Genetic parameter estimates for scrotal circumference and semen characteristics of Line 1 Hereford bulls[1]

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ABSTRACT: The objectives of this study were to estimate heritability for scrotal circumference (SC) and semen traits and their genetic correlations (r_g) with birth weight (BRW). Semen traits were recorded for Line 1 Hereford bulls (n = 841), born in 1963 or from 1967 to 2000, that were selected for use at Fort Keogh (Miles City, MT) or for sale. Semen was collected by electroejaculation when bulls were a mean age of 446 d. Phenotypes were BRW, SC, ejaculate volume, subjective scores for ejaculate color, swirl, sperm concentration and motility, and percentages of sperm classified as normal and live or having abnormal heads, abnormal midpieces, proximal cytoplasmic droplets (primary abnormalities), bent tails, coiled tails, or distal cytoplasmic droplets (secondary abnormalities). Percentages of primary and secondary also were calculated. Data were analyzed using multiple-trait derivative-free REML. Models included fixed effects for contemporary group, age of dam, age of bull, inbreeding of the bull and his dam, and random animal and residual effects. Random maternal and permanent maternal environmental effects were also included in the model for BRW. Estimates of heritability for BRW, SC, semen color, volume, concentration, swirl, motility, and percentages of normal, live, abnormal heads, abnormal midpieces, proximal cytoplasmic droplets, bent tails, coiled tails, distal cytoplasmic droplets, and primary and secondary abnormalities were 0.34, 0.57, 0.15, 0.09, 0.16, 0.21, 0.22, 0.35, 0.22, 0.00 0.16, 0.37, 0.00 0.34 0.00, 0.30, and 0.33, respectively. Estimates of r_g for SC with color, volume, concentration, swirl, motility, and percentages of live, normal, and primary and secondary abnormalities were 0.73, 0.20, 0.77, 0.40, 0.34, 0.63, 0.33, −0.36, and −0.45, respectively. Estimates of r_g for BRW with SC, color, volume, concentration, swirl, motility, and percentages live, normal, and primary and secondary abnormalities were 0.28, 0.60, 0.08, 0.58, 0.44, 0.21, 0.34, 0.20, −0.02, and −0.16, respectively. If selection pressure was applied to increase SC, all of the phenotypes evaluated would be expected to improve. Predicted correlated responses in semen characteristics per genetic SD of selection applied to SC were 0.87 genetic SD or less. If selection pressure was applied to reduce BRW, the correlated responses would generally be smaller but antagonistic to improving all of the phenotypes evaluated. Predicted correlated responses in SC and semen characteristics per genetic SD of selection applied to BRW were less than 0.35 genetic SD.

Key words: beef cattle, fitness, semen, sperm morphology

INTRODUCTION

Economic success of cow-calf production depends on the percentage of calf crop, which in turn depends on the fertility of parents and the survival of progeny (Werth et al., 1991; MacNeil et al., 1994; Tess, 1999). Sire fertility should be established before the breeding season due to its impact on profitability. Semen evaluation is generally an accepted way to estimate potential fertility of bulls. Thus, a breeding soundness evaluation consisting of a physical examination, scrotal circumference (**SC**) measurement, and semen evaluation is recommended (Elmore et al., 1976; Hopkins, 2003). Barth and Waldner (2002) reported that 49 and 73% of bulls evaluated

in January and June, respectively, were of satisfactory breeding soundness. Kennedy et al. (2002) classified 76% of 3,648 yearling bulls as satisfactory potential breeders. Thus, improvement of phenotypes evaluated in a breeding soundness exam may be warranted.

Scrotal circumference may useful in predicting the quality and amount of spermatozoa-producing tissue (Elmore et al., 1976; Coe, 1999; Hopkins, 2003) and age at puberty (Brinks et al., 1978; Lunstra et al., 1978). Scrotal circumference of beef bulls has been reported to be moderately heritable (Koots et al., 1994a; Martinez-Velazquez et al., 2003). Few genetic characterizations exist for phenotypes derived from evaluating semen samples and that are indicative of fertility. Likewise, birth weight may be indicative of calf survival, and there are few estimates of its genetic correlations with components of a breeding soundness examination.

Thus, our objectives were to 1) estimate heritability for birth weight, SC, ejaculate characteristics, and morphology of spermatozoa; 2) estimate genetic and phenotypic correlations among ejaculate characteristics and morphology of spermatozoa; and 3) predict correlated responses in ejaculate characteristics and morphology of spermatozoa when selection pressure is applied to reduce birth weight (**BRW**) or increase SC.

MATERIALS AND METHODS

Bulls were from the line 1 Hereford population maintained by the USDA-ARS Fort Keogh Livestock and Range Research Laboratory (Miles City, MT). The population originated in 1934 with matings of 2 half-sib bulls, Advanced Domino 20th and Advanced Domino 54th, to 50 registered Hereford females. Inbreeding accumulated quickly in the first few generations, but in later generations the rate of inbreeding declined due to the use of planned matings (Knapp et al., 1951). During the period of the present research, pedigree inbreeding increased approximately 2% per generation (MacNeil et al., 1992). From the late 1950s to the present, all bull calves were kept intact, placed on feed after weaning, and fed for 140 (after 1995), 168 (1981–1995), or 196 (before 1981) d to evaluate postweaning growth (MacNeil et al., 1992).

Semen from bulls (n = 841) selected for use at Fort Keogh or for sale was evaluated during the years 1963 and 1967 to 2000. For each bull, the semen collection nearest to 1 yr of age was used. For most bulls it was their first collection. The average age of bulls at evaluation was 446 d. Scrotal circumference was measured from 1976 onward. On a given day, a trained technician collected the semen samples by electroejaculation and measured SC. Scrotal circumference was measured with a flexible measuring tape at the greatest horizontal distance around the scrotum after manually forcing the testicles into the base of the scrotum. Descriptive statistics for all phenotypes are shown in Table 1.

One person (R. A. Bellows) evaluated all semen samples used in this study. During collection, the semen

Table 1. Numbers of observations (n), means (μ), and phenotypic standard deviations (s) for scrotal circumference, birth weight, and semen characteristics of line 1 Hereford bulls at an average age of 446 d

Trait[1]	n	μ	s
Birth weight, kg	3,260	38.5	4.61
Scrotal circumference, cm	626	35.04	2.10
Color	840	2.21	0.87
Volume, mL	840	3.34	1.80
Concentration	841	3.23	1.03
Swirl	841	2.06	1.44
Motility	841	3.26	1.23
Live, %	835	78.21	16.54
Normal spermatozoa, %	837	81.73	12.56
Primary abnormalities, %	839	11.03	10.88
Abnormal heads, %	839	3.25	5.72
Abnormal midpieces, %	839	6.88	8.58
Proximal cytoplasmic droplets, %	839	0.90	3.85
Secondary abnormalities, %	838	7.28	7.20
Bent tails, %	837	1.41	3.35
Coiled tails, %	839	5.82	6.79
Distal cytoplasmic droplets, %	839	0.05	0.58

[1]Subjective scores were assigned for color, concentration, swirl, and motility with 0 = least and 5 = most.

tube was maintained at 36 to 39°C with an insulated water jacket. A water bath and slide warmer were used to maintain the sample at 37°C until sperm motility was assessed and a morphology slide was dry. Measurements collected were ejaculate volume, sperm concentration, semen motility, and percentages of normal, live, abnormal heads, abnormal midpieces, proximal cytoplasmic droplets, bent tails, coiled tails, and distal cytoplasmic droplets. When a particular sperm cell exhibited more than one abnormality, the most obvious abnormality was recorded. Abnormal heads, abnormal midpieces, and proximal cytoplasmic droplets were considered primary abnormalities. Secondary abnormalities consisted of bent tails, coiled tails, and distal cytoplasmic droplets (Field and Taylor, 2003).

Ejaculate volume and semen color score (where 0 = clear and water-like and 5 = rich creamy pearl) were recorded within 3 min of collection. An undiluted drop of neat semen was placed on a microscope slide and given a score for swirl (0 to 5, where 0 = none; 1 = very weak; 2 = weak; 3 = intermediate; 4 = strong; and 5 = very strong) under a light microscope at 100× magnification. Subjective scores were given to each ejaculate for semen concentration (0 = essentially no sperm; 5 = very abundant sperm) and motility (0 = essentially no sperm exhibit progressive movement; 5 = most sperm exhibit rapid forward movement) by viewing a drop of neat semen placed on a warmed glass slide under a cover slip at 100× magnification. The scoring systems used were originally adapted from Harris et al. (1960) and Cummings (1954). Percentages of live, normal, primary abnormalities, and secondary abnormalities were estimated by staining a drop of semen with eosin-nigrosin morphology stain (Lane Manufacturing, Inc., Den-

ver, CO) and counting 100 random spermatozoa at 400× magnification.

Data were analyzed using multiple-trait derivative-free REML methods as implemented by Boldman et al. (1995). The linear model for each trait included fixed classification variables for effects of contemporary group and age of dam (yr) and continuous variables for age of bull at evaluation (d), inbreeding level of the bull (0 to 1), and his dam (0 to 1). The contemporary group was defined as the year and season (spring or fall) of evaluation. Age of dam was classified as 2, 3, 4, and 5 yr of age or more. Random effects included animal, maternal, permanent maternal environmental, and residual effects. A single-trait model was used to estimate heritability of BRW, SC, and semen characteristics. For birth weight, the model was

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}_g\mathbf{u} + \mathbf{Z}_m\mathbf{m} + \mathbf{Z}_c\mathbf{c} + \mathbf{e},$$

where $\mathbf{y}$ is a vector of observations, β is a vector of fixed effects (contemporary group, age of bull at evaluation, age of dam, levels of inbreeding of the bull and his dam), $\mathbf{u}$ is a vector of direct additive genetic effects, $\mathbf{m}$ is a vector of maternal additive genetic effects, $\mathbf{c}$ is a vector of permanent environmental effects due to dam, $\mathbf{e}$ is a vector of random residual effects, and $\mathbf{X}$, $\mathbf{Z_g}$, $\mathbf{Z_m}$, and $\mathbf{Z_c}$ are known incidence matrices connecting the observations to the corresponding fixed and random effects. Maternal additive genetic effects and permanent environmental effects due to dams were not included in analyses of SC and semen characteristics. Following Dodenhoff et al. (1988), standard errors of the heritability estimates were calculated from the inverse of the negative average information matrix, considering it to be an asymptotic dispersion matrix of the estimated parameters.

Correlations of BRW with SC, each semen trait, and the genetic trend in SC were calculated with a 2-trait model:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \beta + \begin{bmatrix} Z_{g1} & 0 \\ 0 & Z_{g2} \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix}$$

$$+ \begin{bmatrix} Z_{m1} \end{bmatrix} \begin{bmatrix} m_1 \end{bmatrix} + \begin{bmatrix} Z_{c1} \end{bmatrix} \begin{bmatrix} c_1 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix},$$

where the effects of each trait are as defined for the single-trait analyses, and subscripts 1 and 2 correspond to BRW weight and SC or a semen trait, respectively.

Correlations among SC, ejaculate characteristics, and sperm morphology were estimated using 3-trait models. The model used included the same fixed effects, the 2 traits of interest, and BRW. Birth weight was included in the analysis because it was measured on all animals, including those that were not evaluated for breeding soundness and thus aided in accounting for any nonrandom selection of the bulls. The 3-trait model used was

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix} = \begin{bmatrix} X_1 & 0 & 0 \\ 0 & X_2 & 0 \\ 0 & 0 & X_3 \end{bmatrix} \beta + \begin{bmatrix} Z_1 & 0 & 0 \\ 0 & Z_{g2} & 0 \\ 0 & 0 & Z_{g3} \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \\ u_3 \end{bmatrix}$$

$$+ \begin{bmatrix} Z_{m1} \end{bmatrix} \begin{bmatrix} m_1 \end{bmatrix} + \begin{bmatrix} Z_{c1} \end{bmatrix} \begin{bmatrix} c_1 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \end{bmatrix},$$

where subscripts 1, 2, and 3 correspond to birth weight, SC or a semen trait, and a second semen trait.

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

Single-trait analysis of birth weight,

$$\text{Var} \begin{bmatrix} u \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_g^2 & A\sigma_{gm} & 0 & 0 \\ A\sigma_{mg} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I\sigma_c^2 & 0 \\ 0 & 0 & 0 & I\sigma_e^2 \end{bmatrix};$$

Two-trait analysis of birth weight,

$$\text{Var} \begin{bmatrix} u_1 \\ u_2 \\ m_1 \\ c_1 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma_{g1}^2 & A\sigma_{g1g2} & A\sigma_{g1m1} & 0 & 0 & 0 \\ A\sigma_{g2g1} & A\sigma_{g2}^2 & A\sigma_{g2m1} & 0 & 0 & 0 \\ A\sigma_{m1g1} & A\sigma_{m1g2} & A\sigma_{m1}^2 & 0 & 0 & 0 \\ 0 & 0 & 0 & I\sigma_{c1}^2 & 0 & 0 \\ 0 & 0 & 0 & 0 & I\sigma_{e1}^2 & 0 \\ 0 & 0 & 0 & 0 & 0 & I\sigma_{e2}^2 \end{bmatrix};$$

Three-trait analysis of birth weight,

$$\text{Var} \begin{bmatrix} u_1 \\ u_2 \\ u_3 \\ m_1 \\ c_1 \\ e_1 \\ e_2 \\ e_3 \end{bmatrix} =$$

$$\begin{bmatrix} A\sigma_{g1}^2 & A\sigma_{g1g2} & A\sigma_{g1g3} & A\sigma_{g1m1} & 0 & 0 & 0 & 0 \\ A\sigma_{g2g1} & A\sigma_{g2}^2 & A\sigma_{g2g3} & A\sigma_{g2m1} & 0 & 0 & 0 & 0 \\ A\sigma_{g3g1} & A\sigma_{g3g2} & A\sigma_{g3}^2 & A\sigma_{g3m1} & 0 & 0 & 0 & 0 \\ A\sigma_{m1g1} & A\sigma_{m1g2} & A\sigma_{m1g3} & A\sigma_{m1}^2 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & I\sigma_{c1}^2 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & I\sigma_{e1}^2 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & I\sigma_{e2}^2 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & I\sigma_{e3}^2 \end{bmatrix};$$

where σ_g^2 is the direct additive genetic variance, σ_m^2 is the maternal additive genetic variance, σ_c^2 is the permanent environmental variance due to dams, σ_e^2 is the

Table 2. Estimates of genetic (σ_g^2), environmental (σ_e^2), and phenotypic (σ_p^2) variances and heritability (h^2) for scrotal circumference and semen characteristics of line 1 Hereford bulls at an average age of 446 d

Trait[1]	σ_g^2	σ_e^2	σ_p^2	h^2
Birth weight,[2] kg	7.02	11.44	20.96	0.34 ± 0.06
Scrotal circumference, cm	1.96	1.49	3.45	0.57 ± 0.09
Color	0.10	0.54	0.64	0.15 ± 0.08
Volume, mL	0.25	2.66	2.90	0.09 ± 0.08
Concentration	0.16	0.77	0.93	0.16 ± 0.08
Swirl	0.35	1.35	1.70	0.21 ± 0.08
Motility	0.29	1.02	1.31	0.22 ± 0.09
Live, %	30.57	105.65	136.22	0.22 ± 0.09
Normal spermatozoa, %	56.40	104.61	161.01	0.35 ± 0.10
Primary abnormalities, %	30.67	72.70	103.37	0.30 ± 0.10
Abnormal heads, %	0.00	12.16	12.16	0.00 ± 0.08
Abnormal midpieces, %	11.83	61.08	72.91	0.16 ± 0.09
Proximal cytoplasmic droplets, %	6.29	10.62	16.91	0.37 ± 0.11
Secondary abnormalities, %	17.50	36.04	53.55	0.33 ± 0.09
Bent tails, %	0.00	8.01	8.01	0.00 ± 0.07
Coiled tails, %	15.12	29.78	44.90	0.34 ± 0.09
Distal cytoplasmic droplets, %	0.00	0.33	0.33	0.00 ± 0.06

[1]Subjective scores were assigned for color, concentration, swirl, and motility with 0 = least and 5 = most.
[2]Heritability of maternal additive effects was 0.17 ± 0.05 and permanent environmental effects due to dams account for 2.3 ± 2.6% of phenotypic variation.

residual variance, σ_{gigj} is the covariance between additive direct genetic effects of traits i and j, σ_{gimk} is the covariance between additive direct and additive maternal genetic effects for traits i and k, σ_{mkml} is the covariance between additive maternal genetic effects for traits k and l, A is the numerator relationship matrix, and I is an identity matrix of rank equal to the number of dams (permanent environmental effects) or animals (residual effects).

For each analysis, iteration continued until the variance of the simplex was less than 1×10^{-9}. Once the convergence criterion was reached, the analysis was done again with different starting values. This process continued until the minimum –2 log likelihood obtained was confirmed by a second analysis with the convergence criteria differing by less than 0.001. The (co)variance components attained from the last restart were used to derive estimates of the genentic parameters.

Correlated responses in scrotal circumference and the semen characteristics with single-trait selection for reduced BRW were predicted. Likewise, correlated responses in the semen characteristics were also calculated when single-trait selection was practiced for increased SC. The equation used was as follows: CR = $\sqrt{h^2} r_{i,j} \sigma_j$, where h^2 is the estimated heritability of the selection criterion, $r_{i,j}$ is the genetic correlation between the selection criterion (trait i) and the correlated phenotype (trait j), and σ_j is the genetic standard deviation of trait j. Selection intensity was assumed constant and equal to 1.0.

RESULTS AND DISCUSSION

Genetic, environmental, and phenotypic variances and heritability estimates are listed in Table 2. Data

for this investigation were collected over a 40-yr period. Physical control of experimental conditions was not entirely possible due to increasing experience of the evaluator, possible unidentified changes in technique, and different operators of the electroejaculator. Our intent was to control these sources of variation statistically by including contemporary group in the model. However, response to the electroejaculator varies between bulls, and any interaction between components of the contemporary group definition and animal may inflate the variances attributed to genotype, environment, or both. Sampling variances of the estimates and the population of inference should also be considered when interpreting these results. Finally, there is variation in the literature in the particular abnormalities classified as primary and secondary, which may complicate some interpretations.

Estimated heritability of SC was 0.57 and was within the range of values reported in the literature (0.32 to 0.71; Morris et al., 1992; Evans et al., 1999). Bourdon and Brinks (1986) and Kriese et al. (1991) estimated the heritability of SC to be 0.53, similar to the estimate reported here. In a review paper, Koots et al. (1994a) reported an average heritability estimate for SC of 0.45.

Heritability estimates for ejaculate color, volume, and concentration were 0.15, 0.09, and 0.16, respectively. Low estimates of genetic variance for these traits indicate substantial environmental influence. Color of the ejaculate was subjectively scored against a written standard, which might have introduced experimental error in the measurement of this phenotype. The heritability estimate for ejaculate volume was supported by the estimate reported by Rege et al. (2000) of 0.11 in 12-mo-old rams. Literature values of 0.13 and 0.17 for

ejaculate concentration (Knights et al., 1984; Rege et al., 2000) agree with the estimate reported here.

Motility has been significantly associated with nonreturn rate on a phenotypic basis (Christensen et al., 1999). In this study, percentage motile spermatozoa and swirl both had moderate heritability estimates of 0.22 and 0.21, respectively. In other studies of yearling bulls, Knights et al. (1984) and Smith et al. (1989) reported estimates of heritability for motility of 0.13 and 0.08, respectively. Percentage of motile spermatozoa may be considered indicative of the proportion of individual spermatozoa that are progressively motile; Rege et al. (2000) reported a heritability estimate of 0.16 in 12-mo-old rams. Rege et al. (2000) also reported an estimate of 0.27 for the heritability of mass motility, which is comparable to swirl in this study. Thus, our research and the literature support a low to moderate heritability for these indicators of vigor of the spermatozoa.

Estimated heritabilities for percentages of live and normal spermatozoa in an ejaculate were 0.22 and 0.35, respectively. Smith et al. (1989) reported an estimate of 0.07 for percentage of normal sperm, which is substantially less than the estimate calculated in this study. Like the current study, data of Smith et al. (1989) were from an inbred population. However, there were data from fewer bulls (n = 549) that were younger (approximately 12 mo), and method III (Henderson, 1953) as implemented by Harvey (1975) was used to estimate the variance components. Knights et al. (1984) used method III and REML to estimate genetic parameters for semen traits in yearling Angus bulls and found the estimates did not differ between methods of analysis. Henderson (1979) suggested that estimators based on procedures like REML may be less biased by selection than method III estimates. To further reduce selection, we also estimated these parameters in analyses with BRW, which was recorded for all animals.

Percentage spermatozoa with primary abnormalities had a heritability estimate of 0.30. Traits that compose primary abnormalities individually had heritability estimates that ranged from 0.00 to 0.37 (Table 2). The estimate for percentage of primary abnormal spermatozoa from this study was similar to the value of 0.31 reported by Smith et al. (1989). This finding is consistent with the common belief that primary abnormalities are at least partially of genetic origin and thus may persist throughout the breeding life of the bull. However, the very low estimate of heritability for percentage of abnormal heads is suggestive of environmental origins for this primary abnormality

Secondary abnormalities most likely arise from faulty epididymal sperm maturation and thus may have a genetic component but may also be induced during sample collection and handling (Barth and Oko, 1989). Heritability of percentage of spermatozoa with secondary abnormalities was estimated to be 0.33. However, 2 of the 3 phenotypes contributing to secondary abnormalities had little variation and heritability esti-

mates of essentially 0.00. Smith et al. (1989) reported an estimate for percentage secondary abnormalities of 0.02. The estimate from this study suggests genetic effects have greater influence on the frequency of secondary abnormalities, particularly coiled tails, than would be indicated by the estimate of Smith et al. (1989).

Estimates of direct additive genetic correlations and covariances between semen characteristics obtained from 3-trait analyses are listed in Table 3. It is possible that the estimated genetic covariances and thus the genetic correlations were affected by the assignment of sperm with multiple abnormalities to only one category of abnormality. However, sperm with multiple abnormalities were very rare and thus any effect is expected to be quite minor. The majority of semen characteristics had favorable genetic correlations with each other. These favorable genetic correlations are promising because they indicate that positive selection applied among bulls for one semen characteristic could benefit the majority of other semen characteristics in their male progeny.

However, there also were a few unfavorable genetic correlations between semen characteristics. Ejaculate volume was negatively correlated with percentages of live and motile sperm (–0.09 and –0.38, respectively). Introduction of excess urine or seminal plasma as part of a typical electroejaculation may affect the covariances of ejaculate volume with percentages of live and motile sperm (M. DeJarnette, Select Sires Inc., Plain City, OH, personal communication). However, semen collections having detectable contamination with urine were discarded. Additional undesirable correlations involved proximal cytoplasmic droplets. Percentage of motility and percentage live spermatozoa had genetic correlations with proximal cytoplasmic droplets of 0.32 and 0.53, respectively.

Birth weight and scrotal circumference were found to have a positive genetic correlation of 0.28. This estimate is much greater than the range of 0.02 to 0.10 previously reported in the literature (Knights et al., 1984; Kriese et al., 1991; Koots et al., 1994b). The present estimate was calculated using an animal model, whereas the literature estimates resulted from sire models. Based on the results of Ferreira et al. (1999), this discrepancy may result in part from the difference in models as well as other differences between the studies including the different populations used for inference.

Estimates of the genetic correlations between BRW and the semen traits from 2-trait analyses are presented in Table 4. Ejaculate color, concentration, and swirl had strong, positive genetic correlations with BRW. Genetic correlations of BRW with spermatozoa motility and percentages of normal and live spermatozoa were smaller but also positive. Percentages of spermatozoa with proximal cytoplasmic droplets, coiled tails, and secondary abnormalities were negatively correlated with BRW.

Table 3. Direct additive genetic correlations (above diagonal) and covariances (below diagonal) among semen characteristics of line 1 Hereford bulls at an average age of 446 d[1]

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

[1]COL = ejaculate color, VOL = ejaculate volume, SW = swirl, CN = concentration, MOT = motility, NORM = percentage of normal spermatozoa, CT = percentage with coiled tails, ABM = percentage with abnormal midpieces, PD = percentage with proximal cytoplasmic droplets, LIVE = percentage of live spermatozoa, 1° AB = percentage primary abnormalities, 2° AB = percentage secondary abnormalities.
[2]NC = 3-trait analysis did not converge.

Estimates of the genetic correlations between SC and the semen traits that were obtained from 3-trait analyses are also presented in Table 4. Genetic relationships among SC and color, volume, concentration and swirl of ejaculate, and motility of spermatozoa were positive and indicated favorable genetic associations between these semen traits and SC. Similarly, favorable negative genetic correlations were found between SC and percentages of spermatozoa with proximal cytoplasmic

Table 4. Genetic correlations (r_g) between birth weight, scrotal circumference, and semen characteristics, and predicted correlated responses (CR) to one phenotypic standard deviation of selection for decreased birth weight ($h^2 = 0.34$) or increased scrotal circumference ($h^2 = 0.57$)
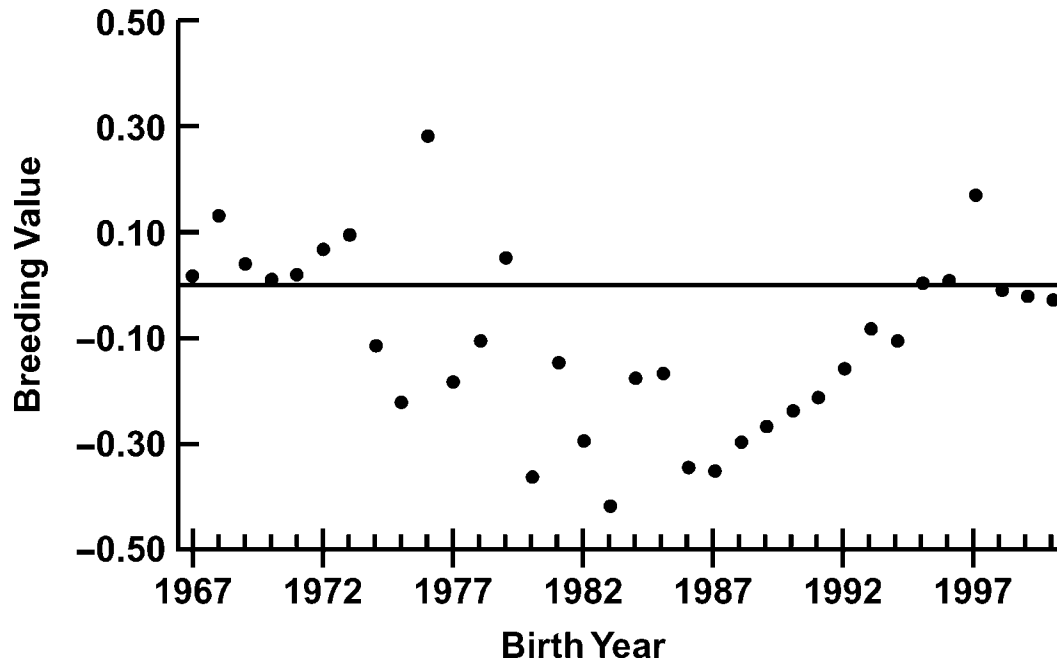
	Birth weight		Scrotal circumference	
Trait[1]	r_g	CR	r_g	CR
Scrotal circumference	0.28	−0.22	–	–
Color	0.60	−0.11	0.73	0.17
Volume	0.08	−0.02	0.20	0.08
Concentration	0.58	−0.13	0.77	0.23
Swirl	0.44	−0.15	0.40	0.18
Motility	0.21	−0.07	0.34	0.14
Live, %	0.34	−1.09	0.63	2.63
Normal spermatozoa, %	0.20	−0.85	0.33	1.87
Primary abnormalities, %	−0.02	0.06	−0.36	−1.51
Abnormal heads, %	NC[2]	0.00	NC	0.00
Abnormal midpieces, %	−0.03	0.06	−0.36	−0.96
Proximal cytoplasmic droplets, %	−0.52	0.71	−0.37	−0.66
Secondary abnormalities, %	−0.16	0.39	−0.45	−1.42
Bent tails, %	NC	0.00	NC	0.00
Coiled tails, %	−0.20	0.43	−0.12	−0.33
Distal cytoplasmic droplets, %	NC	0.00	NC	0.00

[1]Subjective scores were assigned for color, concentration, swirl, and motility with 0 = least and 5 = most.
[2]NC = genetic variance estimates for these phenotypes from single-trait analyses were essentially zero, and the multiple-trait analyses did not converge.

droplets, secondary abnormalities, and coiled tails. The percentage of proximal cytoplasmic droplets was previously found to be 60 to 70% before puberty and decreased markedly after puberty (Lunstra and Echternkamp, 1982). Thus, the negative genetic correlation between SC and percentage proximal cytoplasmic droplets may be a manifestation of the well-documented negative genetic correlation between SC and age at puberty (BIF, 1996).

Given the preceding results and selection intensity equal to 1.0, the predicted response to selection for decreased birth weight would be −1.57 kg. Similarly, the predicted response to selection for increased scrotal circumference was +1.06 cm. The magnitude of the direct response in birth weight to a unit of selection intensity is greater than would be inferred from a generation of selection by independent culling levels for below average BRW and high yearling weight (MacNeil et al., 1998). Likewise, the magnitude of the predicted response to single-trait selection for increased SC is substantial relative to the observed changes in breeding value for SC. The trend in breeding value for SC from 1968 to 2004 of North American Hereford cattle is approximately 0.10 cm per year, based on data from the national cattle evaluation conducted for the American Hereford Association (2005). In comparison, shown in averages are shown in Figure 1 for breeding values by birth year for SC, derived from the bivariate analysis of the present data. The genetic trend from 1980 to 2000 was 0.018 ± 0.002 cm per year, which is substantially less than that of the Hereford breed over the same period. DeJarnette et al. (2004) also suggest there has been no phenotypic trend in SC, semen quantity, or semen quality of Holstein sires since 1969. Thus, given current selection practices, the correlated responses predicted here should be interpreted conservatively.

Predicted correlated responses in SC and semen traits to single-trait selection for decreased BRW birth

Figure 1. Average breeding value, by year of birth, for scrotal circumference of line 1 Hereford bulls born between 1967 and 2000 and for data collected during evaluations of breeding soundness.

weight are also listed in Table 4. Direct selection to decrease BRW may result in undesirable correlated responses in a majority of the semen characteristics. Predicted correlated responses in percentages live and normal spermatozoa to one unit of selection intensity applied to reduce BRW are −1.09 and −0.85%, respectively. Greater values of these traits are desirable and increase the probability of a bull passing a breeding soundness evaluation. Further, the majorities of sperm abnormalities were negatively correlated with BRW and would thus increase if selection was applied to reduce BRW. Thus, intense selection for low BRW carries the risk of undesirable correlated responses in semen characteristics and associated breeding soundness scores.

Predicted correlated responses in the semen traits to single-trait selection for increased SC are also listed in Table 4. The greatest positive impact of selection for increased SC would be on concentration score and the percentage of spermatozoa abnormalities. Percentages of primary and secondary abnormalities would be expected to decrease by 1.51 and 1.42%, respectively, for each 1.0 cm increase in scrotal circumference. Neubauer et al. (2004) indicated that cats producing <40% morphologically normal sperm have greater sperm output, which is achieved by having more sperm-producing tissue than cats producing >60% normal sperm per ejaculate. However, our results suggest that selection for more sperm-producing tissue, as indicated by increased SC, may lead to more male progeny passing breeding soundness evaluations due to improved sperm morphology.

Given the present estimates of additive genetic variance, identification of molecular markers for semen characteristics may be reasonable, if greater selection pressure on semen characteristics is desired. Marker-assisted EPD would facilitate more accurate genetic evaluation without the expense of conducting breeding soundness examinations of bulls that have little chance of being used for breeding. An initial attempt by Casas et al. (2004) to identify quantitative trait loci for male reproductive traits in beef cattle found linkage of FSH concentration in peripheral blood at 8.5 mo at approximately 70 cM on BTA 5 and testicular size and age at puberty at approximately 44 cM on BTA 29.

IMPLICATIONS

These data suggest that correlated responses affecting semen characteristics may be unimportant, given the present emphasis on increasing scrotal circumference leading to improved semen quality. However, if breeders are to place greater emphasis on using indicators of fitness as selection criteria, it may be prudent to consider semen characteristics in selection of seedstock bulls. As a standardized breeding soundness evaluation is a component of the marketing plan for many seedstock producers, requirements for data collection from at least a selected sample of bulls and expected progeny difference calculation for semen characteristics may not be arduous.

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