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Genetic parameters for scrotal circumference, frame score and yearling weight of Mexican Charolais and Charbray young bulls^ª

Parámetros genéticos de circunferencia escrotal, talla corporal y peso al año de toros jóvenes mexicanos Charolais y Charbray

Parâmetros genéticos de perímetro escrotal, escore de frame e peso ao ano de idade de touros jovens mexicanos Charolês e Charbray

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Abstract

Background: Knowledge of genetic correlations and the economics of traits are essential to decide which traits should be used as selection criteria. **Objective:** To estimate heritabilities and genetic, environmental, and phenotypic correlations, and direct (DRS) and correlated (CRS) responses to selection by scrotal circumference (SC), frame score (FS), and yearling weight (YW) of Mexican Charolais (CH), and Charbray (CB) young bulls. **Methods:** Actual SC, height and YW records (10,078 for CH, and 500 for CB) were adjusted to 365 d. The 0.0505 adjustment factor recommended by the Beef Improvement Federation was used to obtain the 365-d adjusted SC for both breeds. Height and age records were used to obtain FS. Data were analyzed using a three-trait animal model. The animal model for each trait included bull breed, contemporary group (groups of young bulls born in the same herd, year, and season of the year), and age of dam as a linear covariate as fixed effects, and direct additive genetic and residual as random effects. **Results:** Heritability estimates for SC, FS and YW were 0.21 ± 0.04 , 0.25 ± 0.04 , and 0.29 ± 0.04 , respectively. The genetic correlation between YW with SC was 0.37 ± 0.16 , and between YW with FS was 0.42 ± 0.16 . The estimate of genetic correlation between SC and FS was low and positive (0.15 ± 0.14). The DRS was 0.38 cm, 0.18 units, and 8.30 kg for SC, FS

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Keywords: Beef cattle, genetic correlations, heritability, males, phenotypic correlations, response to selection.

Resumen

Antecedentes: el conocimiento de las correlaciones genéticas y el aspecto económico de las características son necesarios para decidir qué características usar como criterios de selección. Objetivo: estimar las heredabilidades y correlaciones genéticas, ambientales y fenotípicas, y respuesta directa (DRS) y correlacionada (CRS) a la selección por circunferencia escrotal (SC), talla corporal (FS), y peso al año (YW) de toros jóvenes mexicanos Charolais (CH), y Charbray (CB). Métodos: registros (10.078 para CH y 500 para CB) de SC, altura y YW se ajustaron a 365 d. El factor de ajuste de 0,0505 recomendado por la Beef Improvement Federation se usó para obtener la SC ajustada a 365 d para ambas razas. Registros de altura y edad del animal se usaron para calcular FS. Los datos se analizaron usando un modelo animal para tres características. El modelo animal para cada característica incluyó raza del toro, grupo contemporáneo (grupos de toros jóvenes nacidos en el mismo hato, año y época del año) y edad de la madre como covariable lineal como efectos fijos, y el genético aditivo directo y el error como efectos aleatorios. Resultados: los estimadores de heredabilidad de SC, FS y YW fueron 0.21 ± 0.04 , 0.25 ± 0.04 y 0.29 ± 0.04 , respectivamente. La correlación genética de YW con SC fue 0.37 ± 0.16 , y de YW con FS fue 0.42 ± 0.16 . El estimador de la correlación genética entre SC y FS fue bajo y positivo ($0,15 \pm 0,14$). La DRS fue 0,38 cm, 0,18 unidades, y 8,30 kg para SC, FS y YW. La CRS fue 0,16 cm y 0,08 unidades para SC y FS al seleccionar YW. Conclusiones: se espera que la selección directa de YW sea efectiva. La selección indirecta de SC y FS basada en YW no se espera que sea tan efectiva como la selección directa para mejorar SC y FS.

Palabras clave: correlaciones fenotípicas, correlaciones genéticas, ganado de carne, heredabilidad, machos, respuesta a la selección.

Resumo

Antecedentes: o conhecimento das correlações genéticas, e aspecto econômico de as características são necessário para decidir que características usar como critérios de seleção. Objetivo: estimar herdabilidades e correlações genéticas, ambientais e fenotípicas, e resposta direta (DRS), e correlacionada (CRS) à seleção do perímetro escrotal (SC), escore de frame (FS), e peso ao ano de idade (YW) de touros jovens mexicanos Charolês (CH), e Charbray (CB). Métodos: registros (10.078 para CH e 500 para CB) de SC, altura e YW foram ajustados a 365 d. O fator de ajuste 0,0505 recomendado por a Beef Improvement Federation foi usado para obter o SC ajustado aos 365 d para ambas raças. Registros de altura na garupa e idade do animal foram usados para obter o FS. Os dados foram analisados usando um modelo animal para três características. O modelo animal para cada característica incluiu raça do touro, grupo contemporâneo (grupos de touros jovens nascidos no mesmo fazenda, ano e época do ano) e idade materna como covariável linear como efeitos fixos, e genético aditivo direto e o erro como efeitos aleatórios. Resultados: as estimativas de herdabilidade para SC, FS e YW foram 0.21 ± 0.04 , 0.25 ± 0.04 e 0.29 ± 0.04 , respetivamente. A correlação genética do YW com SC foi 0.37 ± 0.16 , e de YW com FS foi 0.42 ± 0.16 . A estimativa da correlação genética entre SC e FS foi baixa e positiva $(0,15 \pm 0,14)$. A DRS foi 0,38 cm, 0,18 unidades, e 8,30 kg para SC, FS e YW. A CRS foi 0,16 cm e 0,08 unidades para SC e FS al selecionar YW. Conclusões: espera-se que a seleção direta do YW seja eficaz. A seleção indireta de SC e FS com base no YW não se espera que seja tão efetiva como a seleção direta para melhorar SC e FS.

Palavras-chave: bovinos de corte, correlações fenotípicas, correlações genéticas, herdabilidade, machos, resposta à seleção.

Introduction

Estimates of genetic and phenotypic parameters for growth traits of Mexican beef cattle (e.g., Limousin, Charolais, Charbray, Simmental, Simbrah, Indubrazil) are available in the scientific literature (Ríos-Utrera *et al.*, 2011; Ríos-Utrera *et al.*, 2012; Vega-Murillo *et al.*, 2012; Ríos-Utrera *et al.*, 2013). Despite several Mexican breeders associations conduct national cattle evaluations of scrotal circumference as an indicator

of male fertility (sperm volume and quality), and frame score as a measure of lean-to-fat ratio potential, only one study (Torres-Vázquez *et al.*, 2012) has estimated genetic and phenotypic parameters for scrotal circumference (SC), frame score (FS), and yearling weight (YW), and their relationships in Mexican beef cattle.

Multivariate analysis reduce the prediction error variance and in some instances reduce or eliminate bias from selection (Schaeffer, 1984). Additionally, knowledge of genetic relationships among economically important traits helps to decide which traits to include as selection criteria when developing breeding selection objectives and to predict the net impact of selection. Scrotal circumference of yearling bulls is moderately heritable (Koots et al., 1994). Its genetic correlation with age at first calving (Barrozo et al., 2012) and pregnancy rate in female relatives is favorable (Eler et al., 2006). In addition, selection for greater SC may simultaneously increase postweaning growth rate, YW, weight at 18 months of age and FS. Some researchers have reported positive genetic correlation estimates for SC with those traits (Johnson et al., 1993; Crews and Porteous, 2003). The objective of this study was to estimate heritabilities and genetic, environmental, and phenotypic correlations, and direct (DRS), and correlated (CRS) responses to selection of scrotal circumference (SC), frame score (FS), and yearling weight (YW) of Mexican Charolais (CH), and Charbray (CB) young bulls.

Materials and Methods

Population

The study involved Charolais and Charbray cattle breeds. Charolais included upgraded (31/32 Charolais-1/32 Brahman) and fullblood cattle. Charbray consisted of 5/8 Charolais and 3/8 Brahman. The Charolais-Charbray Herd Book of Mexico (CCHBM) provided productive and pedigree data used for the study. Records were collected on a total of 10,078 Charolais and 500 Charbray young bulls, born from 2004 to 2015. The bulls were the progeny of 1,741 sires and 8,755 dams. The pedigree file consisted of 20,906 animals. Connectivity among different Charolais and Charbray herds has been established to some extent through the use of common

semen of Charolais and Charbray sires from U.S.A., France and Mexico, and through auction of bulls and heifers among Mexican breeders.

Measurements

The traits analyzed were SC, FS and YW. Qualified CCHBM technicians measured SC and height of the bulls. Scrotal circumference was measured in centimeters at the widest part of the testis using a flexible tape. Animal height and age records were used to calculate FS. The original database consisted of 28,299 records. The age range of the animals was 320 to 410 d for the three traits; therefore, records outside these ranges were eliminated from the analysis, but the animals remained in the pedigree file. Productive data was edited to remove unreliable SC, FS and YW measurements (\pm 3 standard deviations from the mean) as well as unreliable dates. In addition, contemporary groups with only one bull were eliminated. The pedigree file was checked to make sure all parents were born before their progeny. Consequently, 17,721 records (62.6%) were excluded from the original database. Actual SC, height and YW records were adjusted to a standard animal age of 365 d. Because the CCHBM had not developed their own age adjustment factors for SC, the 0.0505 adjustment factor for Charolais cattle recommended by the Beef Improvement Federation (BIF, 2002) was used to calculate adjusted 365-d yearling SC for each bull of the pure and the composite breeds evaluated. The SC was adjusted with the following formula: SC=Yearling SC + $[(365 - Age) \times 0.0505]$. Adjustments for YW and FS followed the Guidelines for Uniform Beef Improvement Programs, published by the Beef Improvement Federation (BIF, 2002). We analyzed FS instead of hip height because FS is easier to interpret and more applicable than hip height. Table 1 presents descriptive statistics for SC, FS, and YW. For Charolais and Charbray bulls, raw means of SC, FS and YW were 29.9 \pm 2.8 and 28.7 \pm 3.4 cm, 5.0 \pm 1.2 and 5.5 \pm 1.2 units, and 347.6 \pm 48.7 and 332.4 \pm 42.6 kg, respectively.

Model

A three-trait animal model was fitted to estimate variance and covariance components and genetic parameters. The animal model for each trait included

Trait/breed	N	Mean	Min	Max	SD	CV (%)
Scrotal circumference (cm)						
Charolais	10,078	29.9	21.7	40.1	2.8	9.4
Charbray	500	28.7	17.9	36.3	3.4	11.8
Both breeds	10,578	29.8	17.9	40.1	2.8	9.4
Frame score (units)						
Charolais	10,078	5.0	1.0	9.0	1.2	24.0
Charbray	500	5.5	0.5	9.1	1.2	21.8
Both breeds	10,578	5.1	0.5	9.1	1.2	23.5
Yearling weight (kg)						
Charolais	10,078	347.6	135.0	577.8	48.7	14.0
Charbray	500	332.4	223.8	464.3	42.6	12.8
Both breeds	10,578	346.9	135.0	577.8	48.6	14.0

Table 1. Summary statistics for scrotal circumference (SC), frame score (FS), and yearling weight (YW) of young bulls.

N= number of records; Min= minimum value; Max= maximum value; SD= standard deviation; CV= coefficient of variation.

breed of bull, contemporary group, age of dam in days as a linear covariate, direct additive genetic effect and residual. Contemporary group was defined as a group of young bulls born in the same herd, year, and season. The season effect included four classes: January-March, April-June, July-September and October-December. The number of contemporary groups for SC and FS was 1,812; for YW, however, the number of contemporary groups was 1,919. The number of contemporary groups for YW was different to that for SC and FS, because YW measurements were not taken the same day as SC and FS measurements. For all traits, the smaller contemporary group had two bulls, while the larger contemporary group had 58 bulls; however, mean numbers of bulls per contemporary group were 5.5 for YW, and 5.8 for SC and FS.

The three-trait animal model in matrix form was as follows:

y1		Xı	0	0		β1		Zı	0	0		aı		eı	
y 2	=	0	\mathbf{X}_2	0	•	β2	+	0	\mathbb{Z}_2	0	•	a 2	+	e ₂	,
y 3		0	0	X 3		βз		0	0	Z 3		a3		e3	
		_		_	-		-	_		_	-				

Where:

 y_1 , y_2 and y_3 are vectors of single trait phenotypic observations of SC, FS and YW.

 β_1 , β_2 and β_3 are vectors of fixed effects (breed of bull, contemporary group, age of dam).

 $\mathbf{a_1}$, $\mathbf{a_2}$ and $\mathbf{a_3}$ are unknown vectors of random direct additive genetic effects.

 $\mathbf{e}_1, \mathbf{e}_2$ and \mathbf{e}_3 are unknown vectors of random temporary environmental effects.

 X_1 , X_2 and X_3 are known incidence matrices relating phenotypes measured with fixed effects in β_1 , β_2 and β_3 , respectively.

 Z_1 , Z_2 and Z_3 are known incidence matrices relating phenotypes measured with additive genetic effects in a_1 , a_2 and a_3 , respectively.

The first and second moments were assumed to be

$$E\begin{bmatrix}\mathbf{a}\\\mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{0}\\\mathbf{0}\end{bmatrix}, \text{ and } Var\begin{bmatrix}\mathbf{a}\\\mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{G}\otimes\mathbf{A} & \mathbf{0}\\\mathbf{0} & \mathbf{R}\otimes\mathbf{I}\end{bmatrix},$$
$$\mathbf{G} = \begin{bmatrix}\sigma_{a1}^2 & \sigma_{a1,a2} & \sigma_{a1,a3}\\\sigma_{a2,a1} & \sigma_{a2}^2 & \sigma_{a2,a3}\\\sigma_{a3,a1} & \sigma_{a3,a2} & \sigma_{a3}^2\end{bmatrix} \text{ and } \mathbf{R} = \begin{bmatrix}\sigma_{e1}^2 & \sigma_{e1,e2} & \sigma_{e1,e3}\\\sigma_{e2,e1} & \sigma_{e2}^2 & \sigma_{e2,e3}\\\sigma_{e3,e1} & \sigma_{e3,e2} & \sigma_{e3}^2\end{bmatrix};$$
$$\text{ Where:}$$

G is the matrix of genetic variances and covariances.

 \otimes is the right direct product operator or Kronecker product.

A is the matrix of additive genetic relationships among animals, including foundation animals without records. R is the matrix of residual variances and covariances.

I is an identity matrix of order equal to the number of animals with records. In addition, σ_{a1}^2 , σ_{a2}^2 and σ_{a3}^2 are the additive genetic variances for traits 1, 2 and 3, respectively. $\sigma_{a1,a2}$, $\sigma_{a1,a3}$ and $\sigma_{a2,a3}$ are the genetic covariances between traits 1 and 2, 1 and 3, and 2 and 3, respectively.

 σ_{e1}^2 , σ_{e2}^2 and σ_{e3}^2 are the residual variances for traits 1, 2 and 3, respectively.

 $\sigma_{e1,e2}$, $\sigma_{e1,e3}$ and $\sigma_{e2,e3}$ are the residual covariances between traits 1 and 2, 1 and 3, and 2 and 3, respectively.

Traits evaluated were assumed to follow a multivariate normal distribution.

Software, initial values and convergence

Variance and covariance components, as well as genetic correlations, for genetic and temporary environmental effects were estimated with the MTDFREML package (Boldman et al., 1995). Estimates of variance and covariance components from the scientific literature were used as initial values in preliminary analyses (one for each response variable) fitting single-trait animal models. Estimates of variance and covariance components from singletrait analyses were used as priors for the three-trait analysis. The convergence criteria (minimum variance of the function values, -2 log likelihood) were set to $1 \ge 10^{-10}$ in each type of analysis. Iterations were checked to converge at a global maximum rather than to a local one. Results from the first run were used as starting values for up to six cold restarts to ensure convergence to the same solutions.

Description of genetic, residual and phenotypic parameters, and response to selection

Heritability for direct additive genetic effects (\mathbf{h}_{a}^{2}) , and genetic $(\mathbf{r}_{ai,aj})$, residual $(\mathbf{r}_{ei,ej})$ and phenotypic $(\mathbf{r}_{pi,pj})$ correlations between traits i and j were estimated as follows:

 $h_{a}^{2} = \sigma_{a}^{2} / \sigma_{p}^{2},$ $r_{ai,aj} = \sigma_{ai,aj} / (\sigma_{ai}^{2} \sigma_{aj}^{2})^{1/2},$

$$\mathbf{r}_{ei,ej} = \sigma_{ei,ej} / (\sigma_{ei}^2 \sigma_{ej}^2)^{1/2} \text{ and}$$

$$\mathbf{r}_{pi,pj} = \sigma_{pi,pj} / (\sigma_{pi}^2 \sigma_{pj}^2)^{1/2},$$

Where:

 σ_p^2 is the phenotypic variance, which was estimated as $\sigma_p^2 = \sigma_q^2 + \sigma_e^2$.

 $\sigma_{ni,ni}$ is the phenotypic covariance between traits i and j.

 σ_{ni}^2 is the phenotypic variance for trait i.

 σ_{pi}^2 is the phenotypic variance for trait j.

Remaining estimates of variance and covariance were previously defined.

Expected direct response to selection (DRS) was obtained for SC, FS and YW. Expected correlated response to selection (CRS) was obtained for SC and FS from indirect selection on YW, because Mexican Charolais and Charbray breeders use to select bulls based on YW. Responses to selection (one generation away) were calculated from selection of sires based on half-sib progeny records, using the formulas of Van Vleck *et al.* (1987):

DRS=
$$\sqrt{(P/P + \lambda)}$$
 i $h_x \sigma_{px}$
CRS= $\sqrt{(P/P + \lambda)} r_e$ i $h_y \sigma_{py}$

c.

Where:

P is the number of half-sib progeny (5, 10, 20, 50, 100, 200, and 500).

 λ is equal to $(4 - h_x^2)/h_x^2$.

i is the intensity of selection, which was assumed to be 1.

 \mathbf{h}_{r} is the square root of the heritability of trait x (\mathbf{h}_{r}^{2}).

 σ_{px} is the phenotypic standard deviation of trait x.

 \mathbf{r}_{g} is the genetic correlation between traits x and y.

 \mathbf{h}_{y} is the square root of the heritability of trait y.

 σ_{py} is the phenotypic standard deviation of trait y.

Results

Estimates of genetic and residual variance and covariance are presented in Table 2.

Table 2. Genetic (lower triangular), and residual (co)variance (upper triangular) for scrotal circumference (SC), frame score (FS), and yearling weight (YW).

	SC	FS	YW
SC	2.55	0.40	16.80
	0.67		
FS	0.04	0.38	6.07
		0.13	
YW	4.60	2.31	582.28
			235.90

Estimates of phenotypic variance, phenotypic covariance, and phenotypic correlations for SC, FS, and YW are shown in Table 3.

Table 3. Phenotypic variance (on diagonal), phenotypic covariance (below diagonal), and phenotypic correlation (above diagonal) for scrotal circumference (SC), frame score (FS), and yearling weight (YW).

	SC	FS	YW
SC	3.21	0.34	0.42
FS	0.44	0.51	0.41
YW	21.40	8.37	818.18

Estimates of heritability, genetic correlations and residual correlations for the same traits are presented in Table 4.

Table 4. Heritability (on diagonal), genetic correlation (below diagonal), and residual correlation (above diagonal) for scrotal circumference (SC), frame score (FS), and yearling weight (YW).

	SC	FS	YW
SC	0.21 ± 0.04	0.40 ± 0.04	0.44 ± 0.05
FS	0.15 ± 0.14	0.25 ± 0.04	0.41 ± 0.05
YW	0.37 ± 0.16	0.42 ± 0.16	0.29 ± 0.04

The estimates of heritability for SC, FS and YW were 0.21 ± 0.04 , 0.25 ± 0.04 and 0.29 ± 0.04 , respectively. The estimates of the genetic correlations for SC with YW (0.37 ± 0.16) and for FS with YW (0.42 ± 0.16) were similar to corresponding estimates of phenotypic correlations (0.42 and 0.41); however, the estimate of the genetic correlation for SC with FS (0.15 ± 0.14) was less than half the corresponding

phenotypic correlation estimate (0.34). In general, estimates of residual correlations for SC with FS (0.40 \pm 0.04), SC with YW (0.44 \pm 0.05), and FS with YW (0.41 \pm 0.04) were similar to the analogous estimates of phenotypic correlations.

For SC and FS, direct responses to selection were more than two-fold greater than the corresponding correlated responses to selection, independently of the number of half-sib progeny. Direct and correlated responses to selection based on 500 half-sib progeny were about two-fold greater than those based on 5 half-sib progeny. Correlated responses to selection based on 100, 200 and 500 half-sib progeny were similar for SC, as well as for FS (Table 5).

 Table 5. Expected direct (DRS), and correlated responses to selection (CRS) from selection of sires based on different number of half-sib progeny.

		DRS	CRS			
Number of progeny	YW	SC	FS	SC	FS	
5	8.17	0.38	0.18	0.16	0.08	
10	10.20	0.49	0.23	0.20	0.10	
20	12.03	0.60	0.27	0.24	0.12	
50	13.75	0.70	0.31	0.27	0.13	
100	14.50	0.76	0.33	0.29	0.14	
200	14.93	0.79	0.34	0.29	0.15	
500	15.21	0.81	0.35	0.30	0.15	

YW= yearling weight; SC= scrotal circumference; FS= frame score.

Discussion

Scrotal circumference heritability

Scrotal circumference was medium heritable in the Mexican Charolais and Charbray cattle population, suggesting that this fertility trait may be changed by direct selection. However, response to selection would be slow. The heritability estimate for SC reported in the present study is similar to estimates reported by other authors. In particular, the estimate for SC obtained by Everling *et al.* (2001) for Angus-Nelore crossbred cattle with different breed composition is similar to our estimate. In a more recent study carried out in Brazil, Boligon *et al.* (2006) found 0.22 heritability estimate. Gressler *et al.* (2000) reported that SC was 24% heritable in Nelore cattle. In South Africa, Marle-Koster *et al.* (2000) obtained 0.25 heritability estimate for Hereford cattle. In contrast,

Gargantini et al. (2005), in several beef breeds from the Roman L. Hruska U.S. Meat Animal Research Center, found 0.05 heritability estimate for SC. On the other hand, other studies have reported moderate to high heritability for SC. Arthur et al. (2001), Dias et al. (2003), Van Melis et al. (2010), Barrozo et al. (2012) and Corbet *et al.* (2013) reported 0.43 ± 0.06 , $0.35 \pm 0.03, 0.48 \pm 0.01, 0.53 \pm 0.04, and 0.65 \pm 0.08$ heritability estimates, respectively. These values, along with those previously mentioned, including our estimate, reveal great variation in heritability estimates for SC. This variation could be due to different environments, breeds, selection intensity, effects included in the animal model, and type of models (sire model vs animal model; univariate vs bivariate model) among studies (Koots et al., 1994).

Frame score heritability

Similar to SC, FS was medium heritable, suggesting that genetic progress from direct selection on FS adjusted to 365 d of age might be slow as well. Our heritability estimate for FS is similar to the estimate reported by Horimoto et al. (2006) for Nelore cattle raised in Brazil (0.23). However, Johnson et al. (1993) and Torres-Vázquez et al. (2012) found that FS was moderately heritable (0.42) in American Brangus and Mexican Simmental and Simbrah cattle. Except for these three estimates, no other heritability estimates for this trait were found in the literature. In general, heritability estimates for hip height (0.60, 0.46, 0.48)reported in the literature (Afolayan et al., 2007; Yokoo et al., 2010; Regatieri et al., 2012) are higher than our FS estimate. Although FS derives from hip height, this comparison may not be appropriate due to significant loss of variability when a continuous variable (e.g., hip height) is transformed into a categorical variable (e.g., FS), resulting in smaller heritability estimates (Mercadante et al., 2004).

Yearling weight heritability

Yearling weight was a little more heritable than SC and FS in the present study. The current estimate for YW also indicates that this growth trait would respond satisfactorily to direct selection. Our heritability estimate for YW (0.29) is comparable with 0.33 (Crossbred cattle), 0.31 (Canchim cattle), and 0.26 (Nellore cattle) reported by Afolayan *et al.* (2007), Mucari *et al.* (2007) and Boligon *et al.* (2010), respectively. Our figure was smaller than estimates (0.50, 0.38) reported by Bergen *et al.* (2005) and Schiermiester *et al.* (2015), respectively, for Canadian and American crossbred cattle. Moreover, it was greater than the Pico *et al.* (2004) and Assan and Nyoni (2009) estimates (0.14, 0.18), respectively. The literature review by Koots *et al.* (1994) reported 0.33 and 0.35 weighted and unweighted heritability means for YW, respectively, similar to our estimate.

Genetic correlation between SC and FS

The low genetic correlation estimate between SC and FS found in our study indicates that genes involved in the expression of both traits are different. Thus, direct selection for SC would not affect FS. In agreement with this result, the genetic correlation estimate between both traits reported by Johnson *et al.* (1993) was also low (0.20). In contrast, the estimate by Torres-Vázquez *et al.* (2012) for the Mexican Simmental-Simbrah population was high (0.59). No other estimates of this correlation were found in the scientific literature.

Genetic correlation between SC and YW

Our genetic correlation estimate between SC and YW was moderate and positive, suggesting that there would be an increment in YW if emphasis is placed on selection to enhance SC. Other literature reports also indicate that this genetic correlation is moderate and positive. Crews and Porteous (2003), in Canadian Hereford bulls, and Torres-Vázquez et al. (2012) in Simmental and Simbrah bulls, found the same figures as we did (0.38 and 0.36 genetic correlation estimates for SC and YW, respectively). The estimate reported by Garnero et al. (2001), working with Nelore cattle in Brazil, was 0.40. Johnson et al. (1993), Marle-Koster et al. (2000) and Frizzas et al. (2009) also estimated positive genetic correlations for SC and YW in Brangus (0.23), Hereford (0.17) and Nelore (0.21) cattle, but their estimates were lower. In the analysis of published genetic correlation estimates carried out by Koots et al. (1994), the weighted mean estimate was 0.39 for SC and YW. This result closely agrees with our estimate. The study by Mwansa et al. (2000) demonstrated that a two-trait animal model including SC and concomitant body weight would result in more accurate predictions (smaller standard errors of prediction) of expected breeding values for SC than a single-trait animal model.

Genetic correlation between FS and YW

Similar to the genetic correlation estimate found between SC and YW, the moderate and positive estimate for the genetic correlation between FS and YW revealed the presence of pleiotropic gene effects. This means that genes that control FS also control YW; therefore, yearling bulls that excel in FS should also excel in YW. The genetic correlation estimate for FS and YW in our study is very similar to 0.43 and 0.47 estimates reported by Horimoto *et al.* (2006) and Torres-Vázquez *et al.* (2012), respectively, but not as strong as the 0.67 reported by Johnson *et al.* (1993). We did not find other published estimates for this correlation.

Expected responses to selection

Expected direct responses to selection were about two-fold greater than expected correlated responses to selection for SC and FS from indirect selection on YW. Van Vleck *et al.* (1987) reported that situations in which indirect selection is more effective than direct selection are rare.

In conclusion, estimates of heritability for SC, FS and YW were low, but YW tended to be more heritable than SC. Genetic correlation estimates for YW with SC and FS were moderate, but genetic correlation estimate for SC with FS was low. Direct selection for YW is expected to be effective. However, indirect selection for SC and FS based on YW would not be expected to be as effective as direct selection for improving SC and FS.

Conflicts of interest

The authors declare they have no conflicts of interest with regard to the work presented in this report.

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