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Genetic parameters for fatty acids in intramuscular fat from feedlot-finished Nelore carcasses

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Abstract. The aim of the present study was to estimate covariance components and genetic parameters for beef fatty acid (FA) composition of intramuscular fat in the *longissimus thoracis* muscle in Nelore bulls finished in feedlot. Twenty-two FAs were selected. The heritability estimates for individual FAs ranged from 0.01 to 0.35. The heritability estimates for myristic (0.25 ± 0.09), palmitic (0.18 ± 0.07), oleic (0.28 ± 0.09), linoleic (0.16 ± 0.06) and α -linolenic (0.35 ± 0.10) FAs were moderate. Stearic, elaidic, palmitoleic, vaccenic, conjugated linoleic acid, docosahexanoic, eicosatrienoic and arachidonic FAs had heritability estimates below 0.15. The genetic-correlation estimates between the individual saturated FAs (SFAs) were low and negative between myristic and stearic FAs (-0.22 ± 0.84), moderate between palmitic and myristic FAs (0.58 ± 0.56) and negative between palmitic and stearic FAs (-0.69 ± 0.45). The genetic correlations between the individual long-chain polyunsaturated FAs (PUFAs) were positive and moderate (>0.30). However, the genetic-correlation estimates between long-chain PUFAs and α -linolenic acid were low (<0.30), except for the correlation between arachidonic and α -linolenic acids. The genetic correlation estimates of the sums of SFAs with monounsaturated fatty acids and omega 6 FAs were low (0.25 ± 0.59 and -0.02 ± 0.51 respectively), high with PUFAs and omega 9 FAs (-0.85 ± 0.15 and 0.86 ± 0.17 respectively) and moderate with omega 3 FAs (-0.67 ± 0.26). The present study demonstrated the existence of genetic variation and, hence, the possibility to increase the proportion of healthy and favourable beef FAs through selection. The results obtained in the study have provided knowledge to elucidate the additive genetic influence on FA composition of intramuscular fat. In addition, genetic-relationship estimates of intramuscular FA profile help seek strategies for genetic selection or genetic-based diet management to enhance the FA profile in Zebu cattle.

Additional keywords: genetic correlation, genetic variation, heritability, lipid composition, marbling, meat quality, Zebu cattle.

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Introduction

The two main strategies to change meat fatty acid (FA) composition are through genetic manipulation (selection and crossbreeding) and changes in production conditions, such as diet and management decisions (Wood and Enser 1997; Chung

et al. 2007). The majority of studies aiming to estimate genetic parameters for meat FA profile have been conducted on *Bos taurus* breeds and their crosses, with heritability ranging from 0.00 to 0.78 (i.e. Malau-Aduli *et al.* 2000; Pitchford *et al.* 2002; Tait *et al.* 2007; Nogi *et al.* 2011; Ekine-Dzivenu *et al.*

2014). Cesar *et al.* (2014) recently applied the genomic relationship matrix (GBLUP) model and estimated null to moderate heritabilities (0.0–0.46) for meat FA profile in Nelore. According with De Smet *et al.* (2004) and Inoue *et al.* (2011), it is difficult to compare genetic parameter estimates for FA profile obtained in different studies because the genetic variation may be influenced by the differences in enzyme activities related to FA desaturation and by the differences in the degree of animal fattening.

The Zebu breeds are the predominant source of beef in tropical and subtropical regions. Therefore, the results obtained in the present study should indicate whether there is genetic variability for FA profile of intramuscular fat and whether selection is feasible to decrease harmful FA and increase health beneficial FA. Moreover, it is important to understand the genetic relationships within the intramuscular FA profile, so as to elucidate the physiological and metabolic bases that control their composition in Zebu cattle under tropical conditions. The aim of the present study was to estimate covariance components and genetic parameters of beef FA composition of intramuscular fat in the *longissimus thoracis* muscle in Nelore bulls finished in feedlot.

Materials and methods

Animal and management

In total, 963 Nelore bulls finished in a feedlot for a mean feeding days of 120 days (minimum 90 and maximum 150 days), and slaughtered at an average of 24 months of age, were used. The animals belonged to eight different farms located in the south-eastern, north-eastern and mid-western regions of Brazil, which participated in three beef-cattle breeding programs (Nelore Qualitas, Paint and DeltaGen). In these breeding programs, animals were selected on the basis of growth, finishing and sexual-precocity traits.

Breeding seasons were adopted at different periods on these farms. Therefore, calving seasons concentrated from August to October in some farms and from November to January in others, and weaning was performed at 7 months of age. The animals were raised under grazing conditions using *Brachiaria* sp. and *Panicum* sp. as forage, and were given free access to mineral salt. After 1 year of age, the breeding animals were selected and the rest remained in feedlot. During feedlotting, the forage : concentrate ratio ranged from 50 : 50 to 70 : 30, depending on the farm. In general, whole-plant corn or sorghum silage was used as a high-quality forage. Grains of corn and sorghum, and soybeans, soybean meal, or sunflower seeds were used as protein concentrate. The criterion used by farmers for slaughtering the animals was weight (500–550 kg). The descriptive statistics for hot carcass weight and backfat thickness level are shown in Table 1.

Slaughter was undertaken in commercial slaughterhouses (22 kill groups), in accordance with the Brazilian Federal Inspection Service procedures. After 48 h, at 0–2°C, the samples were removed from the *longissimus thoracis* muscle (at least 3.0 kg, including muscle and bone), from between the 12th and 13th ribs from each animal. Samples were placed in airtight plastic bags and stored at –80°C. The percentage of

intramuscular fat in the *longissimus thoracis* muscle was obtained by the method proposed by Bligh and Dyer *et al.* (1959).

Genotyping of animals

In total, 1616 animals were genotyped with a high-density single-nucleotide polymorphism (SNP) chip (Illumina High-Density Bovine BeadChip, 777 000; BovineHD BeadChip assay; 700k, Illumina Inc., San Diego, CA, USA). These animals were feedlot bulls, and some of them were half-sibs of animals with FA records. The SNP markers located on sex chromosomes, monomorphic, with unknown genomic position, and minor allele frequency of <0.05, call rate <90%, and markers with excess heterozygosity, as well as samples with a call rate <90%, were not considered in the analysis. After the SNP quality control, 470 007 SNPs were available for 1556 samples.

FA analysis

Muscle samples were collected, freeze-dried and ground for FA analyses. The beef FAs were extracted from intramuscular fat of the *longissimus thoracis* muscle by using the method described in Folch *et al.* (1957). Lipids were extracted by homogenising the sample with a chloroform–methanol (2 : 1) solution. Sodium chloride (NaCl) at 1.5% was added and the lipids were isolated. The fat extracted was methylated and the methyl esters were formed according to Kramer *et al.* (1997).

Fatty acid analysis in meat was performed at the Meat Science Laboratory (LCC) in the Department of Animal Nutrition and Production at FMVZ/USP, Pirassununga, Brazil. FAs were quantified by gas chromatography (GC-2010 Plus, Shimadzu AOC 20i auto-injector, Tokyo, Japan) using a SP-2560 capillary column (100 m × 0.25 mm in diameter with 0.02-mm thickness, Supelco, Bellefonte, PA, USA). The initial temperature was 70°C, and was then gradually increased (13°C/min) up to 175°C, where it was held for 27 min, until further increasing at a rate of 4°C/min until it reached 215°C, where it was held for 31 min. Hydrogen (H₂) was used as the gas flow at 40 cm³/s. FAs were identified by comparison of retention times of methyl esters of the samples with those of the FA standard C4–C24 (FAME mix, Sigma, Bellefonte, PA, USA), vaccenic acid: C18:1 t11 (V038-1G, Sigma), conjugated linoleic acid (CLA): C18:2 trans-10 cis-12 (UC-61M 100 mg), CLA: C18:2 cis-9 trans-11 (UC-60M 100 mg) and tricosanoic acid (Sigma). FAs were quantified by normalising the area under the curve of methyl esters by using the GS solution 2.42 software. FA concentrations were expressed as a percentage of total FA methyl esters (FAMES) quantified. Twenty FAs (16 individual FAs and 6 groups of FAs) were selected (Table 1).

Quantitative genetic analysis

The contemporary groups (CGs) included animals born on the same farm and in the same year, and from the same management group at yearling. The CGs with fewer than three records were eliminated from the analysis. Records exceeding three standard deviations above or below the mean of each CG were excluded. After data editing, a total of 937 animals with records for beef FA profile remained in the dataset. The model used for the covariance and genetic-parameter estimation included the

Table 1. Descriptive statistics for hot carcass weight (HCW), backfat thickness (BFT), intramuscular fat percentage (IMF), profile of the individual saturated (SFAs), monounsaturated (MUFAs), polyunsaturated (PUFAs) and conjugated linolenic (CLAs) fatty acids and for the total SFAs, MUFAs, PUFAs, omega 3 (n3), omega 6 (n6) and omega 9 (n9), expressed as a percentage of total fatty acid methyl esters, in *longissimus thoracis* muscle from Nelore cattle

The concentration of fatty acids are expressed as a percentage of total fatty acid methyl esters (FAMES) quantified. Total SFAs, C4:0+C6:0+C8:0+C10:0+C11:0+C12:0+C13:0+C14:0+C15:0+C16:0+C17:0+C18:0+C21:0+C24:0; total MUFAs, C16:1+C17:1 c10+C18:1 t11+C15:1 c10+C20:1 c11+C24:1+C22:1 n9+C18:1 n9c+C14:1+C18:1 n9t, total PUFAs, C18:2 n6+C18:3 n3+C18:3 n6+C20:3 n3 cis-8,11,14 (ETE)+C20:3 n6 cis-11,14,17 (DGLA)+C20:4 n6+C20:5 n3+C22:6 n3; n3, C18:3 n3+C20:3 n3 cis-11,14,17+C22:6 n3+C20:5 n3; n6, C18:3 n6+C20:3 n6 cis-8,11,14+C18:2 n6+C20:4 n6; and n9, C18:1 n9c+C18:1 n9t+C24:1 n9+C22:1 n9. s.d., standard deviation

Trait ^A	Nomenclature	Mean	s.d.	Min.	Max.
HCW (kg)		278.0	24.0	145.0	370.0
BFT (mm)		4.90	2.7	1.0	23.0
IMF (%)		0.83	0.42	0.12	3.61
	<i>SFA</i>				
Myristic	C14:0	2.13	0.54	0.66	4.39
Palmitic	C16:0	21.03	2.49	6.85	29.94
Stearic	C18:0	12.56	4.88	0.00	25.86
	<i>MUFA</i>				
Myristoleic	C14:1	0.31	0.22	0.00	2.08
Palmitoleic	C16:1	2.18	0.79	0.16	4.91
Elaidic	C18:1 n9t	1.92	4.46	0.00	21.6
Oleic	C18:1 n9c	30.6	4.98	15.81	44.9
Vaccenic	C18:1 t11	1.29	0.94	0.14	5.67
	<i>PUFA</i>				
Linoleic	C18:2 n6	8.32	3.63	1.14	21.85
Linolenic	C18:3 n6	0.59	0.26	0.00	2.25
Eicosatrienoic (ETE)	C20:3 n3 cis-8,11,14	0.49	0.19	0.00	1.81
Dihomo-gamma-linolenic (DGLA)	C20:3 n6 cis-11,14,17	2.00	0.77	0.00	4.75
α-Linolenic	C18:3 n3	0.89	2.61	0.00	15.29
Docosahexaenoic	C22:6 n3	0.95	0.39	0.00	2.50
Arachidonic	C20:4	1.11	3.14	0.01	26.03
	<i>CLA</i>				
CLA	C18:2 c9 t11	0.22	0.13	0.00	0.66
	<i>Total</i>				
Total SFAs		40.66	6.12	2.56	52.36
Total MUFAs		37.55	8.05	3.75	64.93
Total PUFAs		13.42	5.57	2.07	37.62
n3		3.81	1.55	0.24	11.36
n6		9.35	4.44	0.74	33.87
n9		18.68	14.24	0.14	45.79

random genetic additive effects, the fixed effects of the CG, and the age of the animal at slaughter as a covariable (linear and quadratic effects).

The genetic correlations were estimated by two-trait analysis between the 16 individual FAs, and also between six groups of FAs (sums of saturated FAs (SFA), monounsaturated FAs (MUFAs), polyunsaturated FAs (PUFAs), omega 9, omega 6 and omega 3). The heritability and variance-component (residual and genetic additive variance) estimates for each FA were obtained by one-trait analysis. The covariances and genetic parameters were estimated using the restricted maximum likelihood method, by using the Remlf90 and Airemlf90 softwares (Misztal *et al.* 2002) and considering an animal model (single-step genomic BLUP, ssGBLUP). Initially, the Remlf90 (EM-algorithm) software was applied until the analysis converged, then the covariance estimates obtained by Remlf90

software were utilised as starting values for Airemlf90 (AI-algorithm) software. The ssGBLUP model is a modification of BLUP with the numerator relationship matrix \mathbf{A}^{-1} replaced by \mathbf{H}^{-1} (Aguilar *et al.* 2010), as follows:

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

where \mathbf{A}_{22} is a numerator-relationship matrix for genotyped animals and \mathbf{G} is a genomic-relationship matrix. The single-step GBLUP procedure allows to incorporate into the analysis all information available, including those from genotyped and ungenotyped animals. Thus, it is not necessary that the number of animals with phenotypic records, genotypes and pedigree are the same. The genomic matrix (\mathbf{G}) was calculated following VanRaden *et al.* (2009), as follows:

$$\mathbf{G} = \mathbf{ZDZ}^T q, \quad (2)$$

where \mathbf{Z} is a matrix of gene content adjusted for allele frequencies, \mathbf{D} is a weight matrix for SNP (initially $\mathbf{D} = \mathbf{I}$) and q is a weighting factor. According to Vitezica *et al.* (2011), the normalising factor can be derived by ensuring that the average diagonal in \mathbf{G} is close to that of \mathbf{A}_{22} .

For the traits, the model can be represented by the following matrix form:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{a} + \mathbf{e}, \quad (3)$$

where \mathbf{y} is the vector of observations, $\boldsymbol{\beta}$ is the vector of fixed effects, \mathbf{a} is vector of direct additive genetic effects, \mathbf{X} is known incidence matrix, \mathbf{Z} is incidence matrix of the random additive direct genetic effect (associates vector $\boldsymbol{\beta}$ with vector \mathbf{y}) and \mathbf{e} is the vector of the residual effect. It was assumed that $\mathbf{E}[\mathbf{y}] = \mathbf{X}\boldsymbol{\beta}$; $\text{Var}(\mathbf{a}) = \mathbf{H} \otimes \mathbf{S}\mathbf{a}$ and $\text{Var}(\mathbf{e}) = \mathbf{I} \otimes \mathbf{S}\mathbf{e}$, where $\mathbf{S}\mathbf{a}$ is the covariance matrix for the additive genetic effect, $\mathbf{S}\mathbf{e}$ is covariance matrix for residual effect, \mathbf{H} is relationship matrix, \mathbf{I} is identity matrix and, \otimes is Kronecker product.

The standard deviation of genetic parameters was calculated as an alternative to the standard error. The standard deviation was obtained by repeatedly sampling parameter estimates from their asymptotic multivariate normal distribution, following the idea presented by Meyer and Houle (2013). The Airemlf90 software (Miszta *et al.* 2002) has an option to estimate the standard deviation for functions of covariances (heritability and genetic correlations). The pedigree file contained the identifications of the animal, sire and dam, with a total of 2873 animals (after pruning) in the relationship matrix. The data file contained 937 animals, including 131 sires and 899 cows, with progeny presenting phenotypic data for FA profile.

Results and discussion

The percentage of lipids in the *longissimus thoracis* muscle (Table 1) was lower than those reported by Holloway *et al.* (1990), Huerta-Leidenz *et al.* (1996) and Newman *et al.* (2002) and Cesar *et al.* (2014) for *Bos taurus*, *Bos indicus* and their crossbreds, also finished in feedlot. It is important to highlight, that the animals used in the present experiment were not castrated (bulls) and received a diet with a moderate energy content, since the forage: concentrate ratio ranged from 50 : 50 to 70 : 30 in the farms, resulting in a low percentage of lipid in beef. The descriptive statistics for the profile of the most relevant individual SFAs, MUFAs, CLA cis9 trans11 and PUFAs and for the sums of the SFAs, MUFAs and PUFAs, omega 3, omega 6 and omega 9 are presented in Table 1.

Our mean concentrations agreed with those reported by Prado *et al.* (2003), Kelly *et al.* (2013) and Cesar *et al.* (2014) who also observed palmitic, stearic and oleic FAs at the highest concentrations, although in different proportions (Table 1). These differences observed by the authors could be due to the different degrees of carcass adipose tissue (Prado *et al.* 2003; Wood and Enser, 1997), since lower fat deposition can result in a higher polyunsaturated acid and lower oleic acid deposition (Rule *et al.* 1997). The individual MUFAs and PUFAs with the highest concentrations were oleic (C18:1 n9), vaccenic (C18:1 t11) and linoleic (C18:2 n6) acids (Table 1). In a

study using samples from *longissimus* muscle, Ekine-Dzivenu *et al.* (2014) reported higher and lower concentrations for oleic (40.13%) and vaccenic (0.54%) acids, respectively, than those obtained in the present study. Comparing with other studies, the concentration of linoleic FA obtained in the present study was also relatively high (8.32%). The linolenic and dihomo-gamma linolenic acid (DGLA) FAs presented concentrations of 0.59% and 2.00% respectively. The DGLA concentration was higher than those found by Cesar *et al.* (2014) (0.44%) and Ekine-Dzivenu *et al.* (2014) (0.18%) and lower than the 5.39% estimated by Prado *et al.* (2003).

In the present study, the beef FA profile was composed mainly of SFAs (40.66%) and MUFAs (37.55%), followed by the PUFAs (13.43%). Prado *et al.* (2003), also working with Nelore animals, reported the same tendency for the proportion of saturated and unsaturated FAs, being 43.93% (SFAs), 42.33% (MUFAs) and 12.08% (PUFAs). Pitchford *et al.* (2002), using taurine breeds, and Cesar *et al.* (2014), using Nelore breed, also found similar concentrations between SFAs and MUFAs, namely, 47% and 47.5%, and 47.23% and 48.34%, respectively. Prado *et al.* (2003), Kelly *et al.* (2013) and Cesar *et al.* (2014) estimated a lower proportion of PUFAs, namely 12.08%, 1.26% and 2.87%, respectively, than that obtained in the present study (13.03%).

The heritability estimates for the myristic, palmitic, oleic, linoleic and α -linolenic acids were moderate (Table 2). The heritability estimated for linoleic FA (0.16) was close to that reported by Tait *et al.* (2007), 0.23 in a study using Angus cattle. However, Nogi *et al.* (2011) and Inoue *et al.* (2011) reported higher heritability estimates for linoleic FA in the intramuscular fat of muscle of Japanese black cattle, namely 0.34 and 0.58 respectively. Pitchford *et al.* (2002) estimated heritabilities for the myristic (0.18) and palmitic (0.21) FAs close to those obtained in the present study. Cesar *et al.* (2014) estimated low heritabilities for these FAs, ranging from 0.08 to 0.17. However, Ekine-Dzivenu *et al.* (2014) reported a high estimate for the miristoleic FA (0.51) and Nogi *et al.* (2011) also reported high estimates for myristic (0.70), palmitic (0.65), myristoleic (0.60) and linoleic (0.58) FAs.

The moderate heritability estimate (0.28) for oleic acid obtained in the present study suggests that selection is feasible to change the concentration of this FA in beef. Kim and Ntambi (1999) reported that the palmitoleic and oleic acids are produced from saturated FAs, such as palmitic and stearic acids, by the action of stearoyl-CoA desaturase enzyme. Despite the biological importance of α -linolenic acid (Daley *et al.* 2010) and the moderate heritability obtained, the small additive variance of this FA showed that it could hardly be improved through selection. The stearic, elaidic, palmitoleic, vaccenic, docosahexanoic, eicosatrienoic and arachidonic FAs and CLA had low heritability estimates. Similar results were reported by Ekine-Dzivenu *et al.* (2014) and Pitchford *et al.* (2002) for stearic, Ekine-Dzivenu *et al.* (2014) and Kelly *et al.* (2013) for vaccenic, CLA-cis Cesar *et al.* (2014) and Ekine-Dzivenu *et al.* (2014) for vaccenic, and Cesar *et al.* (2014) for araquidonic FAs.

The heritability estimates for total SFAs, MUFAs, omega 3 and omega 9 were low, suggesting that the genetic additive component had only a small contribution to the phenotypic

Table 2. Additive genetic, residual variance and heritability (h^2) estimates for the profile of the most relevant individual saturated (SFAs), monounsaturated (MUFAs), polyunsaturated (PUFAs) and conjugated linolenic (CLAs) fatty acids and for the sum of the SFAs, MUFAs, PUFAs, omega 3 (n3), omega 6 (n6) and omega 9 (n9), in *longissimus thoracis* muscle from Nelore cattle

The concentration of fatty acids are expressed as a percentage of total fatty acid methyl esters (FAMES) quantified. Total SFAs, C4:0+C6:0+C8:0+C10:0+C11:0+C12:0+C13:0+C14:0+C15:0+C16:0+C17:0+C18:0+C21:0+C24:0; total MUFAs, C16:1+C17:1 c10+C18:1 t11+C15:1 c10+C20:1 c11+C24:1+C22:1 n9+C18:1n9c+C14:1+C18:1 n9t; total of PUFAs C18:2 n6+C18:3 n3+C18:3 n6+C20:3 n3 cis-8,11,14 (ETE)+C20:3 n6 cis-11,14,17 (DGLA)+C20:4 n6+C20:5 n3+C22:6 n3; n3, C18:3 n3+C20:3 n3 cis-11,14,17+C22:6 n3+C20:5 n3; n6, C18:3 n6+C20:3 n6 cis-8,11,14+C18:2 n6+C20:4 n6; and n9, C18:1 n9c+C18:1 n9t+C24:1 n9+C22:1 n9

Fatty acid	Nomenclature	Additive genetic variance	Residual variance	h^2
<i>SFAs</i>				
Myristic	C14:0	0.06	0.18	0.25 ± 0.09
Palmitic	C16:0	0.80	3.70	0.18 ± 0.07
Stearic	C18:0	2.46	18.32	0.12 ± 0.05
<i>MUFAs</i>				
Myristoleic	C14:1	0.005	0.04	0.13 ± 0.05
Palmitoleic	C16:1	0.000345	0.63	0.01 ± 0.01
Elaidic	C18:1 n9t	1.22	15.98	0.07 ± 0.03
Oleic	C18:1 n9c	4.06	10.51	0.28 ± 0.09
Vaccenic	C18:1 t11	0.04	0.33	0.10 ± 0.04
<i>PUFAs</i>				
Linoleic	C18:2 n6	1.07	5.57	0.16 ± 0.06
Linolenic	C18:3 n6	0.003	0.04	0.07 ± 0.04
α -Linolenic	C18:3 n3	0.002	0.003	0.35 ± 0.10
Docosahexaenoic	C22:6 n3	0.016	0.11	0.13 ± 0.06
Arachidonic	C20:4 n6	0.001	2.82	0.01 ± 0.01
Eicosatrienoic Dihomo-gamma-linolenic (DGLA)	C20:3 n6 cis-11,14,17	0.05	0.45	0.10 ± 0.04
Eicosatrienoic (ETE)	C20:3 n3 cis-8,11,14	0.001	0.03	0.14 ± 0.05
<i>CLA</i>				
CLA	C18:2 c9 t11	0.0003	0.01	0.02 ± 0.01
<i>Total</i>				
Total SFAs		2.37	26.12	0.08 ± 0.03
Total MUFAs		3.55	43.45	0.08 ± 0.04
Total PUFAs		4.12	15.97	0.20 ± 0.08
n3		0.11	1.86	0.06 ± 0.03
n6		2.58	9.48	0.21 ± 0.07
n9		8.89	125.3	0.07 ± 0.03

variation of these FAs in zebu cattle. However, moderate heritabilities were obtained for total PUFAs and omega 6. Cesar *et al.* (2014) and Ekine-Dzivenu *et al.* (2014) also estimated a low heritability for SFAs and MUFAs and moderate values for omega 3 and omega 6. Similar to our results, low to moderate heritability estimates for PUFAs (0.05–0.12), MUFAs (0.06–0.20) and SFAs (0.07–0.30) were reported by Malau-Audli *et al.* (2000), Pitchford *et al.* (2002) and Ekine-Dzivenu *et al.* (2014). Nevertheless, other studies have presented higher heritability estimates for these groups of FAs than those in the present study, being 0.47 for PUFAs, 0.35–0.66 for SFAs and 0.35–0.68 for MUFAs in Japanese black cattle (Inoue *et al.* 2011; Nogi *et al.* 2011). Unlike in our study, Kelly *et al.* (2013), working with several breeds, also estimated a high heritability for SFAs (0.54) and MUFAs (0.54) and, therefore, concluded the existence of sufficient genetic variation for response to selection of FAs in subcutaneous fat of cattle. According to Ekine-Dzivenu *et al.* (2014), the wide

range of heritability estimates for several FAs indicates different origins and mechanisms of synthesis, suggesting differences in the genetic mechanisms that rule the FAs in different tissues, cattle breeds or populations. The majority of studies that have estimated genetic parameters for beef FA composition have been conducted in taurine breeds, while the use of zebu breeds has been limited by the low number of records for these traits (Cesar *et al.* 2014).

The genetic-correlation estimates between the individual SFAs, MUFAs and PUFAs are presented in Table 3. The genetic correlations obtained in the present study should be treated with caution, particularly those that showed high standard deviations. It is important to highlight, that despite the high standard deviations obtained, previous researchers supported most of the direction of genetic-correlation estimates found in the present study.

The estimates of genetic correlation between myristic and stearic acids was low, whereas it was moderate between palmitic and myristic acids and between palmitic and stearic

Table 3. Genetic correlation (above the diagonal) and its correspondent standard deviation (below the diagonal) between the individual saturated (SFAs), monounsaturated (MUFAs), polyunsaturated (PUFAs) and conjugated linolenic (CLAs) fatty acids, in *longissimus thoracis* muscle of Nelore cattle

C14:0, myristic acid; C16:0, palmitic acid; C18:0, stearic acid; C18:1 n9c, oleic acid; C18:2 n6, linoleic acid; C18:2 e9 t11, CLA; C18:3 n3, linolenic acid; C14:1, myristoleic acid; C16:1, palmitoleic acid; C18:1 n9t, elaidic acid; C18:1 t11, vaccenic acid; C20:3 n3 cis-8,11,14, eicosatrienoic acid (ETE); C20:3 n6 cis-11,14,17, dihomo-gamma-linolenic acid (DGLA); C18:3 n3, α -linolenic acid; C22:6 n3, docosahexaenoic acid; and C20:4 n6, arachidonic acid

Fatty acid	C14:0	C16:0	C18:0	C14:1	C16:1	C18:1 n9t	C18:1 n9c	C18:1 t11	C18:2 n6	C18:3 n6	C18:3 n3	C22:6 n3	C20:3 n6 cis-11,14,17	C20:3 n3 cis-8,11,14	C20:4 n6	C18:2 e9 t11
C14:0	–															
C16:0	0.36	–														
C18:0	0.64	0.35	–													
C14:1	0.50	0.48	0.66	–												
C16:1	0.35	0.26	0.27	0.32	–											
C18:1 n9t	0.65	0.10	0.21	0.36	0.70	–										
C18:1 n9c	0.33	0.81	0.22	0.28	0.37	0.53	–									
C18:1 t11	0.28	0.23	0.24	0.29	0.19	0.21	0.38	–								
C18:2 n6	0.48	0.25	0.33	0.31	0.55	0.58	0.37	0.23	–							
C18:3 n6	0.33	0.56	0.29	0.23	0.28	0.64	0.27	0.61	0.35	–						
C18:3 n3	0.40	0.35	0.54	0.33	0.29	0.80	0.29	0.65	0.57	0.32	–					
C22:6 n3	0.36	0.63	0.43	0.39	0.24	0.62	0.15	0.33	0.29	0.33	0.33	–				
C20:3 n6 cis-11,14,17	0.30	0.49	0.26	0.58	0.21	0.63	0.31	0.27	0.34	0.50	0.30	0.36	–			
C20:3 n3 cis-8,11,14	0.25	0.38	0.29	0.38	0.65	0.73	0.21	0.29	0.38	0.65	0.53	0.34	0.32	–		
C20:4 n6	0.26	0.44	0.55	0.36	0.36	0.29	0.27	0.48	0.35	0.39	0.18	0.33	0.30	0.28	–	
C18:2 e9 t11	0.38	0.35	0.45	0.51	0.38	0.79	0.63	0.54	0.55	0.51	0.35	0.38	0.37	0.34	0.53	–

acids (Table 3). Ekine-Dzivenu *et al.* (2014) also estimated low genetic correlations (0.78) between these FAs, except between myristic and palmitic FAs. Like in the present study, these authors estimated a low genetic correlation (-0.17) between the shorter-chain (myristic) and longer-chain (stearic) SFAs. Inoue *et al.* (2011) also reported high genetic-correlation estimates between the myristic and palmitic acids (0.70), but lower genetic correlations of these FAs with the longer-chain SFAs (stearic, <0.28). Similar results were reported by Kelly *et al.* (2013), who observed a moderate and positive genetic correlation between myristic and palmitic FAs (0.55) and low genetic correlation between myristic and stearic FAs (-0.09).

According to Drackley (2000) and Mapiye *et al.* (2012), the stearic FAs can be derived in fat deposits from shorter-chain SFAs through elongation. The negative and moderate genetic-correlation estimate between stearic and palmitic acids pointed out that the host animal genes that regulate elongation may lead to a small reduction of stearic and palmitic acid in adipose tissue. The results of Ekine-Dzivenu *et al.* (2014) also supported this fact, since they reported moderate negative genetic correlations between stearic with palmitic FAs. The results obtained in the present study were in agreement with previous reports, where there was a genetic antagonism between medium-chain (C16:0) and longer-chain (C18:0) SFAs.

The genetic-correlation estimates between myristic and myristoleic FAs were positive and moderate, suggesting that the myristoleic FA is predominantly produced from its precursor, myristic acid, through desaturation (Ekine-Dzivenu *et al.* 2014). Additionally, the positive and high genetic correlation between palmitic and palmitoleic acids was obtained. The stearoyl-CoA desaturase is the rate-limiting enzyme required for the biosynthesis of MUFAs from SFAs. The stearoyl-CoA desaturase catalyses the desaturation of palmitoyl-CoA and stearoyl-CoA substrates at the $\Delta 9$ position, to produce *de novo* palmitoleoyl-CoA and oleoyl-CoA respectively (Estany *et al.* 2014). Thus, the results of the present study support the fact that palmitic and myristic acids are converted to palmitoleic and myristoleic acids respectively.

The genetic correlation estimate obtained between oleic acid and one of its precursors, stearic acid, suggests that host animal genes influencing stearic acid are likely to be associated with host genes that are involved in the production of oleic acid. Kelly *et al.* (2013), working with several cattle breeds used for beef production in Australia, also reported a moderate and negative genetic-correlation estimate (-0.46) between oleic and stearic acids. Negative and high to moderate genetic-correlation estimate was obtained for linoleic acid with C14:0, and close to zero with palmitic and stearic acids (Table 3). Ekine-Dzivenu *et al.* (2014) also reported negative genetic correlations of linoleic acid with C14:0 (-0.35) and C16:0 (-0.88), but positive and moderate genetic correlations with C18:0 (0.68). These results pointed out genetic antagonism between the genes that control the concentrations of myristic and the linoleic acid genes. The CLA (*cis*-9 *trans*-11) showed close to zero genetic correlations with C16:0, C14:0 and C18:0. It is important to highlight, that most of the studies that have estimated genetic parameters for PUFAs in beef have reported few PUFAs (Inoue *et al.* 2011; Kelly *et al.* 2013; Ekine-Dzivenu *et al.* 2014).

Myristoleic acid showed negative and moderate genetic-correlation estimates with elaidic acid (-0.74 ± 0.36), and positive and moderate with oleic acids, and near to zero with palmitoleic acid and vaccenic acids. Ekine-Dzivenu *et al.* (2014) found different results for the correlation between myristoleic and vaccenic acids (-0.31), whereas Inoue *et al.* (2011) and Nogi *et al.* (2011) found negative correlations between myristoleic and oleic acids (-0.43 and -0.13 respectively). Although vaccenic acid showed positive and moderate genetic correlations with the oleic acid (0.52 ± 0.38), the high standard deviation value obtained did not allow confirmation of the genetic association between them. Nevertheless, it is important to highlight that a positive genetic correlation with a lower standard deviation between these FAs (0.57 ± 0.46) has been reported by Ekine-Dzivenu *et al.* (2014). Vaccenic acid, an isomer of oleic acid, is the principal ruminant *trans* fatty acid, and it is produced through the biohydrogenation of linoleic acid and α -linolenic acid (Aldai *et al.* 2013).

The genetic-correlation estimates of individual MUFAs with individual PUFAs were mostly negative, suggesting a genetic antagonism between them (Table 3). The vaccenic acid FA is a common intermediate produced during ruminal biohydrogenation of linolenic acid and linoleic acid (Bessa *et al.* 2000). Therefore, the negative correlation between vaccenic acid FA with linolenic acid and linoleic acid suggests that host genes that influence vaccenic acid also influence genes involved in the production of the linoleic acid. Genetic-correlation estimates between CLA and most of the individual PUFAs were low and near zero; only the genetic-correlation estimate between CLA and arachidonic acid was moderate (Table 3).

A possible explanation for the moderate genetic correlation between linoleic and linolenic acids is the fact that linolenic acid is a precursor of linoleic acid (Hirayama *et al.* 2006). It is well known that CLA is produced from ruminal biohydrogenation of linoleic acid to stearic acid in the rumen by *Butyrivibrio fibrisolvens* and other bacteria (Kepler *et al.* 1966; Jenkins 1993). Ekine-Dzivenu *et al.* (2014) estimated a high correlation between linoleic and stearic acids (0.68), but a low estimate of CLAs with stearic (-0.39) and linoleic (-0.25) acids. However, in the present study, close to zero genetic-correlation estimate was obtained between CLA and stearic and linoleic acids. The results of the present study showed that the genetic correlation among the individual long-chain PUFAs, such as arachidonic, eicosatrienoic and docosahexaenoic FAs, were positive and moderate. However, the genetic-correlation estimates between long-chain PUFAs and α -linolenic acid were mostly low, except for the association between arachidonic and α -linolenic acids.

The genetic-correlation estimates of the sums of SFAs with MUFAs and omega 6 were low and near zero, high with PUFAs and omega 9, and moderate with omega 3 (Table 4). Ekine-Dzivenu *et al.* (2014) reported a negative and moderate genetic correlation between PUFAs and SFAs (-0.41) and a positive and low genetic correlation between MUFAs and PUFAs (0.20). However, the genetic correlation estimate between total PUFAs with total MUFAs was negative and high (-0.84 ± 0.19).

Only few studies have estimated genetic correlations among FAs in cattle meat, which limits the discussion and comparison of these results with others. The present study found that selection

Table 4. Genetic (above the diagonal) and standard (below the diagonal) deviation of correlation estimates for the profile of sum of saturated (SFAs), monounsaturated (MUFAs), polyunsaturated (PUFAs), omega 3 (n3), omega 6 (n6) and omega 9 (n9) fatty acids, in *longissimus thoracis* muscle from Nelore cattle

Total SFA, C4:0 + C6:0 + C8:0 + C10:0 + C11:0 + C12:0 + C13:0 + C14:0 + C15:0 + C16:0 + C17:0 + C18:0 + C21:0 + C24:0; total MUFA, C16:1 + C17:1 c10 + C18:1 t11 + C15:1 c10 + C20:1 c11 + C24:1 + C22:1 n9 + C18:1n9c + C14:1 + C18:1 n9t; total PUFA, C18:2 n6 + C18:3 n3 + C18:3 n6 + C20:3 n3 cis-8,11,14 (ETE) + C20:3 n6 cis-11,14,17 (DGLA) + C20:4 n6 + C20:5 n3 + C22:6 n3; omega 3, C18:3 n3 + C20:3 n3 cis-11,14,17 + C22:6 n3 + C20:5 n3; omega 6, C18:3 n6 + C20:3 n6 cis-8,11,14 + C18:2 n6 + C20:4 n6; and omega 9, C18:1 n9c + C18:1 n9t + C24:1 n9 + C22:1 n9

Fatty acid	Total SFA	Total MUFA	Total PUFA	Omega 3	Omega 6	Omega 9
Total SFAs		0.25	-0.85	-0.67	-0.02	0.86
Total MUFAs	0.59		-0.84	-0.29	-0.94	0.20
Total PUFAs	0.15	0.19		0.76	0.76	-0.75
Omega 3	0.26	0.41	0.22		0.75	-0.54
Omega 6	0.51	0.12	0.24	0.28		-0.80
Omega 9	0.17	0.55	0.25	0.22	0.18	

to increase concentrations of PUFAs and omega 6 should result in lowering the concentrations of total SFAs and MUFAs. The PUFAs and omega 6 showed moderate and higher heritability estimates than did SFAs and MUFAs, thus the PUFAs and omega 6 could be used as indicator traits to decrease the total SFAs. The genetic-correlation estimates among omega 3, 6 and 9 suggest that the selection to increase omega 6 should also increase the concentration of omega 3, and decrease the concentration of omega 9 in beef fat. Probably, this is due to the use of a common desaturase enzyme, which is a classic key to the metabolic pathways (Waitzberg and Borges 2002; Lopes and Juzwiak 2003; Hirayama *et al.* 2006).

The beef FA profile is a difficult and costly trait to measure since it depends on a progeny test. Therefore, it is very important to identify the indicator traits that are associated with the FA profile. In this sense, Feitosa *et al.* (2016) suggested that the percentage of intramuscular fat in the *longissimus thoracis* muscle could be used as the indicator trait of FA profile of zebu beef. Moreover, the identification of genomic regions that affect the beef FA composition may become an important and highly applicable tool to improve the nutritional value of zebu beef, given the expensive and difficult nature of collecting phenotypic records. Recently, Lemos *et al.* (2016), using the same dataset as in the present study, identified several genomic regions associated with quantitative trait loci, and harbouring genes such as *ELOVL5*, *ESSRG*, *PCYT1A*, *ABC5*, *ABC6* and *ABC10* related to lipid metabolism and FA composition. These regions can be used in future fine-mapping studies, whose primary function is to search for informative causative mutations and also for customised low-density chips that assist in a more cost-effective genetic evaluation for beef FA profile.

In Brazil, most of the slaughtered male animals are intact bulls, so as to take advantage in terms of higher growth rate when finishing them in feedlot. There have been few studies evaluating the effect of gender status on beef FA in zebu cattle.

The beef from intact Nelore bulls is characterised by lower carcass and beef fatness, and also lower concentrations of PUFAs and MUFAs, a lower PUFA:SFA ratio and higher concentrations of SFAs (Ruiz *et al.* 2005). The present study used a large database of animals belonging to different beef cattle-breeding programs, and animals that are commercialised in various regions of the country. Therefore, the information obtained should contribute to the selection and breeding programs improving beef quality of zebu cattle raised in tropical conditions.

Decreasing SFA intake and increasing unsaturated-fat intake is recommended and has several beneficial impacts on human health (Adams *et al.* 2010). However, some studies have reported that individual SFAs such as the stearic FA have neutral effects on cholesterol concentrations (Yu *et al.* 1995). Moreover, the concentration of oleic FA, which is beneficial for flavour, human nutrition and fat softness (Kelly *et al.* 2013), could be increased, along with stearic acid. The moderate genetic correlation obtained between palmitic and palmitoleic acids, and between myristic and myristoleic acids, suggests that genetic differences in the activity of stearoyl-CoA desaturase gene may have existed among animals used in the present study. There is evidence of genetic differences in elongation activities (Kelly *et al.* 2013), and, in the present study, myristic acid showed a positive correlation with palmitic acid, but a low correlation with the stearic acid, which indicated that some animals exhibited a tendency to elongate specific, but not all, FAs.

The results obtained in the present study have provided knowledge to elucidate the additive genetic influence on fatty acid composition of intramuscular fat. In addition, genetic-relationship estimates among intramuscular FAs help seek strategies for genetic selection and/or genetic-based diet management to enhance the beef FA profile in zebu cattle.

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