

Genetic parameters and trends for traits of the Hereford and Braford breeds in Brazil[☆]



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ABSTRACT

The objective of this study was to estimate genetic parameters and genetic trends of Hereford and Braford breeds for growth traits and visual scores. Data consisting of records for 205-day weight (W205), 550-day weight (W550), 345-day post weaning gain (PWG345), scrotal circumference at 550 days (SC), and muscling (MUS) and frame (FRA) scores also recorded at 550 days of age came from the PampaPlus genetic evaluation system. A series of animal models were fit to the data using Bayesian inference with uninformative priors. Genetic variance for W205 was partitioned into direct (W205_d) and maternal (W205_m) components. Posterior means of heritability estimates and 95% support intervals (2.5% ≤ h² ≤ 97.5%) for W205_d, W205_m, W550, PWG345, SC, MUS, and FRA were 0.12 ≤ 0.13 ≤ 0.14; 0.08 ≤ 0.09 ≤ 0.11; 0.13 ≤ 0.16 ≤ 0.19; 0.04 ≤ 0.10 ≤ 0.18; 0.05 ≤ 0.15 ≤ 0.32; 0.10 ≤ 0.19 ≤ 0.29 and 0.06 ≤ 0.11 ≤ 0.20, respectively. Genetic correlations with W205_d were positive for W550 (0.72 ≤ 0.82 ≤ 0.90), MUS (0.25 ≤ 0.53 ≤ 0.74) and FRA 0.29 ≤ 0.59 ≤ 0.80 and negative for W205_m (− 0.63 ≤ − 0.57 ≤ − 0.50). The genetic correlation of PWG345 and W550 was also positive and large (0.59 ≤ 0.76 ≤ 0.88). Genetic correlations of MUS and FRA with each other (0.30 ≤ 0.53 ≤ 0.73) and with PWG (0.08 ≤ 0.33 ≤ 0.55 and 0.20 ≤ 0.44 ≤ 0.64) and W550 (0.10 ≤ 0.39 ≤ 0.63 and 0.07 ≤ 0.38 ≤ 0.64) were all positive. Use of performance information in selection decisions is supported by positive genetic trends for direct effects on W205_d, PWG345, W550, MUS and FRA. However, the genetic trends were less than the expected gains that would result from use of a recommended selection index, suggesting that the index is not the only criterion currently used in the selection by Pampaplus breeders. It may be concluded that breeders favored larger, more rapidly growing, and more muscular animals in their selection decisions.

1. Introduction

Cumulative and permanent incremental improvement becomes possible due to heritable genetic variation among individuals. Without genetic variability there would be no need to choose among candidates for selection since their future progeny would have the same expected performance. The PampaPlus genetic evaluation system was created in 2008 to facilitate genetic improvement of the Hereford and Braford breeds in Brazil. Within the system, Expected Progeny Differences (EPD) are calculated for growth traits, visual scores and scrotal circumference using BLUP methodology following mixed model theory as

described by Henderson (1984). Reports are generated to provide access to information that can facilitate selection decisions by producers. The genetic evaluation process depends on knowledge of (co)variance components for its implementation. Genetic parameters defined by these components (heritability, repeatability, and genetic correlation) may be specific for each population (Koots et al., 1994 a, b). Heritability determines the potential rate of progress given the selection differentials, and genetic correlations reflect the potential for selection on one trait to impact another (Falconer and Mackay, 1996). In Brazil, since 2008, breeders of PampaPlus genetic evaluation have used the empirical selection index, referred to the IQG (Index of Genetic

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Quality), described by Cardoso and Lopa (2013). However, the relative importance given by empirical weights in the PampaPlus IQG, may not be as efficient in guiding genetic improvement as those developed based on classical economic selection index approaches (Ponzoni and Newman, 1989; Schneeberger et al., 1992; Macneil et al., 1994).

In addition to their use in predicting the EPD, to estimate genetic (co)variance component and genetic parameters are also required to formulate classical selection indexes (Hazel, 1943). Therefore, objectives of this work were to estimate genetic parameters for components IQG for the Hereford and Braford breeds, to predict expected gain in each trait with selection exclusively on IQG, and compare those gains with the observed current progress.

2. Materials and methods

The data consisted of performance records from 58,780 animals that were born between 2007 and 2012. The associated pedigree contained a total of 87,933 individuals. These records came from 50 herds of Hereford and Braford cattle that were located in Rio Grande do Sul (N = 48), Santa Catarina (N = 1), and the Eastern Republic of Uruguay (N = 1).

Traits analyzed were: weaning weight adjusted to 205 days which was partitioned into direct and maternal genetic effects (W205_d and W205_m, respectively), body weight adjusted to 550 days (W550), 345 days postweaning gain (PWG345), scrotal circumference adjusted to 550 days (SC), and muscling (MUS) and frame (FRA) scores that were also recorded at 550 days of age (Cardoso and Lopa, 2013). Tables 1 and 2 present descriptive statistics that characterize these data.

Animals were identified as contemporaries at weaning by concatenating codes for: farm, year of birth, sex, breed composition of the animal and its dam (zebu percentage: 3/8z, 1/4z or 1/2z), nutritional management and date of weaning. Once formed the range in age of calf within group was evaluated and for those groups in which the range in age was greater than 90 days the group was subdivided until the range in ages within each group was 90 days or less. Contemporary groups for the postweaning traits were nested within the weaning contemporary groups (CGW) with animals that were managed similarly after weaning and whose 550-d weight was recorded on the same day were considered members of the same postweaning contemporary group (CGP). For W205, W550, PWG345, and SC means and standard deviations were calculated within each contemporary group. Those animals whose records deviated from the mean of their contemporary group by more than ± 3.5 standard deviations were deleted from the corresponding analyses. Finally, contemporary groups comprised of fewer than 3 animals were deleted. Thus, there were 4056 CGWs and 2883 CGPs remaining in the data.

Table 1 D
descriptive statistics for 205-d weight (W205), 550-d weight (W550), 345-d post weaning gain (PWG345), and scrotal circumference (SC) of Hereford and Braford males and females.

	Braford Females					Hereford Females				
	N ^a	Min ^b	Max ^c	\bar{x} ^d	SD ^e	N	Min	Max	\bar{x}	DP
W205 (kg)	16,010	65.5	555.7	188.74	35.58	9,430	60,65	356,93	171,61	36,20
W550 (kg)	8680	161.0	582.6	305.30	51.37	5,799	150,33	686,16	312,17	60,01
PWG345 (kg)	8678	0.93	346.0	115.66	40.63	5,797	1,17	393,63	139,72	51,95
	Males					Males				
W205 (kg)	14,248	62,49	537,64	199,89	39,40	8,853	61,83	418,97	184,22	39,90
W550 (kg)	3,783	204,49	749,92	436,05	77,48	2,857	174,22	766,20	438,26	95,59
PWG345 (kg)	3,788	10,24	510,13	223,78	67,03	2,858	10,74	637,40	239,10	83,67
SC (cm)	3,370	20,50	44,00	32,30	3,50	2,586	22,00	42,00	33,57	2,99

^a N = number of observations.
^b Min = minimum observed value.
^c Max = maximum observed value.
^d \bar{x} = average value.
^e SD = standard deviation.

Table 2 D
descriptive statistics describing the categorical scores for muscling (MUS) and frame (FRA) of Hereford and Braford cattle at approximately 550 days of age.

Trait	N ^a	\bar{x} ^b	SD ^c	1 ^d	2 ^d	3 ^d	4 ^d	5 ^d
MUS	22,526	3,37	1,00	692	3,522	8,248	6,928	3,136
FRA	22,528	3,27	0,99	1,055	3,479	8,432	7,369	2,193

^a N = number of observations.
^b \bar{x} = average.
^c SD = standard deviation.
^d Number of observations by score.

The Hereford-Braford genealogy was reformed using RENUMF90 (Misztal, 2012), which specifically identifies ancestors of those animals with performance measures. Prior values of the (co)variance components for use as initial estimates for the Bayesian models were obtained from bivariate REML analyses conducted with AIREMLF90 (Misztal, 2012). Subsequently, INTERGEN (Cardoso, 2010) was used to conduct Bayesian analyses of the data. These analyses used the complete animal model with Gibbs sampling for the Monte Carlo Markov Chains (MCMC). The initial values for the components of (co)variance used as a priori values were assumed to be relatively uninformative, but proper to facilitate convergence of full posterior densities. Each analysis consisted of 1800,000 cycles of Gibbs sampling with the initial 180,000 cycles discarded as burn-in. Subsequent samples were thinned to every 40 cycles. Convergence of the MCMC was evaluated from plots of the (co)variance components against cycle number as described in Cardoso (2010).

Systematic independent variables included in the analyses were: contemporary groups (CGW and CGP, as described above); age of dam (2–14 + years) by sex of calf (dams of 2 years with male calves, dams of 2 years with female calves and so on); and a continuous covariate for age of the animal at time of measurement, which had linear and quadratic terms. The bivariate animal model, in matrix notation, was:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} m_1 \\ m_2 \end{bmatrix} + \begin{bmatrix} D_1 & 0 \\ 0 & D_2 \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} c + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

wherein, y_i = vectors of observations, with the subscript denoting the i^{th} trait; β_i = vectors of systematic effects which are related to the data by incidence matrices X_i ; a_i = vectors of direct additive genetic effects which were related to animals with incidence matrix Z_1 and Z_2 ; m_i = vectors of maternal additive genetic effects which were related to animals who are dams with incidence matrix Z_1 and Z_2 ; c_i = vectors of permanent environmental effects to dams as specified in the incidence

matrix D_i ; and $e_i =$ vectors of residual deviations. Maternal additive genetic effects were only considered for W205 and permanent environmental effects to dams only considered for W205 and W550. For the other traits, we considered only the direct additive genetic effects.

In the first stage, the conditional distribution of data (y) can be represented by a multivariate normal distribution:

$$y|\beta, a, m, c \sim N(X\beta + Za + Zm + Dc, R), \text{ where } R = \begin{bmatrix} \sigma_{e_1}^2 & \sigma_{e_1, e_2} \\ \sigma_{e_2, e_1} & \sigma_{e_2}^2 \end{bmatrix} \otimes I$$

wherein R is the residual covariance matrix, with $\sigma_{e_i}^2 =$ the residual variance for trait i and $\sigma_{e_i, e_j} =$ the covariance of residuals for traits i and j .

In the second stage, we specify the *a priori* distributions for the parameters defined in the first stage: $\beta | \beta_0, V_\beta \sim N(\beta_0, V_\beta)$, where β_0 contains the *a priori* average effects based on existing knowledge and V_β contains the respective variances. In the present study it was assumed that $V_\beta \rightarrow \infty$ and thus all inference to β was derived from the data. For the genetic effects we had that:

$$\begin{bmatrix} a_1 \\ a_2 \\ m_1 \\ m_2 \end{bmatrix} \sim N \left(\begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma_{a_1}^2 & \sigma_{a_1 a_2} & \sigma_{a_1 m_1} & \sigma_{a_1 m_2} \\ \sigma_{a_2 a_1} & \sigma_{a_2}^2 & \sigma_{a_2 m_1} & \sigma_{a_2 m_2} \\ \sigma_{m_1 a_1} & \sigma_{m_1 a_2} & \sigma_{m_1}^2 & \sigma_{m_1 m_2} \\ \sigma_{m_2 a_1} & \sigma_{m_2 a_2} & \sigma_{m_2 m_1} & \sigma_{m_2}^2 \end{bmatrix} \otimes A \right)$$

wherein: $\sigma_{a_i}^2$ and $\sigma_{m_i}^2 =$ additive genetic variances of the direct and maternal effects on the i^{th} trait, respectively; and $\sigma =$ genetic covariances among the corresponding effects as indicated by the subscripts. Moreover, for the permanent environmental effects due to dams, the prior distribution was:

$$\begin{bmatrix} c_1 \\ c_2 \end{bmatrix} \sim N \left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma_{c_1}^2 & \sigma_{c_1 c_2} \\ \sigma_{c_2 c_1} & \sigma_{c_2}^2 \end{bmatrix} \otimes I \right)$$

wherein: $\sigma_{c_i}^2 =$ permanent environmental variance due to dams for the i^{th} trait and $\sigma =$ covariance among the corresponding permanent environmental effects as indicated by the subscripts. For the (co)variances the *a priori* distributions were inverted Wishart and all fully conditional posterior distributions have been described previously (Gianola and Fernando, 1986).

Marginal densities of the 40,500 samples in the thinned posterior distributions were summarized as means, standard deviations, 95% support intervals, and genetic trends using univariate and regression procedures of SAS 9.3 (SAS, 2010). Estimates of heritability (h^2) and genetic correlations (r_g) and their standard deviations were also predicted from the posterior distributions of the (co)variances.

Genetic progress due to use of the data in evaluating candidates for selection was assessed using genetic trends for traits that comprise the IQG:

$$IQG = \frac{0.30 \cdot EPD_{TMD}}{\sigma_{TMD}} + \frac{0.15 \cdot EPD_{W550}}{\sigma_{W550}} + \frac{0.15 \cdot EPD_{PWG345}}{\sigma_{PWG345}} + \frac{0.15 \cdot EPD_{SC}}{\sigma_{SC}} + \frac{0.125 \cdot EPD_{MUS}}{\sigma_{MUS}} - \frac{0.125 \cdot |EPD_{FRA}|}{\sigma_{FRA}}$$

where in the numerators of the ratios (0.30, 0.15 and 0.125) represent the empirical importance of each trait to the PampaPlus IQG and σ_i is the genetic standard deviation of the i^{th} trait. The trait abbreviated TMD corresponds to the total maternal weaning weight: $TMD = 0.5W_{205_d} + W_{205_m}$. For all traits, genetic trends were calculated as the linear regression of mean genetic value on year of birth.

3. Results and discussion

3.1. Estimates of genetic parameters

Analysis of the *a posteriori* distributions generated by the Gibbs sampling allowed for inferences with respect to the genetic parameters and their distributions consistent with the properties of Bayesian

Table 3

Means (\bar{x}), standard deviations (SD), modes (M), and 95% support intervals (SI) from the posterior distributions of variance components estimated by Bayesian inference for 205-d weight, (W205), 550-d weight (W550), 345-d postweaning gain (PWG345), scrotal circumference (SC), and muscling (MUS) and frame (FRA) scores of Hereford and Braford candidates for selection.

Trait	Components of variance ^a					
	σ_a^2	σ_m^2	σ_{am}	σ_{mpe}^2	σ_e^2	
W205	\bar{x}	100.62	72.61	− 48.81	101.05	564.52
	SD	4.71	5.5	4.66	2.89	3.44
	M	100.01	72.53	− 48.66	101.48	564.6
	SI	91.54 to 110.03	62.05 to 83.76	− 58.2 to − 39.59	95.39 to 106.68	557.73 to 571.25
W550	\bar{x}	185.81			64.24	1096.89
	SD	26.97			10.67	22.99
	M	181.81			64.34	1095.49
	SI	136.2 to 242.09			42.33 to 86.16	1050.81 to 1140.72
PWG345	\bar{x}	92.25				871.23
	SD	38.17				32.08
	M	63.26				875.54
	SI	38.38 to 184.45				802.63 to 929.11
SC	\bar{x}	0.88				4.85
	SD	0.46				0.52
	M	0.55				4.83
	SI	0.31 to 1.95				3.84 to 5.88
MUS	\bar{x}	0.13				0.56
	SD	0.03				0.02
	M	0.11				0.57
	SI	0.07 to 0.21				0.51 to 0.61
FRA	\bar{x}	0.07				0.57
	SD	0.02				0.02
	M	0.06				0.57
	SI	0.03 to 0.13				0.53 to 0.61

^a $\sigma_a^2 =$ direct additive genetic variance; $\sigma_m^2 =$ maternal additive genetic variance; $\sigma_{am} =$ additive genetic covariance of direct and maternal effects; $\sigma_{mpe}^2 =$ permanent environmental variance due to dams; $\sigma_e^2 =$ residual variance.

inference (Gianola and Fernando, 1986; Tempelman, 1998; Cardoso and Tempelman, 2004). Graphical analysis of the parameter estimates from the thinned MCMC indicated convergence of the chains. After discarding the burn in cycles, Pearson correlations among the various (co)variance component estimates and autocorrelation within chains were approximately zero (− 0.05 to 0.18).

In general, means and *a posteriori* estimates of the (co)variance components (Table 3) were less than corresponding values summarized from the literature (Koots et al., 1994 a,b). However, these estimates were similar to previously estimated values for Hereford and Braford breeds from Uruguay and southern Brazil (De Mattos et al., 2000; Cardoso and Tempelman, 2004, respectively). Similarity of the present estimates to those of Cardoso and Tempelman (2004) may be attributable to the correspondence of methodology and populations between the two studies. Differences among traits in relative variability of the estimates reflect differences in the numbers of observations that were available for each of them.

Estimates of the variance components (Table 3) and heritability (Table 4) for W205 were consistent with Meyer (1993) and of lower magnitude of Torres-Vázquez and Spangler (2016) in Hereford cattle. Reyes et al. (2006) observed additive genetic variance for W_{205_d} Hereford \times Nellore crossbred cattle that was also similar to that found here, but with greater h^2 . Further, Cardoso and Tempelman (2004) also observed similar additive genetic variance for PWG345 to that observed here. These similarities in additive genetic variation may be interpreted as suggesting the studied populations have similar genetic composition. However, the disparity in estimates of h^2 indicates opportunity for

Table 4

Posterior means of estimates of heritability (on diagonal), genetic correlation (above diagonal) and phenotypic correlation (below diagonal), and 95% support intervals (below the estimates) for direct and maternal effects on 205-d weight, (W205_d and W205_m, respectively), 550-day weight (W550), 345-day post-weaning gain (PWG345), scrotal circumference (SC), and muscling (MUS) and frame (FRA) scores of Hereford and Braford candidates for selection.

Trait	W205 _d	W205 _m	W550	PWG345	SC	MUS	FRA
W205 _d	0.13 0.12 to 0.14	– 0.57 – 0.63 to – 0.50	0.82 0.72 to 0.90	0.40 – 0.03 to 0.74	0.23 – 0.45 to 0.73	0.53 0.25 to 0.74	0.59 0.29 to 0.80
W205 _m	– 0.09 0.08 to 0.11	– – 0.40 – 0.62 to – 0.16	– – 0.40 – 0.51 to 0.51	– – 0.02 – 0.51 to 0.51	– 0.06 – 0.51 to 0.62	– – 0.10 – 0.46 to 0.29	– – 0.16 – 0.52 to 0.25
W550	0.50 0.49 to 0.52	–	0.16 0.13 to 0.19	0.76 0.59 to 0.88	0.46 – 0.09 to 0.81	0.39 0.10 to 0.63	0.38 0.07 to 0.64
PWG345	– 0.16 – 0.20 to – 0.12	–	0.75 0.74 to 0.77	0.10 0.04 to 0.18	0.10 – 0.23 to 0.42	0.33 0.08 to 0.55	0.44 0.20 to 0.64
SC	0.26 0.16 to 0.36	–	0.33 0.25 to 0.40	0.26 0.24 to 0.28	0.15 0.05 to 0.32	0.13 – 0.20 to 0.46	0.14 – 0.20 to 0.44
MUS	0.23 0.19 to 0.26	–	0.47 0.45 to 0.50	0.37 0.36 to 0.39	0.27 0.24 to 0.29	0.19 0.10 to 0.29	0.53 0.30 to 0.73
FRA	0.32 0.29 to 0.36	–	0.48 0.45 to 0.51	0.34 0.33 to 0.35	0.26 0.24 to 0.29	0.44 0.43 to 0.45	0.11 0.06 to 0.20

improvement through greater control of environmental variation. The work of Oliveira et al. (2010) characterizing the Brangus - Ibagé of Embrapa Pecuária Sul support this contention. They found reduced environmental variance and consequently increased h^2 for PWG345 based on data collected at the research center when compared to the studies of field data.

Heritability estimates for the selection criteria (Table 4) indicate that the direct effects for these traits are lowly to moderately heritable. For PWG345 the current estimates were generally less than a consensus of the 184 papers reviewed by Koots et al. (1994a). They are similarly less than those from studies of Nellore in Brazil (Garnero et al., 2002; Marcondes et al., 2002; Giannotti et al., 2005; Koury Filho et al., 2009). Again, the large environmental component of variance found in the present study contributes to this disparity. The additive (co)variance components (Table 3) and h^2 (Table 4) estimated for SC were also less than those reported previously for Hereford (Bourdon and Brinks, 1986; Evans et al., 1999; Koots et al., 1994a) and Nellore breed (Yokoo et al., 2007; Dias et al., 2003). Again, the inflated environmental variance contributed to the low estimate of h^2 . Thorton (2010) observed that efficacy of selection has been compromised in developing countries, in part, because of the lack of the appropriate infrastructure. Here, several factors including inconsistency in data collection, substandard equipment, poor rural facilities that do not allow good animal restraint, and erroneous techniques may all contribute to the inflated environmental variances. Further, coordinated livestock improvement programs been unsuccessful due to the lack of technical knowledge and training at the point of implementation (Kahi et al., 2005).

The maternal permanent environment variance due to dams for W550 reflects the part-whole relationship of W205 with W550, since part of the variation referring to W550 comes from the variation of W205, likely due to a residual permanent maternal environment effect from the pre-weaning phase influencing the W550. The absence of a similar partitioning of variance for PWG345 belies the hypothesis of compensatory growth from a restriction of growth prior to weaning.

It was found that SC was modestly heritable and genetically independent of growth (Table 4). The inclusion of SC in the IQG has been motivated by previous estimates of its beneficial genetic correlation with sexual precocity of females. Estimating the genetic correlation between heifer pregnancy and SC in Nellore cattle, Santana et al. (2012, 2015) found positive association ranging from 0.30 to 0.48. Working with the genetic correlation of SC and age at first calving, first calving interval, age of second calving, Silva et al. (2000) in Canchim and Santana et al. (2015) in Nellore, found negative association varying from – 0.25 to – 0.70. However, other studies have found scant relationships of SC to age at first calving and pregnancy rate in Hereford and Angus (Evans et al., 1999; Doyle et al., 2000) and Nellore (Pereira

et al., 2002; Boligon et al., 2007) females. However, relationships of SC with other economically relevant traits in the PampaPlus-assisted Hereford and Braford populations remains an important topic for future work, wherein reproductive traits, measured in females, are collected in volume.

Collection of data for subjective scores requires less infrastructure than for objectively measured traits. The heritability estimates for MUS and FRA in this study were at least as large as estimates for the objectively measured traits. The present estimate of h^2 for MUS was comparable to that observed for Angus, varying from 0.19 to 0.26 (Cardoso et al., 2001, 2004), but less than has been observed for Nellore, ranging from 0.32 to 0.49 (Koury Filho et al., 2009; Yokoo et al., 2009; Boligon and Albuquerque, 2010). Frame score was lowly heritable, but had substantial genetic and phenotypic correlations with the growth traits (Table 4). Thus, selection for growth would be expected to increase stature as a correlated response, in agreement with the findings of Yokoo et al. (2007).

Growth traits were all positively correlated (Table 4) and thus complimentary in the IQG. These data indicate only the relationship of W205_d with W205_m as an important genetic antagonism among components in the IQG. Similar results were found in the paper of Cardoso et al. (2001) with Angus raised in southern Brazil Meyer (1993) in the Australian Hereford. However, authors such as Robinson (1996b) questioned if the totality of this negative correlation can be attributed to genetic origin, and argued that it may also be due to non-genetic effects such as bull interaction with the year or negative covariance between progeny – dams. Selection index is seen as the optimum way to balance selection for these components of weaning weight (Willham, 1972). Currently they are considered jointly through their effect on TMD (Cardoso and Lopa, 2013).

In general, the low estimates of h^2 found here indicate that the individual phenotypes are not accurate predictors of the corresponding breeding values. Thus, to obtain accurate predictors of breeding values for individual animals it will be necessary to amalgamate information from collateral relatives and progeny through a system of genetic evaluation. In this way and through the use of selection indexes there can be some assurance of genetic improvement in the Hereford and Braford populations of southern Brazil and surrounding regions.

3.2. Genetic trends and gains

Genetic gain occurred for most of the traits evaluated in the PampaPlus (Figs. 1–9). In evaluating these trends, it is noteworthy that they span a total of six years. Examination of long-term genetic trends (e.g. Macneil, 2009) reveals the possibility for short-term trends, such as those that are presented here, to be in the opposite direction of the

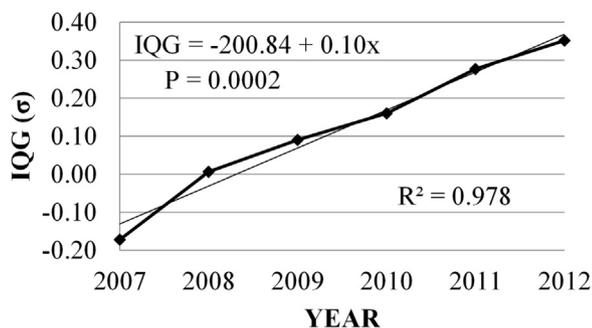


Fig. 1. Genetic trend in Hereford and Braford for the multi-trait index of genetic quality (IQG).

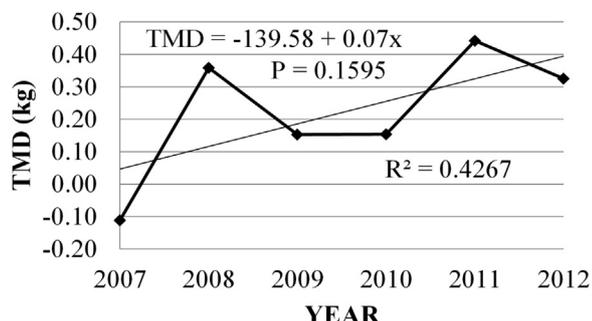


Fig. 2. Genetic trend in Hereford and Braford for total maternal 205-d weight (TMD).

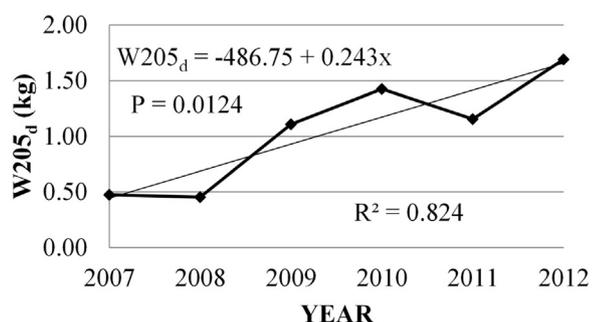


Fig. 3. Genetic trend in Hereford and Braford for direct effects on 205-d weight (W205_d).

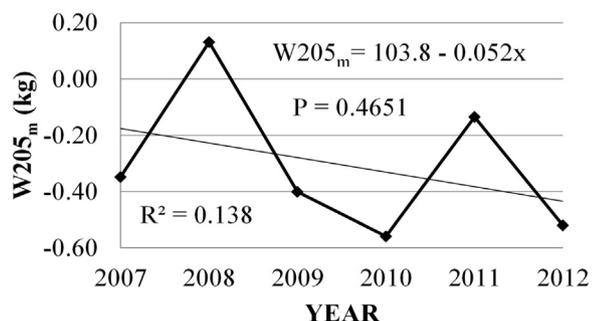


Fig. 4. Genetic trend in Hereford and Braford for maternal effects on 205-m weight (W205_m).

long-term trend simply by chance. Thus, the trends presented here are properly interpreted with a degree of caution.

For the IQG of PampaPlus, which is an empirical index with weights defined subjectively by the technician body of the program, the trend was positive ($P < 0.01$) with an annual gain of 0.1 standard deviation (Fig. 1). If the IQG is distributed normally, then 10 years of selection would be required to increase the aggregate genetic value by one standard deviation. Observed rates of response in the primary selection

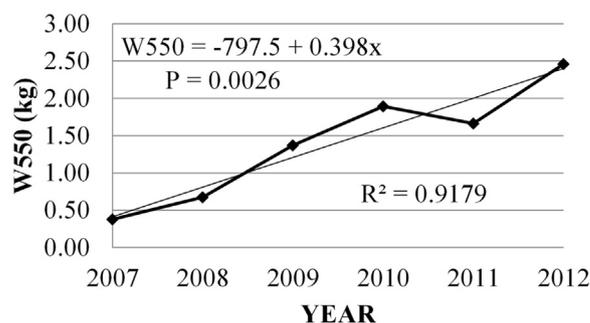


Fig. 5. Genetic trend in Hereford and Braford for direct effects on 550-d weight. (W550).

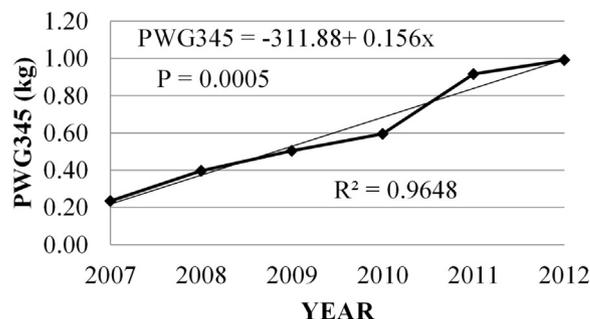


Fig. 6. Genetic trend in Hereford and Braford for direct effects on 345-d post weaning gain (PWG345).

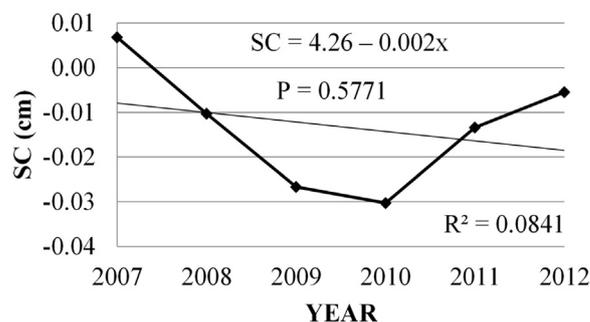


Fig. 7. Genetic trend in Hereford and Braford for direct effects on scrotal circumference (SC).

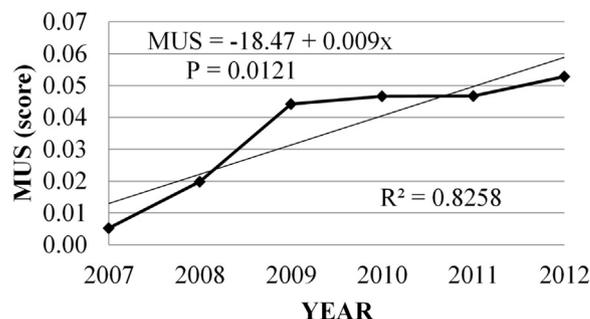


Fig. 8. Genetic trend in Hereford and Braford for direct effects on muscle score (MUS).

criteria (since, $TMD = 0.5W205_d + W205_m$ and $W550 = W205_d + PWG345$) were less than would be expected if selection of animals was exclusively based on the IQG (Table 5). For most traits, the observed response is on the order of 20% of that which would be expected. Thus, the IQG is not the only criterion that is being used by breeders. However, the expected relative gains demonstrate that IQG is an index focused on direct effects on growth with the highest gains expected for W205_d, MUS, FRA and PWG345.

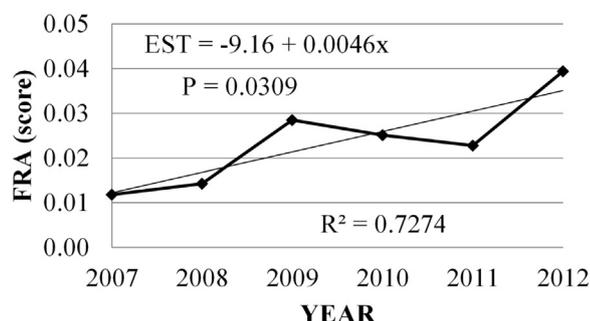


Fig. 9. Genetic trend in Hereford and Braford for direct effects on frame score (FRA).

Table 5

Expected (E)^a and realized (R) genetic gain (ΔG) per year for weaning weight direct (W205_d), weaning weight maternal (W205_m), 345-day post-weaning gain (PWG345), scrotal circumference at 550 days (SC), muscling score (MUS) and frame score (FRA) of Hereford and Braford cattle.

Parameter ^b	W205 _d	W205 _m	PWG345	SC	MUS	FRA
E(ΔG /year)	1.154	- 0.262	0.764	0.038	0.034	0.022
E(ΔG /year/ σ_g)	0.115	0.031	0.080	0.041	0.094	0.083
E(ΔG /year/ σ_g), %	26.0	6.9	17.9	9.1	21.3	18.8
R(ΔG /year)	0.232	- 0.052	0.156	- 0.002	0.009	0.0046
R(ΔG /year/ σ_g)	0.023	0.006	0.016	0.002	0.025	0.017
R(ΔG /year/ σ_g), %	25.7	6.8	18.1	2.4	27.7	19.3
R/E (ΔG /year), %	20.1	19.8	20.4	- 5.3	26.5	20.9

^a Adapted from Costa et al. (2017).

^b E(ΔG /year/ σ_g)/R(ΔG /year/ σ_g) is the annual expected/realized genetic gain per genetic standard deviation unit; %E(ΔG /year/ σ_g)/%R(ΔG /year/ σ_g) is the relative emphasis of the expected/realized gain for each trait; R/E (ΔG /year) is the proportion of the realized genetic gain compared to the expected gain.

The genetic trend in TMD was relatively flat (Fig. 2) and not significant ($P = 0.16$). The TMD combines W205_d and W205_m which trended in opposing directions (Figs. 3 and 4, respectively), although the trend in W205_m was not significant ($P = 0.47$). The genetic trend in W205_d was positive with an estimated annual increase ($P = 0.01$) of 243 g (Fig. 2). This result may be related to W205_d being the trait with the greatest amount of information in the program which began with calves born in 2012 and weaned in 2013. These calves may already have produced progeny that themselves have recorded data for many of the traits that are monitored in PampaPlus. However, the numbers of females with multiple progeny would be quite limited in the present data. In the face of the considerable genetic antagonism between direct and maternal effects on weaning weight that was observed here, their separate consideration in the IQG may be beneficial, particularly if it is deemed undesirable to reduce the maternal ability of the cows.

Among traits that were evaluated at the 550 days, both genetic trends for PWG345 and W550 increased significantly ($P < 0.05$) over the time-course evaluated. However, the genetic trend for SC was essentially zero ($P = 0.58$). Thus, while direct effects on objectively measured growth traits are increasing, the change in SC that was intended by the creators of the IQG has not occurred.

For the subjectively determined scores, positive ($P < 0.05$) genetic trends were observed for both MUS (Fig. 8) and FRA (Fig. 9). While the former trend is viewed as being desirable for the program, the latter is contrary to its intentions. Use of the absolute value and negative weighting or FRA in the IQG was intended to penalize extreme animals, either very large or very small. The goal of the IQG designers was to increase growth while maintaining moderate size. An alternative strategy to achieve this goal would be to develop a restricted selection index (Kemphthorne and Nordskog, 1959) that fixed genetic change in FRA at zero.

This analysis demonstrated that the empirically weighted index does indeed produce genetic change, but it may not be best for a profit

motivated producer. In fact, efficient selection for an economic objective should be based on selection index theory, preferably with EPD for economically relevant traits weighted by economic values (Henderson, 1963). Such an index would combine the EPD into a single valued criterion to serve as the basis for selection decisions (Hazel, 1943; Macneil et al., 1994). Simulation of an appropriate bioeconomic system can be used to derive the necessary economic weights (Macneil et al., 1994), rather than assigning these weights subjectively. Knowledge of the genetic covariances among all the selection criteria present in an index are also necessary in order to predict this expected genetic gain in Hereford and Braford, Costa et al. (2017) showed the greater economic profitability of proposed economic selection indexes in relation to the current empirical PampaPlus IQG.

Finally, current work for developing Brazilian Hereford and Braford population reference for genomic selection (Cardoso et al., 2015; Piccoli et al., 2017) may be integrated in local breeding programs to improve accuracy of predictions and consequently genetic gains obtained for these two breeds.

4. Conclusions

The genetic parameters found here are generally less than those reported in the literature, primarily due to inflated environmental variances. However, there is considerable genetic variability to be used in the selection. Physical control of the environmental variance is likely to entail greater educational efforts and infrastructure in rural areas where the cattle are produced. In the near term, variance components that are used in current PampaPlus genetic evaluations should be updated. Tools to guide breeders in making selection decisions in the form of indexes (such as the IQG) should be improved so as to facilitate accomplishment of their stated goals.

Conflicts of interest

None.

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