Genetic parameter estimates for carcass traits and visual scores including or not genomic information

Article · May 2016

DOI: 10.2527/jas2015-0134

CITATIONS
3

READS
97

13 authors, including:

Daniel Gm Gordo
Aarhus University
32 PUBLICATIONS **219** CITATIONS
SEE PROFILE

Rafael Espigolan
São Paulo State University
43 PUBLICATIONS **195** CITATIONS
SEE PROFILE

Rafael L Tonussi
São Paulo State University
27 PUBLICATIONS **226** CITATIONS
SEE PROFILE

Gerardo Alves Fernandes Júnior
São Paulo State University
37 PUBLICATIONS **95** CITATIONS
SEE PROFILE

Published April 8, 2016

Genetic parameter estimates for carcass traits and visual scores including or not genomic information[1]

D. G. M. Gordo,* R. Espigolan,* R. L. Tonussi,* G.A.F. Júnior,* T. Bresolin,* A. F. Braga Magalhães,* F. L. Feitosa,* F. Baldi,* R. Carvalheiro,* H. Tonhati,* H. N. de Oliveira,* L. A. L. Chardulo† and L. G. de Albuquerque,*[2,3]

*Faculdade de Ciências Agrárias e Veterinárias, Universidade Estadual Paulista, 14884-900, Jaboticabal (Sao Paulo), Brazil; and †Faculdade de Medicina Veterinária e Zootecnia, Universidade Estadual Paulista, 18618-970, Botucatu (Sao Paulo), Brazil

ABSTRACT: The objective of this study was to determine whether visual scores used as selection criteria in Nellore breeding programs are effective indicators of carcass traits measured after slaughter. Additionally, this study evaluated the effect of different structures of the relationship matrix (**A** and **H**) on the estimation of genetic parameters and on the prediction accuracy of breeding values. There were 13,524 animals for visual scores of conformation (CS), finishing precocity (FP), and muscling (MS) and 1,753, 1,747, and 1,564 for LM area (LMA), backfat thickness (BF), and HCW, respectively. Of these, 1,566 animals were genotyped using a high-density panel containing 777,962 SNP. Six analyses were performed using multitrait animal models, each including the 3 visual scores and 1 carcass trait. For the visual scores, the model included direct additive genetic and residual random effects and the fixed effects of contemporary group (defined by year of birth, management group at yearling, and farm) and the linear effect of age of animal at yearling. The same model was used for the carcass traits, replacing the effect of age of animal at yearling with the linear effect of age of animal at slaughter. The variance and covariance components were estimated by the REML method in analyses using the numerator relationship matrix (**A**) or combining the genomic and the numerator relationship matrices (**H**). The heritability estimates for the visual scores obtained with the 2 methods were similar and of moderate magnitude (0.23–0.34), indicating that these traits should response to direct selection. The heritabilities for LMA, BF, and HCW were 0.13, 0.07, and 0.17, respectively, using matrix **A** and 0.29, 0.16, and 0.23, respectively, using matrix **H**. The genetic correlations between the visual scores and carcass traits were positive, and higher correlations were generally obtained when matrix **H** was used. Considering the difficulties and cost of measuring carcass traits postmortem, visual scores of CS, FP, and MS could be used as selection criteria to improve HCW, BF, and LMA. The use of genomic information permitted the detection of greater additive genetic variability for LMA and BF. For HCW, the high magnitude of the genetic correlations with visual scores was probably sufficient to recover genetic variability. The methods provided similar breeding value accuracies, especially for the visual scores.

Key words: beef cattle, fat thickness, genetic correlation, heritability, longissimus muscle area, single nucleotide polymorphism

J. Anim. Sci. 2016.94
doi:10.2527/jas2015-0134

INTRODUCTION

In Brazil, visual scoring systems are used for the improvement of carcass traits in an attempt to identify individuals that exhibit finishing precocity, greater muscling, and better slaughter conformation. These traits have the advantage that they can be evaluated relatively early during the animal's life and do not require submitting the animals to laborious

[1]This work was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) grant numbers 2009/16118-5 and 2014/11537-8.

[2]Present address: Via de acesso Paulo Donato Castellane s/n. Departamento de Zootecnia. CEP: 14884-900, Jaboticabal, Sao Paulo, Brazil.

[3]Corresponding author: lgalb@fcav.unesp.br

Received November 25, 2015.
Accepted February 21, 2016.

measurements, rendering the process more agile and cost effective (Koury Filho et al., 2010).

Visual scores have been associated with growth, reproductive, and ultrasound-measured carcass traits (Yokoo et al., 2009, 2015; Boligon et al., 2012). However, few studies have investigated the relationship between visual scores and traits measured postmortem.

Although carcass traits measured postmortem are economically important, selection for these traits is still rarely performed because they are difficult to measure and depend on the slaughter of the animals and, consequently, on progeny testing for the evaluation of sires, thus delaying the selection process. In this respect, indirect selection for these traits through traits commonly used in selection programs, such as visual scores, may be an alternative.

In Brazil, large beef cattle herds are raised on pasture and the use of multiple-sire mating is common. As a result of this practice, the paternity of many offspring is unknown, a fact contributing to the "impoverishment" of the relationship matrix and, consequently, less accurate genetic parameter estimates.

In the single-step genomic BLUP (**ssGBLUP**) method proposed by Misztal et al. (2009) and Legarra et al. (2009), the traditional numerator relationship matrix is corrected by the genomic matrix and animals with phenotypes and known genotypes, as well as those not genotyped, can be included in the analysis. The application of the genomic matrix together with the traditional matrix to herds with high rates of unknown sires may improve estimation of the relationships between animals and, consequently, of genetic parameters.

The objectives of this study were to determine whether visual scores used as selection criteria in Nellore breeding programs are effective indicators of carcass traits measured after slaughter and to evaluate the effect of different structures of the relationship matrix (**A** and **H**) on the estimation of genetic parameters and on the prediction accuracy of breeding values.

MATERIAL AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from an existing database.

Data and Definition of Traits

The data were obtained from noncastrated Nellore males participating in 3 breeding programs (DeltaGen, Paint CRV Lagoa, and Nelore Qualitas). The animals were raised on pasture, and those destined for slaughter were finished in feedlots for about 90 d.

In the DeltaGen and Paint CRV Lagoa breeding programs, the animals were evaluated for visual scores of conformation (**CS**), finishing precocity (**FP**), and muscling (**MS**) at weaning and yearling. The animals were assessed by trained technicians according to the following procedure: first, the whole contemporary group (**CG**) is observed and the average profile of the CG is determined for each trait, which serves as a baseline. Scores ranging from 1 to 5 were then assigned to the traits of CS, FP, and MS, with 5 corresponding to the highest expression of the trait and 1 to the lowest expression. Conformation is influenced by the size of the animal (especially its length) and by the degree of muscularity. Finishing precocity is evaluated by the measurement of the ratio of rib depth to limb height and by the evidence of fat deposition in the groin and tail of the animal. In the case of MS, evidence of muscle mass at sites such as the shoulder, forearm, loin, rump, and rear is evaluated (Koury Filho et al., 2010). The visual scores used in the present study were obtained at yearling when the animals had a mean age of 506 d.

The following carcass traits were evaluated: HCW, LM area (**LMA**), and backfat thickness (**BF**). At slaughter, HCW was recorded for each animal. After a 24- to 48-h chill, the LM sections between 12/13th ribs were taken from the left side of the carcass and immediately frozen at −20°C for later analyses. Point counting on a plastic grid (where each square corresponds to 1 cm^2) was used to measure LMA, in which the grid was placed on the sample and the sum of all squares corresponds to the LMA of the animal. For the determination of BF, the layer of subcutaneous fat located at an angle of 45 degrees from the geometric center of the sample was measured in millimeters with a caliper. The mean age of the animals at slaughter was 735 ± 84 d.

The CG for all traits was defined by the effects of year, farm, and management group at yearling. The season effect was not included in the CG because the management groups were created within a season; therefore, the season effect is taken into account by the management group effect in CG. For the carcass traits, observations with 3 SD above or below the mean of their CG were excluded. The structure of the data is shown in Table 1.

Marker Genotypes

The animals were genotyped using the BovineHD BeadChip (Illumina, Inc., San Diego, CA), which contains 777,962 SNP markers distributed across the genome. For quality control of the genotypes, only SNP located on autosomes and with a GenCall score higher than 0.70 were used. Single nucleotide polymorphisms at the same genomic position and those with a minor allele frequency < 0.05 and a call rate < 0.90 were excluded. Individuals with a call rate < 0.90 were also eliminated. Finally, the correlation between

Table 1. Structure of the data file for carcass and visual scores in Nelore cattle

Trait[1]	No. of observations	No. of sires	No. of dams	Mean (SD) or mode[2]
LMA, cm^2	1,753	289	1,534	68.57 (8.58)
BF, mm	1,747	289	1,527	4.84 (2.60)
HCW, kg	1,564	244	1,432	277.92 (23.34)
CS	13,524	620	12,260	3
FP	13,524	620	12,260	3
MS	13,524	620	12,260	3

[1]LMA = LM area; BF = backfat thickness; CS = conformation; FP = finishing precocity; MS = muscling.

[2]Mode for visual scores.

SNP within a window of 100 markers was evaluated and 1 SNP of each highly correlated pair ($r^2 \geq 0.995$) was excluded from the analyses. After quality control, 1,634 animals and 369,590 SNP remained.

Quantitative Genetic Analysis

Six analyses using multitrait animal models were performed, with each model including the 3 visual scores and 1 of the carcass traits. For the visual scores, the model included the direct additive genetic and residual as random effects, the fixed effects of CG, and the linear effect of age of animal at yearling. The same model was used for the carcass traits, replacing the effect of age of animal at yearling with the linear effect of age of animal at slaughter.

The general model can be written in matrix form as follows:

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}\alpha + \mathrm{e},$$

in which **y** is the vector of the traits observed, β is the vector of fixed effects, α is the vector of genetic additive direct effects of the animal, **e** is the vector of residual effects, and **X** and **Z** are incidence matrices relating β, α, and **e** to **y**. In this study, it was assumed that E[y] = Xb, var(α) = A ⊗ $\mathbf{S}_a$ or var(α) = **H** ⊗ $\mathbf{S}_a$ and var(e) = **I** ⊗ $\mathbf{S}_e$, in which $\mathbf{S}_a$ is the additive genetic covariance matrix, $\mathbf{S}_h$ is the additive genetic covariance matrix combined with the genomic matrix, **S**e is the residual covariance matrix, **A** is the additive-genetic numerator relationship matrix, **H** is the additive-genetic relationship matrix based on pedigree and genomic information, **I** is the identity matrix, and ⊗ is the direct product between matrices. A pedigree containing the identification of the animal, sire, and dam with a total of 37,685 animals (after pruning) in the relationship matrix was used. The variance and covariance components were estimated by the REML method using the AIREMLF90 program (Misztal et al., 2002).

Table 2. Distribution of visual evaluation scores for conformation (CS), finishing precocity (FP), and muscling (MS) in 13,524 animals of Nellore breed

	Score				
Trait	1	2	3	4	5
CS	810	2,782	4,933	3,521	1,478
FP	924	2,675	4,677	3,448	1,800
MS	1,235	3,099	4,665	2,988	1,537

According to Aguilar et al. (2010), the inverse of **H** ($\mathbf{H}^{-1}$) can be obtained as follows:

$$\mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & \mathbf{G}^{-1} - \mathbf{A}_{22}^{-1} \end{bmatrix},$$

in which $\mathbf{A}^{-1}$ is the inverse of the pedigree-based relationship matrix, $\mathbf{G}^{-1}$ is the inverse of the genomic matrix, and $\mathbf{A}_{22}{}^{-1}$ is the inverse of the pedigree-based relationship matrix for genotyped animals. According to VanRaden (2008), matrix **G can be written as follows:**

$$\mathbf{G} = [(\mathbf{M} - \mathbf{P})(\mathbf{M} - \mathbf{P})']/[2\textstyle\sum_{j=1}^{m} p_j(1 - p_j)],$$

in which **M** is the allele-sharing matrix with *m* columns (*m* = total number of markers) and *n* lines (*n* = total number of genotyped animals) and **P** is a matrix containing the frequency of the second allele (p_j), expressed as 2_{pj}. $\mathbf{M}_{ij}$ is 0 if animal *i* genotyped for SNP *j* is homozygous for the first allele, 1 if it is heterozygous, and 2 if the genotype is homozygous for the second allele.

To facilitate inversion, the program AIREMLF90 uses, by default, a weighted **G** as proposed by VanRaden (2008): $\mathbf{G} = 0.95\mathbf{G}_0 + 0.05\mathbf{A}_{22}$. We also have conducted additional analyses without scaling **G** based on $\mathbf{A}_{22}$.

The accuracies of the breeding values were evaluated using the equations proposed by the Beef Improvement Federation (BIF, 2010).

RESULTS AND DISCUSSION

Although visual scores are categorical variables, a linear model was used for the estimation of genetic parameters because of the large number of phenotypic data available for these traits. The distribution of each visual score is shown in Table 2. Furthermore, Faria et al. (2010) obtained similar genetic parameter estimates for these traits using either a threshold or a linear model.

Heritability Estimates

The heritability estimates for the visual scores (Table 3) obtained with the 2 methods were similar and of moderate magnitude (0.23–0.34), indicating that these traits should respond to direct selection. The

Table 3. Variance components (SE) and heritability estimates for carcass and visual evaluation traits using different relationship matrices

Trait[1]	$\sigma_a^{2\,2}$	$\sigma_e^{2\,2}$	h^2
A[3]			
LMA, cm^2	7.38 (4.84)	47.95 (4.78)	0.13 (0.09)
BF, mm	0.26 (0.17)	3.33 (0.18)	0.07 (0.06)
HCW, kg	51.25 (16.74)	242.5 (16.97)	0.17 (0.03)
CS	0.27–0.33 (0.03–0.04)	0.66–0.70 (0.01–0.03)	0.28–0.34 (0.03)
FP	0.28–0.30 (0.03–0.05)	0.83–0.84 (0.01–0.04)	0.25–0.27 (0.03)
MS	0.26–0.30 (0.03–0.05)	0.85–0.87 (0.01–0.04)	0.23–0.26 (0.03)
H[4]			
LMA, cm^2	15.91 (3.62)	36.53 (3.34)	0.29 (0.06)
BF, mm	0.58 (0.12)	3.04 (0.13)	0.16 (0.05)
HCW, kg	67.25 (7.69)	225.13 (12.86)	0.23 (0.06)
CS	0.27–0.31 (0.03–0.04)	0.69–0.70 (0.01–0.03)	0.27–0.31 (0.03)
FP	0.29–0.32 (0.03–0.05)	0.82–0.83 (0.01–0.03)	0.26–0.28 (0.03)
MS	0.28–0.31 (0.02–0.04)	0.85–0.86 (0.01–0.03)	0.24–0.27 (0.03)

[1]LMA = LM area; BF = backfat thickness; CS = conformation; FP = finishing precocity; MS = muscling.

[2]$\sigma_a 2$ = additive genetic variance; σ_e^2 = residual variance.

[3]**A** = numerator relationship matrix.

[4]**H** = genomic matrix combined with the numerator relationship matrix.

Table 4. Genetic covariances (SE) between visual evaluation and carcass traits using different relationship matrices

Trait[1]	CS[2]	FP[2]	MS[2]
A[3]			
LMA, cm^2	0.26 (0.37)	0.42 (0.38)	0.41 (0.37)
BF, mm	0.06 (0.01)	0.07 (0.02)	0.08 (0.02)
HCW, kg	3.28 (0.53)	1.68 (0.43)	1.81 (0.43)
H[4]			
LMA, cm^2	0.42 (0.21)	0.74 (0.24)	0.91 (0.24)
BF, mm	0.16 (0.01)	0.19 (0.02)	0.16 (0.03)
HCW, kg	2.80 (0.34)	1.63 (0.37)	1.59 (0.37)

[1]LMA = LM area; BF = backfat thickness.

[2]CS = conformation; FP = finishing precocity; MS = muscling.

[3]**A** = numerator relationship matrix.

[4]**H** = genomic matrix combined with the numerator relationship matrix.

estimates were probably similar because the number of animals with phenotypes was expressively higher than the number of genotyped animals and the inclusion of genomic data did not add sufficient information to change these estimates.

On the other hand, the heritabilities for the carcass traits estimated with the ssGBLUP method were higher than those obtained with BLUP. These results agree with those reported by Onogi et al. (2014), who also estimated variance components using BLUP and ssGBLUP and obtained higher genetic variance and heritability estimates for HCW and LMA with ssGBLUP. In the present study, the addition of genomic information to matrix **A** also resulted in higher additive genetic variance estimates with lower SE for the carcass traits, that is, for the traits with a smaller number of observations.

When BLUP was used, the heritability estimates for the carcass traits were of low magnitude (0.07–0.17). In contrast, the use of ssGBLUP provided moderate heritabilities for LMA and HCW (Table 3). More expressive increases in additive genetic variance were observed for LMA and BF (about 2 times higher) when matrix **H** was used instead of matrix **A**. For HCW, the ssGBLUP method also detected greater genetic variation (30%) than BLUP. The smaller increase in additive genetic variance observed for HCW compared with the other carcass traits may be due to the high genetic correlation between this trait and the visual scores (Table 4 and 5) observed in the BLUP method. Therefore, the analysis of HCW was benefited by the large number of data available for the visual scores.

The heritability estimates for LMA obtained here with the 2 methods were lower than those reported in the literature for Zebu animals using matrix **A**, which ranged from 0.35 to 0.63 (Riley et al., 2002; Smith et al., 2007; Rezende et al., 2009). On the other hand, Tizioto et al. (2013) reported a heritability similar to that found in the present study (0.27) using the genomic relationship matrix. A possible reason for the lower heritability estimates found in this paper in comparison with those reported in the literature may be due to the commercial animals studied, which were probably submitted to greater variability of environmental conditions in comparison with those raised in trial stations.

For HCW, the heritability estimates were of low (BLUP) or moderate (ssGBLUP) magnitude (Table 3) and lower than those obtained by Riley et al. (2002) for Brahman animals (0.55). Studying Nellore animals, Rezende et al. (2009) reported a higher heritability (0.38) than that observed in the present study. On the other hand, Ferriani et al. (2013) obtained a similar heritability (0.20 ± 0.08) for animals of the same breed.

Although the ssGBLUP method provided an important increase in the additive genetic variance of BF, the heritability estimates obtained with the 2 methods were of low magnitude and lower than those reported by Riley et al. (2002) and Rezende et al. (2009; 0.63 and 0.52, respectively). However, the heritability obtained when the numerator relationship and genomic matrices were combined (matrix **H**) was similar to that reported by Tizioto et al. (2013) for Nellore animals (0.21).

In the present study, 618 individuals with information for the carcass traits were animals with unknown sires. To verify if the difference in the genetic parameter estimates using matrix **A** and **H** was due to the animals with unknown sires, we also have conducted additional analyses including only the animals with both sire and dam information. We found that the genetic

Table 5. Genetic correlations (SE) between visual evaluation and carcass traits estimated by the numerator relationship matrix (**A**) and the genomic matrix combined with the numerator relationship matrix (**H**)

Trait[1]	CS[2]	FP[2]	MS[2]
A			
LMA, cm^2	0.18 (0.39)	0.31 (0.50)	0.30 (0.47)
BF, mm	0.22 (0.65)	0.28 (0.74)	0.25 (0.68)
HCW, kg	0.80 (0.13)	0.41 (0.17)	0.44 (0.17)
H			
LMA, cm^2	0.20 (0.15)	0.35 (0.15)	0.43 (0.16)
BF, mm	0.39 (0.37)	0.47 (0.63)	0.41 (0.39)
HCW, kg	0.67 (0.14)	0.39 (0.18)	0.38 (0.17)

[1]LMA = LM area; BF = backfat thickness.

[2]CS = conformation; FP = finishing precocity; MS = muscling.

Table 6. Average accuracy estimates for breeding values using different relationship matrices

Trait[1]	Full pedigree	Young males	Females
A[2]			
LMA	0.17	0.26	0.14
BF	0.23	0.25	0.22
HCW	0.42	0.45	0.28
H[3]			
LMA	0.30	0.32	0.26
BF	0.26	0.27	0.27
HCW	0.47	0.54	0.42

[1]LMA = LM area; BF = backfat thickness.

[2]**A** = numerator relationship matrix.

[3]**H** = genomic matrix combined with the numerator relationship matrix.

parameter estimates were close to those obtained when the 618 animals with unknown sires were used (results not shown). Therefore, the numerator relationship matrix did not represent the existing relationship between animals, compromising the estimation of genetic variability for the carcass traits. The addition of genomic information to the numerator relationship matrix contributed to correcting matrix **A** and therefore captured a higher proportion of the genetic variance.

An important finding of the present study was that the variance components and their respective SE obtained when matrix **G** was not scaled based on matrix $\mathbf{A}_{22}$ were similar to those obtained when matrix **G** was scaled based on matrix $\mathbf{A}_{22}$.

Genetic Correlations

The covariances and genetic correlations between the visual scores and carcass traits were positive and generally higher when the ssGBLUP method was used (Tables 4 and 5). These results suggest that long-term selection for higher visual scores should lead to an increase in carcass traits measured postmortem, especially HCW.

Using either method, the genetic correlations between the visual scores and LMA were of moderate magnitude. The highest genetic correlation was observed between MS and LMA. This result is expected because the objective of visual evaluation of MS is to identify evidence of muscle mass in the animal, whereas LMA is related to carcass cut yield. In a previous study using matrix **A**, Gordo et al. (2012) reported similar results, with genetic correlations of 0.39, 0.37 and 0.44 between LMA (in vivo) with body structure (which corresponds to CS of this study), FP, and MS, respectively.

Regarding BF, the genetic correlations with CS, FP, and MS were of moderate magnitude. Matrix **H** permitted the detection of a higher proportion of genetic covariation between the scores and BF (Table 4). The highest genetic correlation was observed with FP, which measures the capacity of the animal to reach the minimum degree of carcass finishing at a nonelevated BW. Similar positive and moderate genetic correlations of BF (in vivo) with FP and MS in Nellore animals have been described by Yokoo et al. (2009) and Gordo et al. (2012), ranging from 0.33 to 0.40. Koch et al. (2004), studying Hereford animals, reported a low genetic correlation of 0.09 between MS and BF.

The 2 methods provided moderate to high genetic correlations between the visual scores and HCW (Table 5). As expected, the highest correlation was obtained with CS. According to Koury Filho et al. (2010), phenotypically, CS scores estimate the amount of meat in the carcass at slaughter of the animal and a higher correlation with HCW is therefore expected.

Muscling scores measure evidence of muscle mass in the animals, and muscles are the main components of carcass weight. The genetic correlation between MS and HCW obtained in the present study was higher than that reported by Koch et al. (2004) for Hereford animals (0.27). Similarly, Bonfatti et al. (2013) found a low genetic association between shoulder muscularity and HCW (0.11).

The SE of the genetic covariances were lower for the ssGBLUP method compared with BLUP. One explanation for this finding is the fact that matrix **H** improves the relationship coefficients and, consequently, additive-genetic relationships. The higher proportion of multiple sires for animals with observations for the carcass traits in relation to the general database leads to impoverishment of the numerator relationship matrix and consequently increases the difficulty in estimating genetic variances and covariances.

Although the genetic correlations between the visual scores and carcass traits were moderate, considering the difficulty and cost of obtaining these traits postmortem, visual scores could be used as criteria for selecting these traits.

Accuracies of Breeding Values

Table 6 shows the accuracies of the breeding values. For the carcass traits, the addition of genomic information resulted in a slight increase in accuracies. The 2 methods provided similar accuracies of breeding values for the visual scores of both young males (up to 2 yr) and females (data not shown). This finding is probably due to the larger number of available information and known parents for the visual scores than the animals with phenotypic data for carcass traits. It should be noted that the number of genotyped animals is small compared with the database of phenotypes for the visual scores. Using a larger number of genotyped animals, these results may show more important differences.

Conclusions

The visual scores of conformation, finishing precocity and muscling can be used as selection criteria to improve HCW, backfat thickness, and LM area. If available, genomic information should be included in the analyses for the estimation of variance and covariance components and breeding values, especially when the number of observations for the trait is small and the percentage of unknown sires is high.

LITERATURE CITED

Aguilar, I., I. Misztal, D. L. Johnson, A. Legarra, S. Tsuruta, and T. J. Lawlor. 2010. A unified approach to utilize phenotypic, full pedigree, and genomic information for genetic evaluation of Holstein final score. J. Dairy Sci. 93:743–752. doi:10.3168/jds.2009-2730

Beef Improvement Federation. 2010. Guidelines for Uniform Beef Improvement Programs. 9th ed. Beef Improv. Fed., Raleigh, NC.

Boligon, A. A., D. R. Ayres, R. J. Pereira, N. P. Morotti, and L. G. Albuquerque. 2012. Genetic associations of visual scores with subsequent rebreeding and days to first calving in Nellore cattle. J. Anim. Breed. Genet. 129:448–456 doi:10.1111/j.1439-0388.2012.00998.x

Bonfatti, V., A. Albera, and P. Carnier. 2013. Genetic associations between daily BW gain and live fleshiness of station-tested young bulls and carcass and meat quality traits of commercial intact males in Piemontese cattle. J. Anim. Sci. 91:2057–2066. doi:10.2527/jas.2012-5386

Faria, C. U., B. C. Pires, A. P. Vozzi, C. U. Magnabosco, W. Koury Filho, M. A. O. Viu, H. N. Oliveira, and R. B. Lôbo. 2010. Genetic correlations between categorical morphological traits in Nelore cattle by applying Bayesian analysis under a threshold animal model. J. Anim. Breed. Genet. 127:377–384. doi:10.1111/j.1439-0388.2010.00860.x

Ferriani, L., L. G. Albuquerque, F. S. B. Baldi, G. C. Venturini, A. B. Bignardi, J. A. II V. Silva, T. C. S. Chud, D. P. Munari, and J. A. Oliveira. 2013. Parâmetros genéticos de características de carcaça e de crescimento de bovinos da raça Nelore. (In Portuguese.) Arch. Zootec. 62:123–129. doi:10.4321/S0004-05922013000100013

Gordo, D. G. M., F. Baldi, R. B. Lôbo, W. Koury Filho, R. D. Sainz, and L. G. Albuquerque. 2012. Genetic association between body composition measured by ultrasound and visual scores in Brazilian Nelore cattle. J. Anim. Sci. 90:4223–4229. doi:10.2527/jas.2011-3935

Koch, R. M., L. V. Cundiff, K. E. Gregory, and L. D. Van Vleck. 2004. Genetic response to selection for weaning weight or yearling weight or yearling weight and muscle score in Hereford cattle: Efficiency of gain, growth, and carcass characteristics. J. Anim. Sci. 82:668–682.

Koury Filho, W., L. G. Albuquerque, S. Forni, J. A. II V. Silva, M. J. I. Yokoo, and M. M. Alencar. 2010. Estimativas de parâmetros genéticos para os escores visuais e suas associações com peso corporal em bovinos de corte. (In Portuguese.) Rev. Bras. Zootec. 39:1015–1022. doi:10.1590/S1516-35982010000500011

Legarra, A., I. Aguilar, and I. Misztal. 2009. A relationship matrix including full pedigree and genomic information. J. Dairy Sci. 92:4656–4663. doi:10.3168/jds.2009-2061

Misztal, I., A. Legarra, and I. Aguilar. 2009. Computing procedures for genetic evaluation including phenotypic, full pedigree, and genomic information. J. Dairy Sci. 92:4648–4655. doi:10.3168/jds.2009-2064

Misztal, I., S. Tsuruta, T. Strabel, B. Auvray, T. Druet, and D. H. Lee. 2002. BLUPF90 and related programs (BGF90). In: Proc. 7th World Cong. Genet. Appl. Livest. Prod., Montpellier, France. Communication no. 28–07.

Onogi, A., A. Ogino, T. Komatsu, N. Shoji, K. Simizu, K. Kurogi, T. Yasumori, K. Togashi, and H. Iwata. 2014. Genomic prediction in Japanese black cattle: Application of a single-step approach to beef cattle. J. Anim. Sci. 92:1931–1938. doi:10.2527/jas.2014-7168

Rezende, F. M., J. B. S. Ferraz, E. Groeneveld, G. B. Mourão, P. S. Oliveira, M. N. Bonin, and J. P. Eler. 2009. Estimation of genetic and phenotypic parameters for meat and carcass trait in Nellore bulls. In: Proc. 60th Annu. Meet. Eur. Fed. Anim. Sci., Barcelona, Spain. p. 20.

Riley, D. G., C. C. Chase, A. C. Hammond, R. L. West, D. D. Johnson, T. A. Olson, and S. W. Coleman. 2002. Estimated genetic parameters for carcass traits of Brahman cattle. J. Anim. Sci. 80:955–962.

Smith, T., J. D. Domingue, J. C. Paschal, D. E. Franke, T. D. Bidner, and G. Whipple. 2007. Genetic parameters for growth and carcass traits of Brahman steers. J. Anim. Sci. 85:1377–1384. doi:10.2527/jas.2006-653

Tizioto, P. C., J. E. Decker, J. F. Taylor, R. D. Schnabel, M. A. Mudadu, F. L. Silva, G. B. Mourao, L. L. Coutinho, P. Tholon, T. S. Sonstergard, A. N. Rosa, M. M. Alencar, R. R. Tulio, S. R. Medeiros, R. T. Nassu, G. L. D. Feijó, L. O. C. Silva, R. A. Torres, F. Siqueira, R. H. Higa, and L. C. A. Regitano. 2013. Genome scan for meat quality traits in Nelore beef cattle. Physiol. Genomics 45:1012–1020. doi:10.1152/physiolgenomics.00066.2013

VanRaden, P. M. 2008. Efficient methods to compute genomic predictions. J. Dairy Sci. 91:4414–4423. doi:10.3168/jds.2007-0980

Yokoo, M. J., R. B. Lôbo, C. U. Magnabosco, G. J. M. Rosa, S. Forni, R. D. Sainz, and L. G. Albuquerque. 2015. Genetic correlation of traits measured by ultrasound at yearling and 18 months of age in Nellore beef cattle. Livest. Sci. 180:34–40. doi:10.1016/j.livsci.2015.07.003

Yokoo, M. J. I., J. N. Werneck, M. C. Pereira, and L. G. Albuquerque. 2009. Correlações genéticas entre escores visuais e características de carcaça medidas por ultrassom em bovinos de corte. (In Portuguese.) Pesqi. Agropecu. Bras. 44:197–202.