs commonly use a threshold of at least 70% morphologically normal and motile sperm as a minimum to be used for inseminations (Rozeboom, 2000).

From results in previous research, there has been consideration in determining ejaculate discards on all combined MD and heritability estimates were reported based on percentage of morphologically abnormal sperm as compared with individual morphological traits. The previously reported heritability of percentage of abnormal sperm has a wide range of 0.07 to 0.34 (Smital et al., 2005; Wolf and Smital, 2009; Marques et al., 2017). There is also a range in the previously reported heritability estimates for total and progressive sperm motilities, with estimates ranging from 0.05 to 0.38 (Smital et al., 2005; Wolf, 2009a, b; Marques et al., 2017). Reported estimates indicate there are moderate correlations between repeated records on boars for sperm motility (Huang and Johnson, 1996; Wolf, 2009b) and to the authors' knowledge, there are no estimates of repeatability for MD traits in boars.

Computer assisted semen analysis (CASA) evaluation allows for highly accurate and repeatable analyses of sperm quality when there is assessment of a single ejaculate (Farrel et al., 1995). To the authors' knowledge, estimates of genetic and phenotypic (co) variances of the specific morphological traits estimated from computer assisted semen analysis (CASA) have not been previously reported. The goals of this study, therefore, were to 1) estimate the heritability and repeatability of sperm quality traits during the summer season 2) estimate phenotypic and genetic correlations between CASA traits and 3) assess the effect of these sperm quality traits on total number of piglets born.

2. Materials and methods

2.1. Boars utilized

Duroc boars ($n = 363$) were utilized for this study. Boars were housed and collected at three boar studs in three states, North Carolina (NC) ($n = 137$), Virginia (VA) ($n = 148$), and Texas (TX) ($n = 78$). The average age in months of boars at all collection time points was 15.5, with a minimum age of 7 months and a maximum age of 40 months (Table 1).

2.2. Genotype information and genomic relationship matrix formation

The DNA was extracted from hair follicles and genotyping was performed on all boars. The SNP genotypes were obtained from Smithfield Premium Genetics (Rose Hill, NC). Boars ($n = 110$) were genotyped on the PorcineSNP80 BeadChip (GeneSeek, Neogen Corp.) and the remaining 253 boars were genotyped on the GeneSeek Genomic Profiler 50k BeadChip (GGP; GeneSeek, Neogen Corp.). Quality control included removal of SNPs with a minor allele frequency of less than 0.05 and SNP with a call rate less than 0.9. Individuals were removed when the call rate was less than 0.9. For all boars, Fimpute 2.2 (Sargolzaei et al., 2014) was used to impute to a set of 45,836 SNP from the GGP Porcine BeadChip.

Table 1

Mean and standard deviation (SD) of sperm quality traits, and variables that affect sperm quality during the seasonal heat stress period (May through October).

Quality Trait/Variable	Mean	SD	Max	Min
Total motility (%)	70.26	14.08	91.9	2.3
Total progressively motile (%)	42.76	13.55	84.7	0.1
Proximal droplet (%)	6.94	4.40	27.6	0.9
Distal droplet (%)	9.57	6.65	31.7	1.1
Distal midpiece reflex (%)	4.27	4.34	20.2	0
Bent tail (%)	1.89	1.38	24.6	0
Total Sperm (billion/collection)	79.81	28.43	166.79	17.63
Mean sperm head elongation	0.41	0.02	0.48	0.33
Rest interval between collections (days)	8.70	3.62	18	1
Collection to processing (days)	1.5	0.81	5	1
Age in months at collection	15.5	6.32	40	7

2.3. Semen analysis

Semen was collected and processed from May through October 2017 to obtain data during the normal heat-stress season in the United States, where the greatest average daily barn temperature was $24.22\text{ }^{\circ}\text{C} \pm 5.36$ throughout the study duration. Boars were collected and semen was shipped over-night to the laboratory at The University of Nebraska-Lincoln (UNL) for processing. Samples were received every-other week during the time frame, totaling 13 weeks, when there was processing of semen. Only samples collected during the week when shipping occurred were sent to UNL. Samples from every ejaculate of each boar were not processed at the UNL laboratory during this 6-month timeframe due to the alternate week shipping schedule. There was an average of 6.5 collections processed at UNL during this period (minimum = 1, maximum = 24). A complete collection schedule was provided to UNL personnel for determination of the rest interval (RI) between the times of sample collections for each boar (Table 1).

Following collection, semen was visually assessed for quality characteristics and evaluated at the boar stud to determine whether the ejaculate met the criteria that it was useful for inseminations. Volume is reported by weight, and concentration was estimated using a spectrophotometer (Metrosperm). Prism software (MOFA Global PRISM 3.5) was then used to estimate total cells from concentration and volume. Semen dosing determinations were made on a total cell basis and semen was extended to the company specific ratio required per sample for breeding. A 3 ml sample was collected by pipetting from each extended sample which was cooled to $18\text{ }^{\circ}\text{C}$ in preparation for shipment to UNL. All boar studs used the same cooling procedure. A sample was sent to UNL for processing regardless of whether the semen was deemed acceptable for inseminations or was discarded for quality issues. Semen was shipped over-night at approximately $18\text{ }^{\circ}\text{C}$ in 3 ml tubes. The majority of samples were processed the day after collection, unless boars were collected on Friday or Saturday. Semen from Friday/Saturday ejaculates were shipped Monday and processed Tuesday. All collections were processed within the timeframe when fresh semen would typically be used for breeding (Knox et al., 2008), thus standardizing the timing of semen quality assessments with that when the semen is typically used for inseminations in pork production enterprises. The average days from collection to processing (DCP) was 1.5 days (Table 1).

Samples were processed using a Hamilton-Thorne Sperm Analyzer IVOS 1.9, CASA system (Hamilton Thorne Biosciences, MA, USA). The Leja4 analysis chambers (Leja, Nieuw-Vannep, Netherlands) were used which contain a $20\text{ }\mu\text{m}$ aliquot of semen. Samples were evaluated at $35\text{ }^{\circ}\text{C}$. Semen quality variables estimated using CASA in this study were the following: total percentage of motile cells (MOT), total percentage of progressively motile cells (PROG), distal droplet percentage of total cells (DIST), proximal droplet percentage of total cells (PROX), bent tail percentage of total cells (BENT), distal midpiece reflex percent of total cells (DMR), and mean sperm head elongation (ELON) which is a mean ratio of width to length of the sperm head. The CASA system cut-off values the motility traits were as follows: PROG = cells with over $45\text{ }\mu\text{m}/\text{second}$ average path velocity (VAP) and 45% path straightness (STR), MOT = cells greater than a VAP of $4\text{ }\mu\text{m}/\text{second}$ with straight line velocity (VSL) of $1\text{ }\mu\text{m}/\text{second}$ or greater. Total sperm cells per ejaculate (TOTSP), quantified in billions, was estimated at the boar stud as previously described.

2.4. Production data

Single sire litter data that corresponded to the samples processed at UNL were available for 121 boars, resulting in a total of 1396 litters with a mean of 11.5 litters per boar ± 8.7 litters. Any doses used for inseminations were assessed as having met the commercial stud quality thresholds for sperm motility and morphology prior to use. Total number of piglets born (TNB) was calculated per farrowing by summing born alive and stillborn piglets.

2.5. Statistical analysis

A genomic relationship matrix was created in R (R Core Team, 2018) in accordance with (VanRaden, 2008):

$$G = \frac{ZZ'}{2\sum p_i(1 - p_i)}$$

Where $Z = M - P$. M was a $n \times m$ matrix of marker alleles that each individual inherited, the P matrix contained allele frequencies multiplied by 2, and p_i was the frequency of the i^{th} allele summed over all loci.

(Co)variance components of the semen parameters were estimated in ASreml 4 (Gilmour et al., 2015) using repeated measure animal models. Univariate models were utilized to estimate the heritability and repeatability of each semen trait. The use of model one allowed for consideration of the following effects and was used to model MOT and PROG:

$$y_{ijklmn} = \mu + CG_i + RI_j + DCP_k + Ext_l + b \text{ Age}_{ijklmn} + \text{Animal}_m + Pe_m + e_{ijklmn}$$

where y is the semen variable measured on the n^{th} ejaculate of the m^{th} boar. Contemporary group (CG_i), is the effect of the i^{th} CG which is a concatenation of farm and collection month, rest interval between collections (RI_j) is the j^{th} effect of days between collections, DCP_k is the k^{th} effect of days between semen collection and semen processing, Ext_l is the l^{th} effect of extender type, and Age is the covariate of months of age at collection. Random effects included Animal_m , the additive genetic effect of the m^{th} boar, Pe_m , the permanent environmental effects for the m^{th} boar, and random residual effect, e_{ijklmn} . It was assumed that $\text{Animal} \sim N(0, G\sigma_a^2)$, where G was the genomic relationship matrix and σ_a^2 was the additive genetic variance. It was also assumed that $Pe \sim N(0, I\sigma_p^2)$, where I is an identity matrix and σ_p^2 was the permanent environmental variance. With model two, there was consideration of the following effects

and this model was used to model DIST, PROX, BENT, DMR, TOTSP, and ELON:

$$y_{ijkl} = \mu + CG_i + RI_j + b \text{Age}_{ijkl} + \text{Animal}_k + Pe_k + e_{ijkl}$$

where y signifies the semen variable measured on the l^{th} ejaculate of the k^{th} boar. Fixed effects in the model included CG_i , RI_j , and Age (as described in Model 1). Random effects included Animal_k , the k^{th} additive genetic effect, Pe_k the permanent environmental effects for animal k , and random residual e_{ijkl} .

In previous research, there was not inclusion of extender type in models for morphological effects as these traits originate from testicular/epididymal disturbances (Vyt et al., 2004), this was also assessed for data in the present study. Extender type had a significant effect on MOT and PROG but not on PROX, BENT, DMR, TOTSP, or ELON, and for this reason, type of extender was only used in the model for MOT and PROG. Sperm motility was previously reported to be affected by storage time (Kommisrud et al., 2002; Vyt et al., 2004). Days between collection and semen processing also did not affect morphological traits, ELON or TOTSP ($P > 0.05$) as these defects occur pre-ejaculation, thus was only included for MOT and PROG as motility was affected by storage time ($P < 0.005$). All other fixed effects included in the models affected the response variable ($P < 0.05$).

Narrow-sense heritability estimates (h^2) were estimated as $h^2 = Va/(Va + Vpe + Ve)$, where Va , Vpe , and Ve were the estimated additive genetic, permanent environmental, and residual variance, respectively. Repeatability (r) was estimated as $(Vpe + Va)/(Va + Vpe + Ve)$. This repeatability represents an estimate of repeated records during one summer season.

Bi-variate repeated measure animal models were used to estimate phenotypic and genetic correlations between the semen traits. These models included the same fixed and random effects per trait as outlined in the univariate models.

Each semen quality trait was tested for an association with TNB. Semen variables were adjusted for fixed effects using the linear model package in R (R Core Team, 2018) with the following models:

$$\text{Model s1: } y_{ijklm} = \mu + CG_i + RI_j + DCP_k + Ext_l + b \text{Age}_{ijklm} + e_{ijklm}$$

$$\text{Model s2: } y_{ijk} = \mu + CG_i + RI_j + b \text{Age}_{ijk} + e_{ijk}$$

Model s1 was used to adjust MOT and PROG and included the fixed effects of CG , which was the i^{th} effect of the concatenation of farm and collection month, rest interval between collections (RI_j) is the j^{th} effect of days between collections, DCP_k is the k^{th} effect of days between semen collection and semen processing, Ext_l is the l^{th} effect of extender type, and Age is the covariate of months of age at collection. Model s2 was used to adjust DIST, PROX, BENT, DMR, TOTSP, and ELON. Fixed effects in the model included CG , RI , and Age . An average per boar, per adjusted sperm quality trait, was then calculated to be used as the independent variable in the regression analysis with TNB.

Total number born was adjusted for fixed effects including female contemporary group (FCG_i), which was a concatenation of service month and sow farm, and the j^{th} effect of mating parity (PR_j). A Poisson distribution was specified for the TNB model using the generalized linear model package in R (R Core Team, 2018).

$$\text{TNB model: } y_{ijk} = \mu + FCG_i + PR_j + e_{ijk}$$

An average adjusted TNB was estimated per boar and was used as the dependent variable (y_{ij}) in the regression analysis of TNB on each adjusted mean semen variable (SV_i ; from models s1 and s2), with the following model using the linear model package in R (R Core Team, 2018):

$$y_{ij} = \mu + SV_i + e_{ij}$$

To assess if the semen quality traits had a significant association with TNB, the regression coefficients for the semen quality traits were assessed to ascertain if these were significantly different than zero.

3. Results

Mean values of the sperm variables during the study are presented in Table 1. The narrow-sense heritability estimates of the sperm quality traits are presented in Table 2. Heritability estimates for the traits ranged from 0.08 to 0.24, with MOT having the lowest heritability and DMR having the highest heritability. Repeatability estimates are presented in Table 3. Results for repeatability estimates indicated there were moderate to high correlations between values resulting from repeated records during the summer season with estimates ranging from 0.21 to 0.62. For most traits, the repeatability was greater than twice the heritability estimate indicating permanent environmental effects explained a larger proportion of the phenotypic variance than additive variance.

Values for phenotypic and genetic correlations between the traits are presented in Table 2. There was the greatest phenotypic correlation between MOT and PROG (0.81 ± 0.01), and the least phenotypic correlation between ELON and TOTSP (0.00 ± 0.03). Total motility and PROG were negatively phenotypically correlated with all morphological defects (-0.27 to -0.59), and had positive phenotypic correlations with ELON (0.45 and 0.41 respectively). The MD traits had positive phenotypic correlations with each other with results ranging from 0.14 to 0.48. Values for total sperm had the least overall phenotypic correlations with the values for other traits ranging from 0.00 to 0.19, though interestingly, for TOTSP there were positive phenotypic correlations with the morphological defects DIST and DMR (0.19 and 0.12 respectively).

There was the greatest genetic correlation between MOT and ELON (0.62 ± 0.30), followed closely by PROX and TOTSP

Table 2
Heritability estimates (on diagonal), genetic correlations (above diagonal), and phenotypic correlations (below diagonal), with corresponding standard errors for sperm quality variables for Duroc boars when semen is collected during the summer season.

	% Total Motility	% Progressively motile	% Proximal droplets	% Distal droplets	% DMR	% Bent tail	Mean elongation	Total Sperm
% Total Motility	0.08 ± 0.06	0.62 ± 0.25	-0.44 ± 0.32	-0.24 ± 0.31	-0.37 ± 0.30	NE	0.62 ± 0.30	0.13 ± 0.29
% Progressively motile	0.81 ± 0.01	0.10 ± 0.06	-0.52 ± 0.27	-0.34 ± 0.33	-0.27 ± 0.26	-0.24 ± 0.30	0.31 ± 0.28	0.06 ± 0.32
% Proximal droplets	-0.46 ± 0.03	-0.49 ± 0.03	0.21 ± 0.10	0.60 ± 0.18	0.20 ± 0.26	NE	-0.30 ± 0.26	-0.61 ± 0.28
% Distal droplets	-0.31 ± 0.03	-0.40 ± 0.02	0.35 ± 0.04	0.18 ± 0.07	0.59 ± 0.18	0.16 ± 0.39	0.02 ± 0.30	-0.29 ± 0.31
% DMR	-0.27 ± 0.03	-0.28 ± 0.03	0.14 ± 0.03	0.48 ± 0.02	0.24 ± 0.07	0.56 ± 0.34	0.40 ± 0.27	0.33 ± 0.22
% Bent tail	-0.59 ± 0.02	-0.49 ± 0.02	0.38 ± 0.03	0.22 ± 0.03	0.17 ± 0.03	0.13 ± 0.06	NE	0.10 ± 0.33
Mean elongation	0.45 ± 0.02	0.41 ± 0.03	-0.62 ± 0.02	-0.16 ± 0.03	-0.02 ± 0.03	-0.10 ± 0.02	0.15 ± 0.07	0.28 ± 0.29
Total Sperm	-0.05 ± 0.02	-0.08 ± 0.03	0.02 ± 0.03	0.19 ± 0.02	0.12 ± 0.03	0.05 ± 0.03	0.00 ± 0.03	0.16 ± 0.05

NE = Not estimable, DMR = distal midpiece reflex. Heritability estimates are presented in bold on the diagonal.

Table 3
Estimates of repeatability with corresponding standard errors for sperm quality traits from Duroc boars collected during the summer season.

Variable	Repeatability
% Total motility	0.36 ± 0.03
% Progressively motile	0.36 ± 0.03
% Proximal droplets	0.62 ± 0.02
% Distal droplets	0.39 ± 0.03
% DMR	0.32 ± 0.03
% Bent tail	0.21 ± 0.03
Mean elongation	0.44 ± 0.03
Total Sperm	0.24 ± 0.03

(-0.61 ± 0.28). As was the case with phenotypic correlation estimates, the genetic correlation estimates between MOT and PROG with the morphological defect traits were negative (-0.24 to -0.52). The genetic correlations were not estimable between BENT and the semen quality traits of MOT, PROX, and ELON. The standard errors associated with the genetic correlations were large, and the estimates were not always statistically different from zero mainly due to the sample size of the study ($n = 363$). Many of these genetic correlations, however, have not been described previously and these estimates serve as the first evidence of the genetic relationships among these traits.

Five semen quality traits affected TNB with regression coefficients differing from zero. For total motility ($P < 0.0001$), there was a positive association with TNB while, DIST ($P = 0.0003$), PROX ($P = 0.0002$), BENT ($P = 0.05$) and DMR ($P = 0.002$) were negatively associated with TNB. Values for regression coefficients for TNB are reported in Table 4. There were no significant associations between TNB and PROG, ELON, or TOTSP.

4. Discussion

In the present study, there was estimation of the heritability of 0.08 ± 0.06 for total sperm motility during the summer season after shipping and storage. Wolf (2009b) also reported a heritability of 0.08, with a repeatability analysis of multiple terminal sire breeds, including for the Duroc breed. The results in Table 1 indicate that the average total motility throughout the present study was 70% of total spermatozoa. It should be noted that this estimate occurred after semen had been cooled, stored, shipped, warmed and processed. The characteristics of sperm in semen samples, therefore, were determined in a similar timeframe as inseminations would have occurred in pork production enterprises during the summer. The average total sperm motility in the current study is similar to the average motility after 24 h from the time of collection reported by Schulz et al. (2014) of 71.3% for Duroc boars. Total sperm motility had a moderate repeatability (0.36 ± 0.03), which is similar to the average repeatability among the breeds assessed in a previous study (Wolf, 2009b) of approximately 0.33, indicating there are permanent environmental effects that markedly effect MOT. For the progressively motile sperm variable, the heritability estimate (0.10 ± 0.06) was slightly less than the heritability estimate reported by Wolf and Smital (2009) of 0.13. The repeatability for PROG has not previously been reported and was estimated at 0.36 ± 0.03 in the current study.

The negative genetic correlation of PROG with all MD traits has previously been reported by Wolf (2009a). This negative relationship exists because cells with morphological abnormalities affect the capacity of the sperm cell to be progressively motile. For example, cells with bent tails have a “drag defect” that affects the movement of the cell (Zini et al., 1998; Brito, 2014). These negative correlations between MOT and PROG with all MD traits indicate selecting for MOT or PROG could potentially result in a decrease in morphological defects in semen samples of boars.

There was a positive association in the present study between MOT and TNB. It has previously been reported that total sperm

Table 4
Estimates of regression coefficients from models that regressed average total number born per boar on averaged semen quality parameters per boar using Duroc boars collected during the summer season.

Variable	Regression coefficient	P value
% Total motility	0.05	< 0.001
% Progressively motile	0.01	0.28
% Proximal droplets	-0.14	< 0.001
% Distal droplets	-0.06	< 0.001
% DMR	-0.08	< 0.001
% bent tails	-0.26	0.05
Mean elongation	11.82	0.29
Total Sperm	0.00	0.84

Sperm quality traits and total number born were adjusted for fixed effects prior to being averaged and used in the regression model.

motility affects both farrowing rate and litter size (Rozeboom, 2000), and it has also been reported that there are favorable genetic correlations between number of motile sperm with total number of piglets born (0.35), and conception rate (0.35) (Smital et al., 2005). Though the regression coefficient of 0.05 from the current study is small, this estimate indicates that a 20% decrease in total sperm motility could lead to there being one less piglet produced per litter. It should be reiterated that the difference in TNB in the current study resulted inseminations where all semen used for matings met the commercial stud quality threshold, which is typically 70% motile sperm. This finding indicates that even when semen is considered to have acceptable total sperm motility, there is still economic value in having a greater total sperm motility per semen dose. Overall, results from the present and previous research indicates there is potential for boars to be selected for motile and progressively motile sperm that would result in a decrease in semen collections that would be excluded due to not meeting the total motility threshold for breeding, therefore, there would be an increase in progeny per boar through gains in both farrowing rate and TNB.

Semen collections in which there is less than 70% morphologically normal sperm are also commonly rejected for insemination of females in pork production enterprises (Rozeboom, 2000). In the present study, cytoplasmic droplets were the most common morphological defect (Table 1). Distal droplets are more common than proximal droplets on boar spermatozoa, with both types of droplets having a negative effect on farrowing rate and litter size (Waberski et al., 1994; Rozeboom, 2000). The regression coefficient for PROX of -0.14 indicates that when there is less than a 10% incidence in PROX there is a one piglet reduction in litter size. As the mean PROX reported in the present study was 6.94% (Table 1), substantial potential piglet losses could be occurring due to these sperm morphological defects.

In the present study, for proximal droplets and distal droplets there were heritability estimates of 0.21 ± 0.10 and 0.18 ± 0.07 , respectively, and repeatability estimates were 0.61 ± 0.02 and 0.39 ± 0.03 , respectively. To the best of our knowledge there are no published heritability or repeatability estimates for cytoplasmic droplet percentage in boars. The values for heritability estimates in the present study indicate that selection against cytoplasmic droplet presence is possible, which is promising considering the effect of droplets on production traits as previously reported by (Waberski et al., 1994; Rozeboom, 2000) and in the current study. The genetic correlation between DIST and PROX of 0.60 ± 0.18 indicates that both droplet types were under similar genetic control and selecting against either droplet type should reduce the incidence of the other droplet type.

The next most commonly occurring morphological defect detected in the present study was DMR. The DMR is a bend in the distal region of the mid-piece and is commonly associated with a distal droplet entrapped in the bend. Both DMR and bent tails results in a “drag-like” defect that affects sperm motility. The difference between DMR and bent tails is the midpiece quality. With DMR sperm, the midpiece is still complete and smooth, whereas with bent tails that involve the midpiece or total tail, the mitochondrial sheet is usually fractured (Brito, 2014). The effect of heat-stress on DMR percentage in boars has not been previously reported. In bulls, however, a relatively greater DMR percentage was highly correlated with the extent of heat-stress conditions (Menegassi et al., 2015). The results of the current study indicate DMR percentage was negatively associated with total number of piglets born, indicating its potential importance to efficiencies in pork production enterprises.

The average BENT percentage was 1.89% (Table 1). The effect of bent tails on fertility of boar semen for breeding has not previously been reported, however in humans, with a relative increase in bent tail percentages there is greater infertility (Jouannet et al., 1988). The heritability estimate for BENT in the current study was 0.13 ± 0.06 , and the repeatability estimate was 0.21 ± 0.03 . Neither the heritability nor repeatability of BENT has previously been assessed. Percentage of bent tails was negatively associated with TNB. There was an estimated regression coefficient of -0.26, indicating that for every 1% increase in bent tails, there would be decrease of 0.26 piglets born in a litter. This finding indicates that a small percentage increase above the average for BENT could markedly affect the TNB.

The heritability and repeatability of ELON has not previously been estimated in any species. There are effects on sperm head shape when boars are heat-stressed, and change in head shape has been reported to negatively affect sperm motility and fertility (Boyer and Almond, 2017). The relationship between sperm head size and total motility was observed in the present study with there being a phenotypic correlation of 0.45 ± 0.02 , and genetic correlation of 0.62 ± 0.30 , indicating sperm head size may have a function in sperm motility.

Heat stress negatively affects total sperm per ejaculate (Stone, 1982; Flowers, 1997), which leads to a reduction in the number of semen doses per ejaculate (Flowers, 1997). The heritability for total sperm production during the summer season in the present study was 0.16 ± 0.05 with this value being intermediate between values of previous estimates (0.10 to 0.17) in samples collected throughout the year (Wolf, 2009a, 2010; Marques et al., 2017). Repeatability for TOTSP was 0.24 ± 0.03 , which is similar to the estimate of repeatability reported by Huang and Johnson (1996) of 0.26. Phenotypic correlations between TOTSP and all traits were close to zero, except for DIST (0.19 ± 0.02), and DMR (0.12 ± 0.03), with the increase in TOTSP there was a slight increase in some morphological defects in the present study. The genetic correlation between TOTSP and DMR (0.33 ± 0.22) also indicates this unfavorable relationship. In contrast to the phenotypic correlations, there was a negative genetic correlation between TOTSP, DIST, and PROX in the current study (-0.29 ± 0.31 and -0.61 ± 0.28 , respectively). Oh et al. (2006) also reported there was a negative correlation between total sperm and percentage of morphologically abnormal cells (-0.12). Analyzing the morphological defects as individual traits instead of combined as one trait allows for a preliminary understanding of the relationships with each other and the relationships with other non-morphological sperm traits. Though the standard errors corresponding to these genetic correlation estimates were large in the present study, these estimates serve as the initial evidence that the relationship between morphological traits and other economically important traits, such as TOTSP, vary depending on the morphological defect.

Results from the present study indicate selection for semen quality when heat-stress conditions of the summertime prevail could result in improvements in sperm quality characteristics of boar semen. It is recognized that the standard errors for the genetic correlations in the present study were large, with not all estimates being statistically different from zero. Many of these relationships

have not, however, previously been described, and with the moderate to strong correlations estimated between many of the sperm quality traits, the results of the study indicate there is need for further research with larger datasets.

5. Conclusion

The goal of this study was to estimate the heritability and repeatability of sperm quality during the summer season when sperm production and quality is typically less, as well as assess how sperm quality traits are correlated both phenotypically and genetically. Heritability estimates for the sperm quality traits ranged from 0.08 to 0.24. Of the traits for which there are previously reported estimates of heritability from samples taken throughout the year, the estimates when heat stress conditions prevailed were similar, which may indicate selecting for sperm quality, regardless of whether there is heat-stress is feasible when selecting for quality during periods when heat stress prevails. Traits that positively affect litter size such as total sperm motility had negative genetic correlations with all morphological abnormality traits suggesting that selecting for total motility could decrease the incidence of sperm morphological defects while potentially increasing total number of piglets born. The substantial permanent environmental effect for all sperm quality traits suggests that collecting data on boars prior to the use of their semen for artificial insemination should be considered to manage semen quality in the boar stud. Overall, results indicate that sperm quality could be selected for when heat-stress conditions prevail and that several sperm quality traits had significant associations with litter size.

Conflict of interest

None reported. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

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