

Genetic covariance components within and among linear type traits differ among contrasting beef cattle breeds

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ABSTRACT: Linear type traits describing the skeletal, muscular, and functional characteristics of an animal are routinely scored on live animals in both the dairy and beef cattle industries. Previous studies have demonstrated that genetic parameters for certain performance traits may differ between breeds; no study, however, has attempted to determine if differences exist in genetic parameters of linear type traits among breeds or sexes. Therefore, the objective of the present study was to determine if genetic covariance components for linear type traits differed among five contrasting cattle breeds, and to also investigate if these components differed by sex. A total of 18 linear type traits scored on 3,356 Angus (AA), 31,049 Charolais (CH), 3,004 Hereford (HE), 35,159 Limousin (LM), and 8,632 Simmental (SI) were used in the analysis. Data were analyzed using animal linear mixed models which included the fixed effects of sex of the animal (except in the investigation into the presence of sexual dimorphism), age at scoring, parity of the dam, and contemporary group of herd-date of scoring. Differences ($P < 0.05$) in heritability estimates, between at least two breeds, existed for 13 out of 18 linear type traits. Differences ($P < 0.05$)

also existed between the pairwise within-breed genetic correlations among the linear type traits. Overall, the linear type traits in the continental breeds (i.e., CH, LM, SI) tended to have similar heritability estimates to each other as well as similar genetic correlations among the same pairwise traits, as did the traits in the British breeds (i.e., AA, HE). The correlation between a linear function of breeding values computed conditional on covariance parameters estimated from the CH breed with a linear function of breeding values computed conditional on covariance parameters estimated from the other breeds was estimated. Replacing the genetic covariance components estimated in the CH breed with those of the LM had least effect but the impact was considerable when the genetic covariance components of the AA were used. Genetic correlations between the same linear type traits in the two sexes were all close to unity (≥ 0.90) suggesting little advantage in considering these as separate traits for males and females. Results for the present study indicate the potential increase in accuracy of estimated breeding value prediction from considering, at least, the British breed traits separate to continental breed traits.

Key words: beef, breeds, cattle, type traits

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INTRODUCTION

Linear type traits describing skeletal, muscular, and functional characteristics of the animal are

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routinely scored globally in both dairy (Veerkamp and Brotherstone, 1997; Berry et al., 2004; Kern et al., 2015) and beef (Mc Hugh et al., 2012; Mazza et al., 2014) cattle. While genetic parameters of type traits have been extensively researched in Holstein-Friesian dairy cattle (VanRaden et al., 1990; Veerkamp and Brotherstone, 1997; Kern et al., 2015), fewer studies have been undertaken in beef cattle. Nonetheless, type traits are often included in multi-trait genetic evaluations as predictors of performance in both dairy (VanRaden et al., 1990; Berry et al., 2004) and beef (Gutierrez and Goyache 2002; Mc Hugh et al., 2012) cattle. The majority of previous studies have considered type traits in both males and females as being genetically the same trait. It is possible, however, that the genetic control of such traits may be sex-dependent (van der Heide et al., 2016). If sexual dimorphism exists for type traits, then these traits may need to be considered as genetically different traits in genetic evaluations. Genetic parameters for type traits may also differ by breed, similar to what has been previously demonstrated for other performance traits in cattle (Utrera and Van Vleck, 2004; Hickey et al., 2007). Knowledge of possible differences in genetic parameters among breeds is of increasing importance as some populations move towards using a multi-breed, multi-trait statistical model in the pursuit of greater precision of genetic evaluations. The objective, therefore, of the present study was to determine if genetic covariance components for linear type traits differed among five contrasting cattle breeds and also if these traits differed genetically by sex. The results from the present study will be useful in informing breeding programmes of the importance, or lack thereof, of considering a trait in different sexes or breeds to be genetically different traits.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for the present study as data were obtained from the existing Irish Cattle Breeding Federation (ICBF) national database (<http://www.icbf.com>).

Linear Type Trait Data

As part of the Irish national beef breeding program, routine scoring of linear type traits is carried out on both registered and commercial beef herds by trained classifiers (Mc Hugh et al., 2012; Berry and Evans 2014); each classifier scores animals

from a range of different breeds and crossbreeds. A total of 18 linear type traits assessed across all breeds were retained for analysis in the present study. Traits analyzed represented muscular ($n = 6$), skeletal ($n = 6$) and functional ($n = 4$) characteristics of the animal, as well as docility and body condition score. Linear type trait data were available on 248,181 animals. Animals were discarded if the sire, herd, or classifier were unknown or the parity of the dam was not recorded; 230,109 records remained. Parity of the dam was stratified into 1, 2, 3, 4, and ≥ 5 . Only animals scored between 6 and 16 mo between the years 2000 and 2016 were retained; 179,921 records remained. Only animals that were deemed to be $\geq 87.5\%$ Angus, Charolais, Hereford, Limousin or Simmental based on the available pedigree information were retained; 140,936 records remained. Only animals from sires with at least five progeny in the data set were retained. Furthermore, only data from classifiers that scored ≥ 500 animals since the year 2000 were kept. Contemporary group was defined as herd-by-scoring date. Each contemporary group had to have at least five records and all records within contemporary group were from a single breed. Each trait was separately standardized to a common variance within classifier-by-year as described in detail by Brotherstone (1994). Following all edits, data were available on 81,200 animals in 1,811 herds all scored by 20 classifiers; 3,356 Angus (AA), 31,049 Charolais (CH), 3,004 Hereford (HE), 35,159 Limousin (LM), and 8,632 Simmental (SI).

Analysis

Covariance components for each trait in each breed were estimated using linear animal mixed models in ASREML (Gilmour et al., 2009). Preliminary analyses were undertaken to detect any dam permanent environmental effect or genetic contribution of the dam to the linear scores, but neither improved the fit to the data and so were not considered further in the mixed model. The following model was used in all analyses:

$$y_{ijklm} = HSD_i + Sex_j + AM_k + DP_l + Animal_m + e_{ijklm}$$

where y_{ijklm} is the linear type trait, HSD_i is the fixed effect of herd-by-scoring date ($i = 8,844$ levels), Sex_j is the fixed effect of the sex of the animal ($j = \text{male or female}$), AM_k is the fixed effect of the age in months of the animal at scoring ($k = 11$ classes from 6 to 16 mo), DP_l is the fixed effect of the parity of the dam

($l = 1, 2, 3, 4$, or ≥ 5), $Animal_m^l$ is the random additive genetic effect of animal m where $a \sim N(0, A\sigma_a^2)$ with σ_a^2 representing the additive genetic variance; and e_{ijklm}^l is the random residual effect, where $e \sim N(0, I\sigma_e^2)$ with σ_e^2 representing the residual variance. Box's M (Box, 1949) was then used to test the homogeneity of the covariance matrices among the breeds.

In a separate series of analyses, the CH and LM datasets (i.e., the largest datasets) were separately stratified by sex. Further edits were carried out to ensure each sex-specific contemporary group still had more than five animals. Of the remaining 29,541 CH animals, there were 14,253 females and 15,288 males; of the remaining 34,071 LM animals, there were 16,634 females and 17,437 males. Univariate and bivariate analyses were conducted in ASREML using the previously described model without the fixed effect of the sex of the animal.

Likelihood ratio tests were used to evaluate whether sexual dimorphism existed. The log-likelihood value from the original unconstrained bivariate model was compared to that from a constrained model where either the genetic variance in both sexes were constrained to be identical or the genetic correlation between the sexes was constrained to be 0.99.

Eigenstructures

Eigenstructures were calculated to determine if the covariance structures among traits within a trait category (i.e., skeletal, muscular, or functional) differed by breed. Covariance components estimated from the bivariate analyses were arranged into a multi-trait covariance matrix within the skeletal, muscular, and functional traits separately. Any non-positive definite covariance matrix were banded. Eigenvectors and eigenvalues were calculated using the covariance matrices in the individual breeds for the muscular traits, the skeletal traits, and the functional traits separately.

Differences in the covariance structures among traits were evaluated as:

$$E'_{CH} CO_i E_{CH} = D$$

where E_{CH} is a matrix consisting of the eigenvectors in CH, CO_i is the estimated covariance matrix among traits in $breed_i$ and D is the resulting matrix. D was then rescaled to \tilde{D} , a matrix with diagonal elements of 1. Whether the off-diagonals of the \tilde{D} matrix were different from zero was investigated when the CO_i was used; the closer to zero the off-diagonal elements were, i.e., the lower the standard deviation, the more similar the covariance matrices were to the CH. Further analysis was

conducted using AA as the reference breed in place of CH to determine the differences in the covariance structures between AA and HE.

Impact of Incorrect Covariance Parameters on the Estimation of Breeding Value

Calculations were undertaken to quantify the impact of using the covariance components of a given breed to estimate the breeding values for an unmeasured trait in another breed. For illustrative purposes, height of withers was assumed to represent the trait where estimated breeding values were desired but no estimated breeding values were assumed available for this trait; the CH was used as the reference breed for comparison purposes. Five linear type traits, namely width of chest, hind-leg rear view, body condition score, development of loin and development of inner thigh were chosen as predictor traits. These traits were chosen based on a function of both the strength of their genetic correlation with height at withers (favoring the stronger correlation) and the variability in the correlation across breeds, while taking cognisance of the genetic correlation between that trait and the index traits already included in the index.

The efficiency of the index (Eu) was calculated as outlined by Ochsner et al. (2017) as:

$$Eu = \frac{b'_u G_{12_t}}{\sqrt{b'_u G_{11_t} b_u}} \left(\sqrt{b'_t G_{12_t}} \right)^{-1}$$

where G_{12_t} represents the true genetic covariances between height at withers (i.e., goal trait) in CH and the five predictor traits, G_{12_t} is a 5×5 matrix representing the true genetic covariances among the five predictor traits in CH, b_t is a $n \times 1$ vector of the coefficients applied to the estimated breeding values derived as:

$$b_t = G_{11_t}^{-1} G_{12_t}$$

and, b_u is a $n \times 1$ vector of the coefficients estimated as above but by replacing genetic covariances from the CH breed (i.e., the "true" parameters) with those of the breed under investigation.

RESULTS

Variance Components of the Linear Type Traits by Breed

The within breed heritability estimates for the linear type traits (Tables 1 and 2) ranged from 0.00

Table 1. Scale of measurement, number of records (*n*), mean (μ), genetic standard deviation (SD_g) and heritability estimates (h^2) of the functional and muscular linear type traits

Trait	Scale	Angus ^a			Charolais ^a			Hereford ^a			Limousin ^a			Simmental ^a		
		<i>n</i> = 3,220–3,356			<i>n</i> = 23,070–31,048			<i>n</i> = 2,390–3,004			<i>n</i> = 30,491–35,158			<i>n</i> = 6,638–8,632		
		μ	SD_g	h^2	μ	SD_g	h^2	μ	SD_g	h^2	μ	SD_g	h^2	μ	SD_g	h^2
Functional		1–10														
Locomotion	low–high	7.7	0.28	0.12	7.7	0.32	0.12	7.8	0.00	0.00	8.1	0.17	0.04	8.1	0.18	0.04
Foreleg front view	toes out–toes in	5.3	0.24	0.13	6.2	0.24	0.09	5.5	0.00	0.00	6.2	0.16	0.06	6.7	0.20	0.06
Hind-leg side view	straight–sickled	7.2	0.21	0.08	7.3	0.27	0.09	7.3	0.24	0.11	7.6	0.24	0.08	7.4	0.21	0.06
Hind-leg rear view	toes out–toes in	5.3	0.16	0.04	6.0	0.26	0.06	5.6	0.00	0.00	6.4	0.21	0.04	5.6	0.25	0.06
Muscular		1–15														
Development of hind quarter	low–high	8.0	0.43	0.22	9.7	0.60	0.30	8.1	0.35	0.14	11.5	0.52	0.25	10.9	0.51	0.24
Development of loin	low–high	8.2	0.37	0.13	9.4	0.52	0.21	8.7	0.31	0.10	10.6	0.45	0.17	9.9	0.47	0.18
Thigh width	narrow–wide	8.2	0.38	0.14	9.7	0.55	0.22	8.2	0.40	0.16	10.2	0.53	0.23	9.9	0.55	0.24
Development of inner thigh	low–high	8.5	0.37	0.14	10.4	0.62	0.28	8.3	0.43	0.20	11.1	0.54	0.24	10.4	0.51	0.23
Width of withers	narrow–wide	8.9	0.51	0.22	9.4	0.51	0.21	8.9	0.41	0.16	10.3	0.46	0.19	10.2	0.54	0.22
Width behind withers	narrow–wide	7.5	0.39	0.13	8.6	0.46	0.18	7.9	0.40	0.15	9.5	0.43	0.17	9.1	0.48	0.18

^aStandard error of the heritability estimates in Angus ≤ 0.05 . Standard error of the heritability estimates in Charolais ≤ 0.02 . Standard error of the heritability estimates in Hereford ≤ 0.05 . Standard error of the heritability estimates in Limousin ≤ 0.02 . Standard error of the heritability estimates in Simmental ≤ 0.03 .

Table 2. Scale of measurement, number of records (*n*), mean (μ), genetic standard deviation (SD_g), and heritability estimates (h^2) of the skeletal and other linear type traits

Trait	Scale	Angus ^a			Charolais ^a			Hereford ^a			Limousin ^a			Simmental ^a		
		<i>n</i> = 3,124–3,356			<i>n</i> = 21,341–31,044			<i>n</i> = 2,993–3,004			<i>n</i> = 30,494–35,156			<i>n</i> = 6,637–8,631		
		μ	SD_g	h^2	μ	SD_g	h^2	μ	SD_g	h^2	μ	SD_g	h^2	μ	SD_g	h^2
Skeletal		1–10														
Width of chest	narrow–wide	6.6	0.20	0.07	6.9	0.24	0.10	6.5	0.00	0.00	6.2	0.24	0.10	6.8	0.30	0.15
Depth of chest	shallow–deep	7.4	0.29	0.15	7.2	0.24	0.13	7.3	0.36	0.25	7.0	0.27	0.15	7.6	0.26	0.14
Height of withers	small–tall	5.8	0.38	0.19	6.8	0.65	0.43	5.7	0.44	0.30	6.6	0.47	0.29	7.2	0.52	0.34
Length of pelvis	short–long	7.1	0.35	0.17	7.4	0.42	0.23	7.0	0.45	0.27	7.8	0.37	0.19	8.0	0.37	0.20
Length of back	short–long	6.8	0.36	0.17	7.7	0.49	0.30	6.8	0.47	0.29	7.7	0.42	0.23	8.0	0.37	0.20
Width at hips	narrow–wide	6.5	0.21	0.06	6.9	0.29	0.13	6.9	0.00	0.00	6.7	0.30	0.14	7.1	0.30	0.14
Other		1–10														
Body condition score	lean–fat	7.0	0.18	0.03	5.8	0.35	0.13	7.2	0.00	0.00	6.6	0.31	0.11	7.1	0.23	0.05
Docility	aggressive–docile	8.7	0.36	0.21	8.9	0.34	0.15	9.2	0.26	0.11	9.2	0.37	0.17	9.3	0.30	0.09

^aStandard error of the heritability estimates in Angus ≤ 0.05 . Standard error of the heritability estimates in Charolais ≤ 0.02 . Standard error of the heritability estimates in Hereford ≤ 0.06 . Standard error of the heritability estimates in Limousin ≤ 0.02 . Standard error of the heritability estimates in Simmental ≤ 0.03 .

(three of the four functional traits in HE) to 0.43 (height in CH). Heritability estimates for the functional traits were generally the lowest of all the traits, and were all ≤ 0.13 ($SE \leq 0.04$). Heritability for the muscular traits varied from 0.10 ($SE = 0.04$) for development of loin in HE to 0.30 ($SE = 0.02$) for

development of hind quarter in CH. Heritability for the skeletal traits ranged from 0.00 for both width of chest and width at hips in HE to 0.43 ($SE = 0.02$) for height of withers in the CH.

The CH animals generally had the highest heritability estimates for the linear type traits

describing the size of the animal; height of withers (0.43; SE = 0.02), length of back (0.30; SE = 0.02), development of hind quarter (0.30; SE = 0.02), development of inner thigh (0.28; SE = 0.02) and body condition score (0.13; SE = 0.02). For 13 of the 18 linear type traits, heritability estimates differed ($P < 0.05$) between at least two breeds. Heritability estimates for width of withers, width behind withers, depth of chest, length of pelvis, and hind-leg side view did not differ between breeds. The genetic standard deviation of the linear type traits differed greatly between the breeds with no genetic variation in six of the traits (i.e., locomotion, foreleg front view, hind-leg rear view, width of chest, width at hips, and body condition score) being detected in HE.

Within Breed Phenotypic and Genetic Correlations Among the Linear Type Traits

Irrespective of breed, the strongest positive phenotypic correlation existed between width of withers and width behind withers, ranging from 0.81 (SE = 0.01) in SI to 0.87 (SE = 0.01) in CH (Table 5). The strongest negative phenotypic correlations generally existed among the functional traits or between the functional and muscular traits; hind-leg side view and locomotion in CH (−0.57; SE = 0.01), hind-leg rear view and locomotion in LM (−0.11; SE = 0.01; Table 7), hind-leg side view and development of loin in AA (−0.38; SE = 0.02; Table 4), hind-leg side view and development of inner thigh in HE (−0.16; SE = 0.02).

In general, the pair-wise genetic correlations among traits were stronger than their respective phenotypic correlations but of the same sign. The genetic correlations among the muscular traits and among the skeletal traits were typically stronger in the continental breeds (CH, LM, SI) than in the British breeds (AA, HE). Within breed, genetic correlations among the muscular traits were moderate to strong, varying from 0.58 (SE = 0.15) for development of loin and width of withers in HE (Table 6) to 0.99 (SE = 0.01) for development of hind quarter and development of inner thigh in CH (Table 5). Moderate to strong genetic correlations also existed between the skeletal traits in all five breeds, ranging from 0.33 (SE = 0.12) for pelvic length and width of chest in SI (Table 8) to 0.98 (SE = 0.01) between height of withers and both length of pelvis and length of back in CH. The genetic correlations among the functional traits varied considerably among the breeds ranging from −0.08 (SE = 0.29) between foreleg front view and

locomotion in SI to 0.87 (SE = 0.14) between the same traits in AA (Table 1).

Box's M test for homogeneity of the covariance matrices among the breeds revealed that all covariance matrices estimated within breed differed from each other except for when the AA and HE were compared. The majority of the pair-wise estimated within-breed genetic correlations differed ($P < 0.05$) between at least two breeds. The fewest differences in correlations were between when the AA and HE were compared; the greatest number of within-breed estimated genetic correlations among traits was observed when the CH was compared to either the AA or the HE.

Eigenstructures

The rescaled \tilde{D} matrices calculated using the breed-specific covariance matrices of the skeletal, functional and muscular traits in LM (compared to the CH as the reference breed) had off-diagonal elements close to zero; the mean (standard deviation) of the absolute values of the off-diagonals was 0.14 (0.17) for the skeletal traits, 0.17 (0.23) for the muscular traits and 0.05 (0.04) for the functional traits. The off-diagonal elements of \tilde{D} calculated from the covariance matrices of the linear type traits in AA were furthest from zero; the mean (standard deviation) of the absolute values of the off-diagonals was 0.21 (0.23) for the skeletal traits, 0.19 (0.19) for the muscular traits and 0.12 (0.04) for the functional traits

Impact of Incorrect Covariance Parameters on the Estimation of Breeding Value

The impact of using the genetic covariance components of the LM to predict genetic merit for height at withers in CH was least but still the efficiency of selection was just 0.62; the efficiency was 0.61 when the covariance components of the SI were used. When the genetic covariance components of the CH were replaced with those of the AA, the efficiency of the index was just 0.29.

Sexual Dimorphism

Although the genetic variance for the linear type traits was greater in male than female LM, no differences existed in the heritability estimates between the two sexes in LM (Table 3). The genetic variance of the type traits in CH was numerically greater in males than females for 14 of the 18 traits. The genetic variance of the type traits in CH was

greater in females than males for development of hind quarter, width at hips, body condition score and docility. Nevertheless, differences ($P < 0.05$) in the heritability estimates between sexes only existed for length of back (males 0.36; females 0.12), height of withers (males 0.68; females 0.29) and development of hind quarter (males 0.23; females 0.33) in CH. In both CH and LM, genetic correlations between the same linear type traits in both sexes were all greater than 0.90 (Table 3).

DISCUSSION

Even though the homogeneity of covariance matrices has long been a topic of interest in multivariate analysis (Box, 1949; Box, 1953), previous studies that estimated the genetic parameters of linear type traits in beef cattle either did so on a single breed (Gutierrez and Goyache, 2002; Mantovani et al., 2010; Mazza et al., 2014; Vallée et al., 2015) or by collating multiple breeds and crosses into a single analysis (Mc Hugh et al., 2012); none have attempted to quantify if differences among breeds

exist in genetic parameters of linear type traits. The absence of such information in the scientific literature may be due to classifiers often only performing linear type scoring on a single breed, thus contributing to confounding between a classifier effect and breed; 12 of the 20 classifiers included in the present study scored at least four of the five breeds. Linear type trait information from all breeds (and crossbreeds) is collated into a centralized database in Ireland thus facilitating the analysis in the present study; such a centralized system is not present in many countries with some breed societies responsible for the collection, collation and analysis of the data relating to their breed only. While differences in variance components of linear type traits among breeds have not been quantified previously, differences in genetic parameters among breeds have been reported previously for carcass traits (Marshall, 1994; Utrera and Van Vleck, 2004; Pabiou et al., 2009; Kause et al., 2015) and birth and weaning weights (Phocas and Laloë, 2004). Studies are also lacking that investigated the possible existence of sexual dimorphism on variance components for

Table 3. The genetic standard deviation (SD_g), heritability estimate (h^2) and genetic correlation (r_g) of the linear type traits in male and female Limousin and Charolais animals

Trait	Limousin ^a					Charolais ^b				
	Male		Female		r_g	Male		Female		r_g
	SD_g	h^2	SD_g	h^2		SD_g	h^2	SD_g	h^2	
Functional										
Locomotion	0.19	0.05	0.13	0.03	0.98	0.29	0.08	0.26	0.09	0.97
Foreleg front view	0.14	0.04	0.00	0	—	0.26	0.09	0.17	0.06	0.99
Hind-leg side view	0.24	0.08	0.15	0.04	0.99	0.23	0.06	0.16	0.04	0.98
Hind-leg rear view	0.19	0.03	0.16	0.02	0.99	0.24	0.05	0.17	0.03	0.98
Muscular										
Development of hind quarter	0.54	0.26	0.45	0.23	0.93	0.50	0.23*	0.57	0.33*	0.97
Development of loin	0.46	0.18	0.37	0.14	0.97	0.50	0.21	0.43	0.21	0.96
Thigh width	0.51	0.21	0.47	0.23	0.92	0.56	0.23	0.48	0.23	0.93
Development of inner thigh	0.53	0.21	0.49	0.23	0.94	0.53	0.23	0.53	0.27	0.96
Width of withers	0.45	0.19	0.38	0.17	0.97	0.53	0.23	0.44	0.21	0.96
Width behind withers	0.43	0.18	0.34	0.13	0.95	0.46	0.2	0.40	0.18	0.91
Skeletal										
Width of chest	0.19	0.07	0.18	0.06	0.98	0.23	0.09	0.15	0.05	0.90
Depth of chest	0.26	0.14	0.20	0.09	0.98	0.17	0.06	0.17	0.07	0.98
Height of withers	0.47	0.27	0.40	0.24	0.94	0.89	0.68**	0.47	0.29**	0.99
Length of pelvis	0.29	0.12	0.32	0.12	0.99	0.37	0.18	0.32	0.16	0.99
Length of back	0.37	0.19	0.36	0.19	0.98	0.55	0.36**	0.36	0.12**	0.99
Width at hips	0.23	0.09	0.27	0.12	0.95	0.18	0.06	0.25	0.11	0.98
Other										
Body condition score	0.32	0.13	0.28	0.1	0.99	0.24	0.07	0.30	0.12	0.98
Docility	0.30	0.11	0.32	0.13	0.98	0.29	0.11	0.31	0.14	0.99

^aStandard errors for h^2 and r_g in Limousin were all ≤ 0.03 .

^bStandard errors for h^2 and r_g in Simmental were all ≤ 0.04 .

* $P < 0.05$, ** $P < 0.01$.

Table 4. Phenotypic (below the diagonal) and genetic (above the diagonal) correlations between linear type traits in Angus^a

	LOCO	FL-FV	HL-SV	HL-RV	DHQ	DL	TW	DIT	WOW	WBW	CW	CD	WH	PL	BL	HW	BCS	DOC
LOCO		0.87	-0.57	0.41	0.34	0.43	0.23	0.12	0.52	0.84	0.33	0.19	-0.10	0.21	0.15	0.15	0.66	0.52
FL-FV	0.28		-0.10	0.17	0.62	0.83	0.78	0.63	0.66	0.64	0.33	0.45	0.31	0.49	0.38	0.68	0.68	0.37
HL-SV	-0.38	-0.02		0.16	-0.50	-0.66	-0.13	-0.46	0.07	-0.13	0.47	0.01	0.01	-0.05	-0.02	0.09	0.15	-0.09
HL-RV	0.21	0.08	-0.04		0.33	0.07	0.05	0.30	0.12	0.33	0.43	-0.29	-0.46	-0.28	-0.61	0.09	-0.17	0.36
DHQ	0.20	0.13	-0.13	0.18		0.87	0.83	0.77	0.66	0.78	0.57	0.27	0.13	-0.003	0.35	0.41	0.69	0.43
DL	0.28	0.13	-0.14	0.13	0.64		0.74	0.93	0.77	0.89	0.33	0.26	0.22	0.18	0.37	0.43	0.53	0.76
TW	0.16	0.13	-0.07	0.15	0.64	0.64		0.71	0.77	0.75	0.75	0.45	0.18	0.29	0.4	0.85	0.75	0.63
DIT	0.14	0.11	-0.14	0.15	0.77	0.62	0.68		0.73	0.82	0.43	0.22	0.15	0.15	0.3	0.46	0.78	0.68
WOW	0.22	0.11	-0.08	0.07	0.58	0.68	0.66	0.59		0.95	0.65	0.18	0.25	0.20	0.3	0.73	0.63	0.67
WBW	0.25	0.09	-0.10	0.10	0.61	0.72	0.63	0.60	0.85		0.65	0.23	0.28	0.13	0.36	0.87	0.84	0.56
CW	0.14	0.14	-0.04	0.14	0.39	0.45	0.52	0.41	0.48	0.48		0.72	0.84	0.46	0.69	0.84	0.63	0.35
CD	0.09	0.09	0.01	0.05	0.30	0.39	0.47	0.33	0.41	0.38	0.70		0.84	0.87	0.68	0.86	0.60	0.55
WH	0.08	0.07	-0.01	0.05	0.23	0.32	0.40	0.27	0.39	0.34	0.45	0.59		0.80	0.95	0.86	0.42	0.53
PL	0.12	0.09	-0.01	0.08	0.25	0.33	0.40	0.29	0.37	0.33	0.42	0.54	0.73		0.71	0.84	-0.16	0.63
BL	0.12	0.08	-0.03	0.05	0.27	0.36	0.41	0.30	0.39	0.36	0.41	0.51	0.70	0.70		0.78	0.60	0.34
HW	0.15	0.13	-0.01	0.13	0.32	0.43	0.53	0.39	0.49	0.46	0.50	0.52	0.54	0.55	0.67		0.87	0.50
BCS	0.20	0.15	-0.07	0.12	0.39	0.48	0.47	0.42	0.43	0.48	0.41	0.46	0.28	0.29	0.27	0.44		0.81
DOC	0.18	0.07	-0.13	0.06	0.22	0.24	0.24	0.24	0.27	0.24	0.16	0.16	0.17	0.18	0.18	0.20	0.18	

LOCO = locomotion, FL-FV = foreleg front view, HL-SV = hind-leg side view, HL-RV = hind-leg rear view, DHQ = development of hind quarter, DL = development of loin, TW = thigh width, DIT = development of inner thigh, WOW = width of withers, WBW = width behind withers, CW = width of chest, CD = depth of chest, WH = height of withers, PL = length of pelvis, BL = length of back, HW = width at hips, BCS = body condition score, DOC = docility.

^aStandard errors for the phenotypic correlations ranged from 0.01 to 0.02. Standard errors for the genetic correlations varied from 0.02 to 0.49.

linear type traits in beef cattle. Knowledge of the extent, if any, of breed differences in variance components, as well as the presence of sexual dimorphism for variance components is becoming more important as initiatives attempt to combine data from multiple sources in the pursuit of more accurate genomic evaluations.

Sexual Dimorphism

Sexual dimorphism in mammals and many other organisms is due to evolution by natural selection, specifically sexual selection. Sexual selection, a concept coined by Darwin, arises due to competition among the same sex of a species and due to mating preferences of one sex to the other (Kirkpatrick, 1987). Male and female mammals differ in many anatomical and physiological features concerning their role in the development and maintenance of their offspring, their body size, coloration, display characteristics, and mating behavior (McPherson and Chenoweth, 2012; van der Heide et al., 2016). Historically, sexual dimorphism tended to occur in mammals due to competition among males for access to females; males would fight one another and the winner, generally the biggest, strongest animal would mate with the females (Katz, 2008). This competition is, however,

reduced in domestic animals where breeding males are less likely to be selected for their size or aggressiveness but are selected on numerous other desirable traits. Sexual dimorphism has previously been researched in beef cattle for numerous important traits, such as growth rate (Koch and Clark, 1955; Marlowe and Gaines, 1958) and birth weight, weaning weight and post-weaning gain (van der Heide et al., 2016), but no study has been published that investigated the existence of sexual dimorphism on variance components for linear type traits in beef cattle.

While differences in the heritability estimates existed in three of the 18 linear type traits between the sexes in CH (development of hind quarter, height of withers and length of back), no differences existed in LM. All genetic correlations, in both CH and LM, were ≥ 0.90 . It has been proposed previously that traits with a correlation >0.80 can be assumed to be genetically the same trait (Robertson, 1959) despite that fact that a correlation of 0.80 translates to only 64% of the variance in one trait being explained by the other. Combined, the results from the present study suggest little existence of appreciable sexual dimorphism on variance components in linear type traits and thus stratifying genetic evaluations into males and females is unlikely to be beneficial.

breeds than in the British breeds, when rescaled to the mean, the extent of additive genetic variance was similar for all muscular traits.

The strong genetic correlations among the muscular traits are consistent with the correlations reported previously in Chianina beef cows (Forabosco et al., 2005), in the Rendena dual-purpose cattle breed (Mazza et al., 2014), and in Piemontese cows (Mantovani et al., 2010). Genetic correlations between width of withers and width behind withers were extremely strong across all five breeds, ranging from 0.90 to 0.96 suggesting redundancy; this is not unexpected since both traits are measures of animal width taken in close spatial proximity. Moreover, the redundancy is present across all breeds.

The mean and standard deviation of the off-diagonal elements of \hat{D} when calculated from the covariance matrix of LM were close to zero, indicating that the covariance matrix of LM and the covariance matrix of CH were the most similar. Similarly, the mean and standard deviation of \hat{D} calculated using the eigenvector matrix from AA with the covariance matrix from HE suggests the covariance matrices of these breeds were similar to one another.

Skeletal Traits

The heritability estimates of the skeletal linear type traits (0.00–0.43) are in the range of previous estimates reported in beef cattle; Gutierrez and Goyache (2002) reported heritability estimates of between 0.10 and 0.23 for the skeletal traits in Asturiana de los Valles beef cattle while Forabosco et al. (2005) reported heritability estimates in the range of 0.21 to 0.30 for Chianina beef cattle. The heritability estimates reported in the present study are also consistent with heritability estimates (0.23 to 0.38) relating to skeletal traits in dairy cattle (Veerkamp and Brotherstone, 1997; Berry et al., 2014).

The greatest differences in within-breed heritability estimates existed for height of withers (0.19 in AA; 0.43 in CH) and length of back (0.17 in AA; 0.30 in CH). The higher heritability estimate for height of withers in CH is due to a larger genetic standard deviation (0.65) concurrent with a marginally smaller residual standard deviation (0.75) in CH than in AA. The differences in heritability estimates of length of back in CH and AA are due to CH having a slightly lower residual standard deviation (0.75) than AA (0.79). The lower heritability and

genetic variation for height at withers in AA may be related to AA, not only being generally smaller than CH, but also reaching mature height earlier than CH (Arango et al., 2002) and thus having less variability in height at withers at younger ages.

Excluding height at withers, and with the exception of the two skeletal traits in HE with no genetic variation (width of chest and width at hips), the other skeletal traits across all breeds expressed similar genetic variation when rescaled to the respective breed mean (0.03 to 0.07). This implies that, once scaled to the breed mean for that trait, the extent of additive genetic variance was similar within these traits and across the breeds.

Regardless of breed, genetic correlations among the skeletal traits were all generally moderate to strong, corroborating genetic correlation estimates among skeletal traits in beef cattle from other populations such as Asturiana de los Valles beef cattle (Gutierrez and Goyache, 2002) and beef cattle from the Czech Republic (Vesela et al., 2005). Overall, the strongest pairwise genetic correlations existed between the skeletal traits in CH while the weakest genetic correlations existed in AA. The skeletal traits were also moderately to strongly correlated with the muscular traits, signifying that the more muscular animals also have a tendency to score higher for skeletal type traits (Grona et al., 2002).

Functional Traits

While few previous studies have reported heritability estimates for functional traits in beef cattle, the heritability estimates reported in the present study are comparable to what has been reported previously in CH cattle (0.02 to 0.11; Vallée et al., 2015). The heritability estimates are, however, slightly lower than those reported in Brazilian Holstein cows (0.08 to 0.19; Kern et al., 2015) and Irish Holstein-Friesians (0.14 to 0.19; Berry et al., 2004). Excluding the three functional traits with no genetic variation in HE, the genetic standard deviation was similar (0.16 to 0.32) across the other functional traits in all breeds.

Unlike the skeletal and muscular traits, the genetic correlations among the functional traits did not follow any particular pattern with the correlations differing greatly among the breeds. The differences among the breeds, in both the variances and genetic correlations among the functional traits, may be due to the level of environmental influence. Environmental factors such as housing

type, diet and hoof trimming schedules will affect the feet and legs of an animal potentially influencing the linear type classification (Fatehi et al., 2003). The differences in heritability estimates and genetic correlations observed among the linear type traits in the five breeds may be real differences in parameters among populations or may be due to the small sample size of HE and AA available for analysis in comparison to the continental breeds, or a combination of the two (Koots and Gibson, 1996).

The covariance structures of the functional traits in LM and SI were similar to the covariance structure of CH, as indicated by the means and standard deviations of the off-diagonal elements of \hat{D} . Larger differences in the covariance structures existed between CH and AA, signifying these breeds were more different to one another than CH was to LM or SI.

Efficiency of Index When Using Incorrect Genetic Parameters

The efficiency associated with using the genetic parameters of LM in place of CH was poor despite the general similarity in estimated inter-trait genetic covariances among all 18 traits; this observed poor efficiency was due to the traits chosen to be included in the selection index to be contributors to variability in the goal trait but also variable between breeds. The efficiency of the index when CH was replaced by SI was similar to that observed for the LM which is not overly surprising given the relative similarities of in the origin of these breeds (Kelleher et al., 2017). The large reduction in index efficiency associated with using the genetic parameters of AA suggests that AA should ideally not be included in multi-breed genetic evaluations with the continental breeds as this may lead to a marked reduction in accuracy. It should be noted nonetheless, that the index efficiency presented here was based on true breeding values which may not always be available and thus represents an upper threshold to this efficiency.

CONCLUSION

While the sex of an animal had little to no effect on the heritability estimates and genetic correlations among linear type traits, differences among the breeds in both the heritability estimates and in the genetic correlations among the linear type traits did exist. The greatest differences existed between the continental breeds and the British breeds suggesting that the accuracy of genetic evaluations

may benefit from considering, at least, these breed groups separately in future evaluations.

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