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CÂMPUS DE JABOTICABAL

SELEÇÃO GENÔMICA PARA A COMPOSIÇÃO DE ÁCIDOS GRAXOS DA CARNE EM BOVINOS NELORE

Hermenegildo Lucas Justino Chiaia

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Orientador: **Prof. Dr. Fernando Sebastián Baldi Rey**

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UNIVERSIDADE ESTADUAL PAULISTA

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TÍTULO DA TESE: SELEÇÃO GENÔMICA PARA A COMPOSIÇÃO DE ÁCIDOS GRAXOS DA CARNE EM BOVINOS NELORE

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Hermenegildo Lucas Justino Chiaia – Solteiro, nascido aos 5 de Junho de 1982 na cidade do Huambo – Angola, filho de Elias Chiaia e de Joaquina Luís Balombo Justino. Formado em Medicina Veterinária pela Faculdade de Ciências Agrárias da Universidade Agostinho Neto, em Junho de 2009. Em Agosto de 2012 iniciou o curso de mestrado em Genética e Melhoramento Animal, na Faculdade de Ciências Agrárias e Veterinárias da "Universidade Estadual Paulista "Júlio de Mesquita Filho" no Campus de Jaboticabal em São Paulo, sob orientação do Professor Dr. Fernando Sebastián Baldi Rey, obtendo o título de Mestre em 2014. Em 2017 concluíu o curso de doutorado em Genética e Melhoramento Animal, na Faculdade de Ciências Agrárias e Veterinárias da "Universidade Estadual Paulista "Júlio de Mesquita Filho" no Campus de Jaboticabal em São Paulo, sob orientação do Professor Dr. Fernando Sebastián Baldi Rey, obtendo o título de Doutor.

“Nada é exatamente como queremos, então não deixe p□a amanhã o que pode ser feito hoje, imprevistos acontecem a todo momento.”

Israel Ziller.

“A pátria é do tamanho do saber do seu povo”

Simón Bolívar.

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Aos meus pais “Elias Chiaia e Joaquina Luís Balombo Justino”

À minha nova família “Gilmara Pereira da Silva e Arthur Elias da Silva Chiaia” dedico esta obra, pois os laços que nos unem superam todas as barreiras do Universo.

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SUMÁRIO

SELEÇÃO GENÔMICA PARA A COMPOSIÇÃO DE ÁCIDOS GRAXOS DA CARNE EM BOVINOS NELORE

RESUMO – Existem diferentes métodos e pseudo-fenótipos utilizados em predições genômicas, sendo necessário determinar o ideal para a característica de interesse. Os ácidos graxos da carne que contribuem de forma prejudicial para a saúde humana têm recebido considerável atenção nos últimos anos. O objetivo desse estudo foi avaliar a acurácia de predição genômica de diferentes métodos (SNP-BLUP, BayesC, BayesCπ e Bayesian Lasso) e pseudo-fenótipos (fenótipo ajustado para os efeitos fixos, valor genético estimado via pedigree e valor genético genômico obtido pelo método *single step* GBLUP) em dados simulados e reais de perfil de ácidos graxos no músculo *Longissimus thoracis* da raça Nelore terminados em confinamento. A proposta de inclusão do GEBV obtido pelo método passo único genômico BLUP (ssGBLUP) como pseudofenótipo nesta pesquisa é inédita em predição genômica, para responder um dos problemas frequentes ao utilizar a matriz advinda da informação genealógica, pela maioria dos produtores de gado de corte utilizarem o sistema de acasalamento que utiliza reprodutores multiplos. Foram utilizados cerca de 963 bovinos machos inteiros da raça Nelore terminados em confinamento e genotipados com um painel de 777.962 SNPs do Ilumina BovineSNP BeadChip. A informação genômica pode servir para melhorar o perfil de ácidos graxos em animais do grupo Zebu, por ter-se observado valores genômicos preditos com com acurácia de baixa a moderada magnitude. Nenhum dos métodos foi melhor para todos os ácidos graxos em termos de acurácia, no entanto, o método SNP-BLUP permitiu realizar avaliação menos viesada. O método ssGBLUP apresentou-se como ferramenta alternativa para obter GBVs como pseudo-fenôtipo mais acurado em situações de pedigree incompleto, pela alta proporção de de reprodutores múltiplos, sendo mais apropriado que o EBV e o fenótipo ajustado aos efeitos fixos para predizer o valor genômico dos animais.

Palavras-chave: Perfil de ácidos graxos, predição genômica, Zebu

GENOMIC SELETION FOR BEEF FATTY ACID COMPOSITION IN NELORE CATTLE

Abstract – There are different methods and pseudo-phenotypes used in genomic predictions, being necessary to determine the ideal for each trait of interest. Beef fatty acids that contribute to human health have received considerable attention in the last years. Thus, the objective of this study was to evaluate genomic predition accuracy of different methodologies (SNP-BLUP, BayesCπ, BayesC and Bayesian Lasso) pseudo-phenotypes (adjusted phenotype, estimated breeding value and genomic estimated breeding value by ssGBLUP) in simulated and real data of fatty acid profile in the *Longissimus thoracis* muscle of Nelore cattle finished in feedlot. The inclusion of the GEBV obtained by single step genomic BLUP (ssGBLUP) method as pseudo-phenotype in this research is innovator in genomic prediction, to answer one of the frequent problems when using the matrix derived from pedigree, by the mating system that uses multiple sires for many cattle breeders. A total of 963 Nelore bulls with phenotype for fatty acid profiles, were genotyped using the Illumina Bovine HD Bead Chip with 777,962 SNPs. Genomic information can assist in improving fatty acid profile in Zebu animals, since the use of genomic information yielded genomic values for fatty acid profile with accuracies ranging from low to moderate. None of the methods excelled in terms of accuracy, however the SNP-BLUP method allows obtaining less biased genomic evaluations. The ssGBLUP model is an appropriate alternative to obtaining more reliable and less biased GEBVs as pseudo-phenotypes in situations of missing pedigree, due to high proportion of multiple sires, being more appropriate than the EBVs or adjusted phenotypes for fixed effect to predict direct genomic values.

Keywords: Fatty acid profile, genomic selection, Zebu

CAPITULO 1 - CONSIDERAÇÕES GERAIS

1.1 - Introdução

Existem diferentes métodos e pseudo-fenótipos utilizados em predições genômicas, sendo necessário determinar o ideal para a característica de interesse. A inclusão do valor genético genômico estimado (GEBV) obtido pelo método passo único genômico BLUP (ssGBLUP) como pseudofenótipo nesta pesquisa é inédita em predição genômica, para responder um dos problemas frequentes ao utilizar a matriz advinda da informação genealógica, pela maioria dos produtores de gado de corte utilizarem o sistema de acasalamento que utiliza reprodutores multiplos.

Vários estudos têm apontado os benefícios do consumo de produtos cárneos e lácteos produzidos pelos ruminantes, em especial, àqueles alimentados sob condições de pastejo (WOOD et al., 2003; MACRAC et al., 2005; NUERNBERG et al., 2005). Atualmente, há uma contínua e crescente preocupação por parte da população e dos órgãos públicos quanto ao consumo excessivo de gorduras, bem como o perfil de ácidos graxos em produtos de origem animal e seu impacto sobre a saúde do consumidor.

O perfil de ácidos graxos da gordura intramuscular presente na carne é de importância para a saúde humana, uma vez que esta não pode ser extraída ou removida (SMET et al., 2004). A composição dos ácidos graxos tem sido amplamente estudada, pois também está relacionada com atributos sensoriais, como a suculência, aroma e maciez da carne. Para os padrões internacionais de qualidade da carne, a quantidade de gordura intramuscular ou marmorização depositada no músculo *Longissimus* é o principal determinante do valor da carcaça e preditor de palatabilidade (FERRAZ & FELÍCIO, 2010).

A carne bovina é considerada um alimento altamente nutritivo, sendo uma fonte importante de proteínas, micronutrientes e vitaminas do complexo B, mas a mesma apresenta alto teor de gordura com composição indesejável, como alta porcentagem de ácidos graxos saturados (AGS). O alto consumo de AGS está associado ao aumento nos níveis séricos de colesterol e de lipoproteínas de baixa densidade (LDL), que são fatores de risco à ocorrência de doenças cardiovasculares (KATAN et al., 1994).

Vários estudos têm comprovado grandes mudanças na composição de ácidos graxos da carne, por alterações provocadas nas estratégias de alimentação, principalmente em animais monogástricos (JAKOBSEN, 1999; DEMEYER & DOREAU, 1999) e em ruminantes (WOOD et al., 2003). No entanto, os fatores genéticos que afetam a composição dos ácidos graxos em bovinos merecem maior investigação, pois, alguns estudos relatam diferenças entre raças para a composição de ácidos graxos (HUERTA-LEIDENZ et al., 1996; MALAU-ADULI et al., 1997; RULE et al., 1997; PITCHFORD et al., 2002).

O sistema de acasalamento que utiliza vários touros em um mesmo grupo de vacas é o mais utilizado em sistemas de produção de bovinos de corte devido ao seu baixo custo e facilidade de manejo (ARAÚJO et al., 2012). Tipicamente, um progenitor pode ser acasalado com 30 vacas durante a estação de monta. Apesar das muitas vantagens práticas da utilização de reprodutores múltiplos, este sistema não permite a identificação da paternidade das progênies, resultando em um cenário de incerteza de paternidade para os animais jovens assim como pais das matrizes. Como consequência, a utilização de reprodutores múltiplos determina pedigrees incompletos, o que afeta negativamente a confiabilidade das avaliações genéticas e, consequentemente, o progresso genético pela seleção (CARDOSO & TEMPELMAN, 2003).

A obtenção das estimativas de valores genéticos é geralmente baseada na metodologia dos modelos mistos, que permite a inclusão de dados genealógicos e fenotípicos do animal e seus parentes para obter predições lineares não viesadas (BLUP) do valor genético dos indivíduos (HENDERSON, 1975). A inclusão de dados fornecidos pelos marcadores moleculares cobrindo todo genoma no processo de predição do mérito genético, além dos dados fenotípicos e genealógicos, na seleção genômica (MEUWISSEN et al., 2001), permite um aumento na acurácia dos valores genéticos genômicos estimados (GODDARD & HAYES, 2009), utilizando métodos que vão desde regreções de cuumeria (RR-BLUP) também chamado de SNP-BLUP (MEUWISSEN et al., 2001) aos métodos bayesianos como o LASSO (*least absolute shrinkage and selection operato*r) bayesiano como exemplo (CAMPOS et al., 2009).

Em estudos de seleção genômica, diferentes pseudo-fenótipos como fenótipo ajustado para os efeitos fixos (Yc), valor genético estimado (EBV) e valor genético estimado desregredido (dEBV) têm sido considerados (BODDHIREDDY et al., 2014; MOROTA et al., 2014). Em situações em que a matriz de parentesco está incompleta pela presença de reprodutores múltiplos, as estimativas dos valores genéticos a serem utilizados como pseudo-fenótipos para a estimação dos efeitos dos SNPs em seleção genômica podem não ser acuradas.

Para reduzir o erro advindo do parentesco obtido pela informação de genealogia e aumentar a confiabilidade das avaliações genéticas, uma alternativa pode ser a implementação do método ssGBLUP proposto por Legarra et al. (2009) e Misztal et al. (2009), que combina a matriz de parentesco obtida por informação de pedigree e a matriz de informação genômica numa matriz conjugada para predizer o GEBV. Deste modo pode-se melhorar a acurácia de predição genômica, pela melhoria da confiabilidade do pseudo-fenótipo utilizado na avaliação genômica, substituindo o EBV pelo GEBV.

Recentemente, Tonussi et al. (2017) apresentaram valores genéticos 30% mais acurados usando ssGBLUP em relação ao BLUP tradicional em uma população simulada de bovinos de corte com presença de reprodutores múltiplos. Esses autores recomendam o uso da informação genômica, especialmente para situações de incerteza de informação no pedigree em que o método ssGBLUP é uma alternativa apropriada para obter valores genéticos mais acurados e para animais jovens genotipados com incerteza de informação no pedigree.

Em função do limitado número de estudos e da importância do perfil de ácidos graxos sobre os atributos sensoriais da carne e a saúde humana, é primordial o desenvolvimento de trabalhos de seleção genômica para a composição de ácidos graxos em bovinos, em especial da raça Nelore, visto que representa mais de 80% do rebanho brasileiro. Além disto, é importante implementar as metodologias de seleção genômica para a aplicação dos resultados nas condições de produção de carne do Brasil, particularmente, devido as diferenças genéticas e ambientais (clima e manejo) dos rebanhos em relação aos de outros países de clima temperado, em que essas informações genômicas vêm sendo obtidas e utilizadas nas avaliações genéticas.

Objetivos

1 - Avaliar a acurácia de predição genômica dos métodos SNP-BLUP, Bayesian Lasso, BayesC, e BayesCπ para perfil de ácidos graxos em Nelore terminados em confinamento.

2 - Determinar o melhor pseudo-fenótipo (em relação ao fenótipo ajustado, valor genético estimado usando matriz de parentesco obtida pelo pedigree e valor genômico estimado pela combinação da matriz genômica com a matriz de parentesco aditivo obtido pelo pedigree), para predizer os valores genômicos pelo melhor método da pesquisa referente ao primeiro objetivo em dados simulados e reais de perfil de ácidos graxos em Nelore terminados em confinamento.

1.2 - Revisão de literatura

1.2.1 - Perfil de ácidos graxos

Segundo o relatório de perspectivas agrícolas da Organização para a Cooperação e Desenvolvimento Econômico e da Organização das Nações Unidas para Agricultura e Alimentação (OCDE/FAO, 2011), no período 2011-2020, os países em desenvolvimento, como o Brasil, serão a grande força do crescimento da produção, do consumo e do comércio agrícola mundial. No Brasil, o mercado interno é decisivo, uma vez que absorveu em 2015 cerca de 81,38% da produção de carne bovina (BEEFPOINT, 2016). O mercado interno e externo está cada vez mais exigente em relação à qualidade dos produtos, assim, conhecer melhor os atributos da carne mais valorizada pelos consumidores, constitui um elemento imprescindível para o delineamento de estratégias comerciais para a conquista e manutenção de mercados.

O incremento nos preços internacionais da carne, como consequência da maior demanda por alimentos, sobretudo por fontes de proteínas de origem animal, bem como a conjuntura econômica interna favorável, tem estimulado uma expansão da produção de carne bovina no Brasil (USDA, 2017). Avanços tecnológicos vêm revolucionando a pecuária, com um processo de intensificação nos sistemas de produção, como por exemplo, o aumento do número de animais terminados em

confinamento entre 1992 e 2010, a qual passou de 825.000 para quase 3 milhões de cabeças (ANUALPEC, 2011).

O Brasil, pelo seu potencial forrageiro tropical, é caracterizado por sistemas de produção de recria e engorda de bovinos, grande parte baseada numa alimentação a pasto. A carne produzida neste tipo de sistema, quando consumida em quantidades moderadas, não deveria trazer problemas à saúde humana (PRADO et al., 2003), uma vez que possui características desejáveis como baixo conteúdo de gordura, tipicamente variando entre 2-4% de gordura intramuscular no músculo *Longissimus*, um perfil de ácidos graxos com altos níveis de ácidos graxos ômega-3 (n-3) e uma melhor qualidade dietética que se traduz em óptima relação ômega 6 com ômega 3 (n-6/n-3), bem como poliinsaturado com saturado (AGPI/AGS) (FRENCH et al., 2000; MONTOSSI & SAÑUDO, 2007; DEPETRIS & SANTINI, 2009; PINHO et al., 2011), quando comparada à carne de bovinos confinados.

Os AGS predominantes na gordura de bovinos são os ácidos mirístico (C14:0), palmítico (C16:0) e esteárico (C18:0) (LAWRIE, 2005). Cabe ressaltar que o C14:0 tem potencial para aumentar as concentrações de colesterol sérico 4 a 6 vezes maiores em relação ao C16:0 (MENSINK & KATAN, 1992). Por outro lado, o tecido gorduroso de ruminantes é uma fonte natural de isômeros de ácido linoleico conjugado (CLA), como o cis-9, trans-11 (FRENCH et al., 2000), que são sintetizados no rúmen como consequência do processo de biohidrogenação de ácidos graxos realizado pelos microrganismos (TAMMINGA & DOREAU, 1991).

O CLA possui efeitos favoráveis à saúde humana, aumentando a atividade imunoestimulatória, antimutagênica e antioxidante (IP, 1997). Além disto, os ácidos graxos poliinsaturados (AGPI) presentes na gordura de bovinos, como os ácidos linoléico (C18:2n-6) e linolênico (C18:3n-3), e monoinsaturados (AGMI), como o ácido oléico (C18:1 n-9), oferecem proteção ao sistema cardiovascular, uma vez que o consumo balanceado dos mesmos está associado à redução nos níveis séricos de colesterol e aumento nas lipoproteínas de alta densidade (HDL) (PENSEL, 1998; TAPIERO et al., 2002).

Estudos indicaram que o tecido adiposo de bovinos *Bos taurus indicus* é menos saturado em relação aos animais *Bos taurus taurus taurus* (HUERTA-LEIDENZ et al., 1996; PERRY et al., 1998). No Brasil, Prado et al. (2003) não observaram diferenças na proporção de AGS, AGMI e AGPI da gordura intramuscular do músculo *Longissimus* de bovinos *Bos taurus indicus* e bovinos mestiços *Bos taurus indicus* vs. *Bos taurus taurus* alimentados a pasto. Já, Rossato et al. (2010), destacaram que a carne de animais da raça Nelore é nutricionalmente mais saudável, quando comparada à carne de bovinos da raça Angus, pois apresenta menores percentuais de colesterol e maiores quantidades de ácidos graxos n-3, precursor do CLA (C18:1 trans).

Bressan et al. (2011) mostraram que o sistema de produção tem importante influência quando se comparam animais de raças *Bos taurus taurus* e *Bos taurus indicus*. Neste sentido, os autores relataram que em confinamento, as raças *Bos taurus taurus* apresentaram menor percentagem de AGS e maior de AGMI em relação *Bos taurus indicus* e níveis semelhantes de AGPI. Além disto, os autores detectaram maiores concentrações de C14:0 e menores de C16:0 em carne proveniente de animais *Bos taurus indicus*. Resultados semelhantes foram obtidos em estudos anteriores por Perry et al. (1998), Menezes et al. (2009) e Rossato et al. (2010), quando os autores compararam raças *Bos taurus taurus* e *Bos taurus indicus* terminadas em confinamento.

Segundo Menezes et al. (2009), Rossato et al. (2010) e Bressan et al. (2011), a carne de animais *Bos taurus indicus* apresenta maior proporção de perfil de ácidos graxos prejudiciais para a saúde humana, quando os animais são confinados. De acordo com Bressan et al. (2011), nesta condição, bovinos *Bos taurus taurus* têm uma maior aptidão para dessaturar os AGS, que estão presentes em maior quantidade em grãos.

De acordo com pesquisadores do Brasil (MENEZES et al., 2009; SILVA et al., 2009), sistemas de produção de carne semi-intensivos a intensivos, caracterizados por recria a pasto até os 20 a 30 meses de idade, terminação em confinamento, com períodos variando entre 70 e 131 dias e com dietas contendo entre 40 a 50% de volumoso, têm resultado em maiores percentagens de gordura intramuscular na

carne e um perfil de ácidos graxos, que poderia segundo HMSO (1994) prejudicar a saúde humana, com uma relação AGPI/AGS menor que 0,45 e relação n-6/n-3 maior que 4.

Consequentemente, o país deve promover estudos científicos de avaliação dos produtos cárneos, visando a produção de informação objetiva em projetos inovadores, a fim de melhorar a competitividade da cadeia da carne. Também, é importante a capacitação de recursos humanos nesta área de pesquisa, incluindo aspectos relacionados aos processos de produção, transformação e comercialização que afetam a preferência dos consumidores.

1.2.2 - Seleção genômica

Por muitos anos, o perfil de ácidos graxos em animais destinados à produção de carne tem recebido considerável interesse pelas suas implicações para a saúde humana e para as características associadas à de qualidade da carne (XIE et al., 1996; WOOD et al., 1999; GANDEMER et al., 1999). Como a maioria das características de interesse econômico na produção animal, a composição de ácidos graxos é influenciada por fatores ambientais e genéticos.

Em bovinos, estudos de seleção genômica têm sido realizados utilizando painéis de SNPs de alta densidade, com milhares de marcadores genéticos, para características tais como produção de leite e seus componentes (GLANTZ, 2012; DING et al., 2013), crescimento (SNELLING et al., 2010; PRYCE et al., 2012) e eficiência de conversão alimentar (MUJIBI et al., 2011; BOLORMAA et al., 2013). Também realizaram-se alguns estudos sobre a aplicação de informações genômicas para características de carne, como a composição de ácidos graxos (REECY et al., 2010; RAMAYO-CALDAS et al., 2012; SAATCHI et al., 2013; CHEN et al., 2015; ONOGI et al., 2015).

Com o desenvolvimento de milhares de marcadores do tipo SNP que cobrem com maior abrangência o genoma bovino, maiores níveis de desequilíbrio de ligação entre os marcadores e entre os marcadores com os QTL são obtidos e, consequentemente, as chances de encontrar marcadores associados às características produtivas. Como consequência, a utilização de informações

genômicas para a predição dos valores genéticos das características de importância econômica pode contribuir na melhoria da qualidade de carne.

Com a aplicação de seleção genômica, os custos de produção poderão ser reduzidos consideravelmente, sobretudo para características que dependem de teste de progênie para sua avaliação genética, uma vez que diminuirá o intervalo de geração e incrementará a acurácia de seleção, sobretudo a idades jovens (SCHAEFFER, 2006). Normalmente, na estimação dos valores genômicos é utilizada uma população de referência na qual os animais possuem registros fenotípicos de características e informações genotípicas (CALUS & VEERKAMP, 2007). Posteriormente, as estimativas dos efeitos dos marcadores são utilizadas para predizer os valores genômicos de animais de outra população (por exemplo, candidatos à seleção) com informação genotípica, mas que não possuem dados fenotípicos (MEUWISSEN et al., 2001; GODDARD & HAYES, 2009).

A acurácia de predição dos valores genômicos é condicionada à quantidade de informação fenotípica na população de referência, densidade e tipo de marcadores utilizados (SNPs ou haplótipos), herdabilidade da característica e metodologia utilizada para a estimação dos efeitos dos marcadores (MEUWISSEN et al., 2001; MUIR, 2007; SOLBERG et al., 2008; HASSEN et al., 2009; BOLORMAA et al., 2013). Várias metodologias têm sido propostas para a estimação dos efeitos dos marcadores, como “ridge regression” (WHITTAKER et al., 2000), Best Linear Unbiased Predictor (BLUP) (MEUWISSEN et al., 2001) e inferência Bayesiana, utilizando vários tipos de distribuições a *priori* para os efeitos e variâncias dos QTL (MEUWISSEN et al., 2001; XU, 2003; YI & XU, 2008).

A partir de resultados de simulação, os modelos hierárquicos ou bayesianos resultaram em maiores acurácias na estimação dos efeitos dos QTL (ZHANG et al., 2011). Hayes (2009) demonstrou que a metodologia e distribuição mais adequada para a estimação dos efeitos dos QTL é condicionada à característica que está sendo considerada, uma vez que o número de QTL assim como a proporção da variância genética que é explicada pelos marcadores varia em função da característica.

Vários pesquisadores têm mostrado que o perfil de ácidos graxos da carne de bovinos apresenta variação genética para responder à seleção (INOUE et al., 2011; NOGI et al., 2011, WU et al., 2012; YEON et al., 2013). Entretanto, devido à dificuldade e alto custo para se obter medidas fenotípicas do perfil de ácidos graxos, provavelmente, tem sido limitada a sua implementação em programas de melhoramento genético. A identificação de regiões do genoma responsáveis por variação genética do perfil de ácidos graxos da carne deverá contribuir para a compreensão da síntese de ácidos graxos da carne, bem como aumentar as oportunidades para melhorar a composição da gordura da carne por meio de seleção genômica (BOUWMAN et al., 2011).

Em estudo com número significativamente maior de animais, apresentado por Reecy et al. (2010), analisaram o perfil de ácidos graxos da carne de 2.285 bovinos da raça Angus com painel de 54K, usando o método BayesC. Os pesquisadores concluíram que uma grande proporção da variação na composição de ácidos graxos da carne de bovinos da raça Angus está associada a um número relativamente baixo de SNPs.

Yeon et al. (2013) realizaram estudos para identificar variantes genéticas de *Fatty acid sinthase* (FASN) e associação com a composição de ácidos graxos, em bovinos Hanwoo na Coréia do Sul. Os autores observaram 6 variantes genéticas localizadas nos exons 20, 24, 32, 34 e 39, e concluíram que os SNPs localizados em regiões codificadoras (exons 20, 32 e 39) de FASN apresentam associação significativa com a composição dos ácidos graxos.

Saatchi et al. (2013) realizaram estudos de associação e seleção genômica ampla para determinar a extensão em que os marcadores moleculares poderiam ser responsáveis por variação em composição de ácidos graxos do músculo esquelético de bovinos Angus e identificar as regiões genômicas associadas a essa variação. Os autores trabalharam com um painel de 54K, tendo verificado que até 54% da variação na composição dos ácidos graxos da carne era explicada pelos marcadores do tipo SNP e a acurácia na predição do valor genômico genético direto variou de -0.06 a 0.57.

Ainda são limitados os trabalhos de seleção genômica para o perfil de ácidos graxos em bovinos (CHEN et al., 2015; ONOGI et al., 2015). Neste sentido, Chen et al. (2015), realizaram estudos de associação e predição genômica, visando avaliar a acurácia de predição genômica na composição dos ácidos graxos da carne, usando os métodos GBLUP e bayesianos. Os autores trabalharam com bovinos de raças taurinas e seus cruzamentos, tendo concluído que a composição de ácidos graxos na carne bovina é influenciada por alguns genes de efeito maior e muitos genes de efeito menor, existindo potencial de predizer o valor genômico da composição de ácidos graxos em bovinos de corte com moderada a alta acurácia para ácidos graxos que apresentam estimativa de herdabilidade moderada a alta.

Onogi et al. (2015), avaliaram a habilidade preditiva do método passo único genômico BLUP (ssGBLUP) na composição de ácidos graxos da carne de bovinos Japanese black, com fenótipo de 3088 animais, dos quais 952 machos foram genotipados. Na referida avaliação, a acurácia de predição foi maior para o método ssGBLUP em relação ao BLUP para todas as características, sendo que, numa avaliação empirica os ganhos em acurácia do método ssGBLUP em relação ao BLUP aumentam à medida que o desvio dos valores fenotípicos dos animais aumenta.

1.2.3 - Métodos de predição dos valores genômicos

A obtenção das predições de valores genéticos é geralmente baseada na metodologia dos modelos mistos, que permite a inclusão de dados genealogicos e fenotipicos do animal e seus parentes para obter predições lineares não viesadas (BLUP) do valor genético dos indivíduos (HENDERSON, 1975). A inclusão de dados fornecidos pelos marcadores moleculares cobrindo todo genoma no processo de predição do mérito genético, além dos dados fenotípicos e genealógicos, na seleção genômica (MEUWISSEN et al., 2001), permite um aumento na acurácia dos valores genéticos estimados (GODDARD & HAYES, 2009).

A predição do valor genômico, pode envolver múltiplos passos (*multi-step*) (VANRADEN, 2008; HAYES et al., 2009) ou passo único (*single-step*) (AGUILAR et al., 2010; CHEN et al., 2011). Para predizer os valores genômicos por *multi-step*, os

valores genéticos que serão utilizados como pseudo-fenótipos, são estimados pelo melhor preditor linear não viesado (BLUP), o qual considera a matriz de parentesco baseada apenas no pedigree. Em seguida, estes pseudo-fenótipos são utilizados em modelo de predição genômica para estimar os efeitos dos marcadores na população de referência, nesse caso, todos os animais devem estar genotipados e, por último, predizer os valores genômicos por um índice de seleção (HAYES et al., 2009) que é formado por uma média da habilidade de transmissão genética gerada a partir das informações dos passos anteriores. As ponderações do índice são realizadas com base na herdabilidade e acurácia das características analisadas (MISZTAL et al., 2009).

Os efeitos dos marcadores podem ser estimados com diferentes pressuposições quanto a sua distribuição, com distribuição normal e variância homogênea para todos os SNPs no método SNP-BLUP, variância heterogênea para os efeitos dos SNPs no método BayesA, parte dos SNPs sem efeito com probabilidade π e uma fracção de efeito com probabilidade 1-π com variância heterogênea no método BayesB (MEUWISSEN et al., 2001); parte dos SNPs sem efeito com probabilidade π e uma fracção de efeito com probabilidade 1-π com variância homogênea no método BayesC; com π fixo no caso do BayesCπ (HABIER et al., 2011) e exponencial dupla no método Bayesian Lasso (PARK & CASELLA, 2008).

As etapas do método *multi-step* dependem de muitos parâmetros e suposições, os quais são extremamente difíceis de verificar, sobretudo na seleção de animais. Os principais problemas estão relacionados a má qualidade e definição dos pseudo-fenótipos, por exemplo, para animais com pequeno número de progênies, como acontece em alguns casos de bovinos de corte.

Assim, quando apenas uma parcela da população for genotipada, pode-se utilizar o método *single-step* (AGUILAR et al., 2010), o qual apresenta vantagens por ser de fácil aplicação, pois permite considerar simultaneamente as informações fenotípicas dos animais genotipados e não genotipados. Esse método também é adequado para análises multi características e permite a predição indireta de valores

genéticos em animais jovens através dos efeitos dos SNPs com acurácia de uma avaliação completa (CHEN et al., 2011; LOURENÇO et al., 2014).

1.2.4 - Pseudo-fenótipos

Em avaliações genéticas, os valores genéticos dos animais são preditos por meio de dados fenotípicos e de pedigree, com uso da metodologia dos modelos mistos. A matriz de parentesco aditivo é obtida por meio do valor esperado da proporção de loci idênticos por descendência, geralmente denominado de coeficiente de parentesco. Porém, ao utilizar informações de marcadores genéticos de alta densidade, tal matriz pode ser substituída pela matriz de parentesco genômica (**G**), que é construída apenas com as informações dos marcadores de animais genotipados. Na matriz **G**, os coeficientes são dados pela proporção de *loci* idênticos por estado, os quais geralmente capturam mais informação do que o coeficiente de parentesco obtido pela informação de pedigree (PÉRTILE et al., 2016). Existe a possibilidade de se utilizar uma matriz que combina a informação das matrizes **A** e **G**, denominada **H**, que permite gerar predições tanto para indivíduos genotipados e não genotipados simultaneamente conforme proposto por Legarra et al.(2009) e Misztal et al. (2009), tendo apresentado resultados mais acurados em trabalhos de diferentes autores (WANG et al., 2012; TONUSSI et al., 2017).

Segundo Berry et al. (2016), o desenvolvimento de avaliações genômicas acuradas em bovinos de corte é mais difícil do que em bovinos de leite por várias razões, que incluem a presença de múltiplas raças, a dificuldade de mediçaõ para determinar os fenótipos e a falta de inseminação artificial; além disso, é comum o uso de reprodutores múltiplos, que apesár da vantagem em termos de gestão deste sistema de acasalamento, não permite a identificação da paternidade, o que torna a estrutura de pedigree incompleta, constituindo uma das principais dificuldades em avaliações genéticas acuradas.

Para estimar o efeito dos marcadores em avaliação genômica é necessário determinar a variável resposta, denominada pseudo-fenótipo. Diferentes pseudo-fenótipos, incluindo o Yc, EBV e dEBV têm sido considerados para a estimação do efeito dos marcadores (BODDHIREDDY et al., 2014; MOROTA et al., 2014;

FERNANDES JÚNIOR et al., 2016). Estes, apresentam diferentes graus de confiabilidade, afetando a predição dos valores genômicos (treinamento dos SNPs) e consequentemente a habilidade de predição dos marcadores.

De certo modo, o uso de EBVs como variável resposta pode ser uma escolha conveniente, pois espera-se que esta medida seja um preditor mais confiável do mérito genético dos indivíduos, se houver uma quantidade considerável de informações para o seu cálculo, quando comparado ao uso de medidas fenotípicas. Porém, Garrick et al. (2009) destacaram alguns problemas potenciais dessa abordagem e propuseram usar o dEBV para estimar os efeitos dos marcadores. Embora alguns estudos tenham apontado benefícios na utilização de dEBV como variável resposta (OSTERSEN et al., 2011), outros estudos não confirmaram essa vantagem (GUO et al., 2010). Uma análise mais cuidadosa das discrepâncias sugere que haja mais benefício em usar o dEBV quando a quantidade de informação usada para predizer o EBV é menor e mais heterogênea entre os animais de referência.

Alguns estudos de seleção genômica em bovinos de corte, relataram melhor habilidade de predição genômica quando o fenótipo ajustado foi usado como pseudo-fenótipo para treinar os efeitos de marcadores em comparação ao EBV obtido pelo BLUP (SILVA et al., 2016; FERNANDES JÚNIOR et al., 2016). Em bovinos de corte, o EBV obtido via BLUP é menos apropriado devido à estrutura de pedigree e ao pequeno tamanho da população de treinamento. De acordo com Muñoz et al. (2011), a melhoria no EBV do modelo BLUP pode ser obtido simplesmente corrigindo erros no pedigree ou usando abordagens mais complexas, como a aplicação de uma matriz de parentesco genômica no modelo BLUP como alternativa à matriz de parentesco aditivo baseada em valores esperados derivados do pedigree.

Saatchi et al. (2013) consideraram o fenótipo como pseudo-fenótipo na predição dos valores genômico para perfil de ácidos graxos. Na literatura, não foram encontrados trabalhos sobre a seleção genômica para o perfil de ácidos graxos em bovinos zebu criados em condições tropicais utilizando diferentes pseudo-fenotipos. A seleção genômica ainda é pouco aplicada em bovinos de corte, especialmente

para fenótipos que são de difícil medição, provavelmente, devido à falta de população de referência suficientemente grandes e pseudo-fenótipos não confiáveis. Este fato motiva a realização do presente trabalho que visa determinar o melhor pseudo-fenótipo para estimar os efeitos de marcadores em bovinos Nelore para perfil de ácidos graxos.

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CHAPTER 2 - GENOMIC PREDICTION FOR BEEF FATTY ACID PROFILE IN NELORE CATTLE[a]

ABSTRACT - The objective of this study was to compare SNP-BLUP, BayesCπ, BayesC and Bayesian Lasso methodologies to predict the direct genomic value for saturated, monounsaturated, and polyunsaturated fatty acid profile, omega 3 and 6 in the *Longissimus thoracis* muscle of Nelore cattle finished in feedlot. A total of 963 Nelore bulls with phenotype for fatty acid profiles, were genotyped using the Illumina Bovine HD Bead Chip (Illumina, San Diego, CA) with 777,962 SNP. The predictive ability was evaluated using cross validation. To compare the methodologies, the correlation between DGV and pseudo-phenotypes was calculated. Our results indicate that none of the methods excelled in terms of accuracy, however, the SNP-BLUP method allows obtaining less biased genomic evaluations, thereby; this method is more feasible when taking into account the analyses' operating cost. Despite the lowest bias observed for EBV, the adjusted phenotype is the preferred pseudo-phenotype considering the genomic prediction accuracies regarding the context of the present study.

Keywords: *Bos taurus indicus*, lipid profile, meat quality, genomic prediction

RESUMO - O objetivo do presente estudo foi comparar as metodologias SNP-BLUP, BayesCπ, BayesC e Bayesian Lasso para predizer o valor genômico direto para o perfil de ácidos graxos saturados, monoinsaturados e poliinsaturados, ômega 3 e 6 no músculo *Longissimus thoracis* de bovinos Nelore terminados em confinamento. Cerca de 963 touros Nelore com fenótipo para perfil de ácidos graxos, foram genotipados com um painel de 777.962 SNPs (Illumina BovineHD BeadChip). Calculou-se a correlação entre DGV e pseudo-fenótipos para comparar as acurácias das medodologias de predição genômica. Os resultados indicam que nenhum dos métodos se destacou em termos de precisão, entretanto, o método SNP-BLUP permite obter avaliações genômicas menos viesadas, sendo mais viável quando se considera o custo operacional das análises. Apesar das estimativas menos viesadas observadas para o EBV, é preferível o fenótipo ajustado como pseudo-fenótipo por ter apresentado as melhores estimativas de acurácias no presente estudo.

Palavras-chave: *Bos taurus indicus*, perfil lipídico, qualidade da carne, seleção genômica

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2.1 - Introduction

Nowadays, there is a continuing and growing concern about excessive fat consumption and its impact on human health, especially those from animal sources. The high consumption of saturated fatty acids (SFA) is associated with high serum cholesterol and low density lipoproteins levels (LDL),which are risk factors for the occurrence of cardiovascular diseases (KATAN et al., 1994). The predominant SFA in the cattle meat fat are myristic, palmitic, and stearic fatty acids (FAs) (LAWRIE, 2005; ROSSATO et al., 2009). The polyunsaturated fatty acids (PUFA) present in the beef fat such as linoleic (C18:2n-6) and linolenic (C18:3n-3), and monounsaturated (MUFA) as oleic acid (C18:1n-9), provide protection to the cardiovascular system, once the balanced consumption of them is associated with reduce serum cholesterol and an increase in high density lipoprotein (HDL) (PENSEL, 1998; TAPIERO et al., 2002).

Furthermore, the fat presented in ruminants meat is a natural source of conjugated linoleic acid (CLA) isomers (FRENCH et al., 2000), which are synthesized in the rumen (TAMMINGA & DOREAU, 1991) and has favorable effects on human's health, increasing the immunostimulatory, antimutagenic, and antioxidant activities (IP, 1997). There is a growing market demand for sources of healthier lipid profile, and several strategies have been used to improve the beef FA profile, such as dietary manipulation and animal breeding. In these sense, Cesar et al. (2014) and Aboujaoude et al. (2016) reported that selection for beef fatty acids (FAs) profile in Nelore cattle is very feasible, since there is additive genetic variation for most beef fatty acids in Nelore cattle. However, the high cost to obtain the phenotypic information and the fact that this trait can be only obtained after slaughter limits the genetic improvement trough traditional selection. Although the FAs profile is not considered as selection criteria, genomic selection is a relevant tool to increase genetic progress for this trait, because the animal can be evaluated early in life, even at birth, reducing the generation interval and at a low cost.

Several methods have been proposed to predict the genomic breeding values (GEBV) such us SNP-BLUP (Single Nucleotide Polymorphisms-Best Linear Unbiased Predictor), LASSO (Least Absolute Shrinkage and Selection Operator) and

Bayesian methods. SNP-BLUP assumes a normal distribution for SNP effect, with average equal to zero and common variance for all markers (MEUWISSEN et al., 2001). LASSO assumes a double exponential distribution for the SNPs effect (PARK & CASELLA, 2008; DE LOS CAMPOS et al., 2009). BayesC and BayesCπ, which considered a variable with binomial distribution that reports whether a marker (SNP) has (1) or not (0) effect on the trait under study, with π variable probability to be zero and a normal distribution with probability 1-π, assuming that part of the effect markers follows a normal distribution. The BayesC differs from BayesCπ mainly due to the value of π being fixed in the first one and estimated from the analyzed data in BayesCπ. All of these methods differ in the assumptions about the genetic model associated with quantitative traits, and the best method is the one that reflects the biological nature of polygenic traits, in terms of genic effects (RESENDE et al., 2008).

Studying an Angus population, Saatchi et al. (2013) concluded that genomic selection for beef FA profile using Bayesian models is feasible. Recently, Onogi et al. (2015) evaluated the predictive ability of genomic selection in FA composition of Japanese Black cattle, using single-step genomic best linear unbiased method. The genomic selection has potential to increase the genetic gain for hard measure traits, as FA profile, however, the most suitable model to evaluate those traits are still being studied. It is important to highlight that in tropical and subtropical regions the indicine breeds are the predominant source of beef and, up to date, there are no studies about genomic selection for beef FA profile in Nelore cattle under tropical conditions. Therefore, the objective of this study was to compare the predictive ability of SNP-BLUP, Bayesian Lasso, BayesC, and BayesCπ methods for beef FA profile of Nelore cattle finished in feedlot.

2.2 - Material and methods

2.2.1 - Data

A total of 937 Nelore bulls finished in feedlot for a minimum period of 90 days and slaughtered with an average of 24 months of age, were analyzed. The animals belonged to eight different farms located in the Southeast, Northeast, and Midwest regions of Brazil, which participate in three beef cattle breeding programs (Nelore

Qualitas, Paint and Delta Gen). In these breeding programs animals are selected based on growth, finishing, and sexual precocity traits.

Breeding seasons differed among these farms; therefore, calving seasons were concentrated from August to October in some farms and from November to January in others. Weaning was performed at seven months of average age. Animals were raised on grazing conditions using *Brachiaria sp*. and *Panicum sp*. forages, and had free access to mineral salt. At approximately 1 year of age, the breeding animals were selected and the remaining animals were kept in feedlot with a forage:concentrate ratio ranging from 50:50 to 70:30, depending on the farm. In general, whole-plant corn or sorghum silage was used as high quality forage; and corn grains and/or sorghum, and soybeans, soybean meal, or sunflower seeds were used as protein concentrate.

The farmers used a mean live weight between 500 and 550 kg as criteria for slaughtering the animals. The slaughters were carried out in commercials slaughterhouses, in accordance with the Brazilian Federal Inspection Service procedures. After 48 h post mortem stored between 0 and 2 °C, samples from 2.54 cm thick were removed from the *Longissimus thoracis* muscle, between the 12 and 13th ribs from each animal, were placed in plastic bags, and stored at −80 °C until further analyses.

2.2.2 - Fatty acid profile analyses

The beef fatty acids (FAs) were extracted from intramuscular fat of the *longissimus thoracis* muscle using the method by Folch et al. (1957) and the methyl esters were formed according to Kramer et al. (1997). The FA profile in meat was performed at the Meat Science Laboratory (LCC) in the Department of Animal Nutrition and Production at FMVZ/USP.

The FAs were quantified using a gas chromatography (GC-2010 Plus - Shimadzu AOC 20i auto-injector) with a SP-2560 capillary column (100 m × 0.25 mm in diameter with 0.02 mm thickness, Supelco, Bellefonte, PA). The initiating temperature was 70°C with gradual warming (13°C min−1) up to 175 °C, holding for 27min, and later a further increase of 4°C min−1 until 215°C was reached and held

for 31 min. Hydrogen (H_2) was used as the carrier gas with 40 cm^3 s^{-1}. Fatty acids were identified by comparison of retention time of methyl esters of the samples with standards of FAs C4–C24 (F.A.M.E mix Sigma®), vaccenic acid (V038-1G, Sigma®), linoleic acid (UC-61 M 100 mg), conjugated linoleic acid (CLA) (UC-60M 100 mg, Sigma®) and tricosanoic acid (Sigma®). Fatty acids were quantified by normalizing the area under the curve of methyl esters using Software GS solution 2.42. Fatty acids content were expressed in percentage of total FA methyl ester quantified.

Based on the quantified acids (Table 1), twenty one FAs (14 individuals and 7 groups of FAs) were selected due to their importance in human health.

2.2.3 - Genotyping of animals

Animals were genotyped using the Illumina BovineHD BeadChip (Illumina, San Diego, CA) with 777,962 SNP. Quality control was performed excluding those SNPs markers with unknown genomic position, located on sex chromosomes, monomorphic and markers with minor allele frequency (MAF) less than 0.05, call rate less than 90%, and excess of heterozygosity. Samples with a call rate less than 90% were also excluded. After quality control, there were 934 or less samples (Table 1) and 470,007 SNPs left in the dataset for analyses.

2.2.4 - Estimation of SNPs effects and genomic value prediction

To evaluate the prediction ability within the four different methods (SNP-BLUP, Bayesian Lasso, BayesC, and BayesCπ), the cross-validation methodology was used. To perform the cross-validation, the data set was randomly divided into four subsets of similar size and the validation was done in each subset at a time. This process was repeated four times and each group was once considered to be the validation group. An exception has been made for the arachidonic FA, where the cross-validation was composed of two training groups and one validation group due to the reduced data after quality control. The SNP effects were predicted in the training population with known phenotype and genotype. The DGV of animals in the validation set was predicted based on the SNPs effects values estimated on the training population. The figure 1 shows the distribution of animals in the training and

validation set in each cross-validation design made by principal components analyses which was performed based on the genomic matrix.

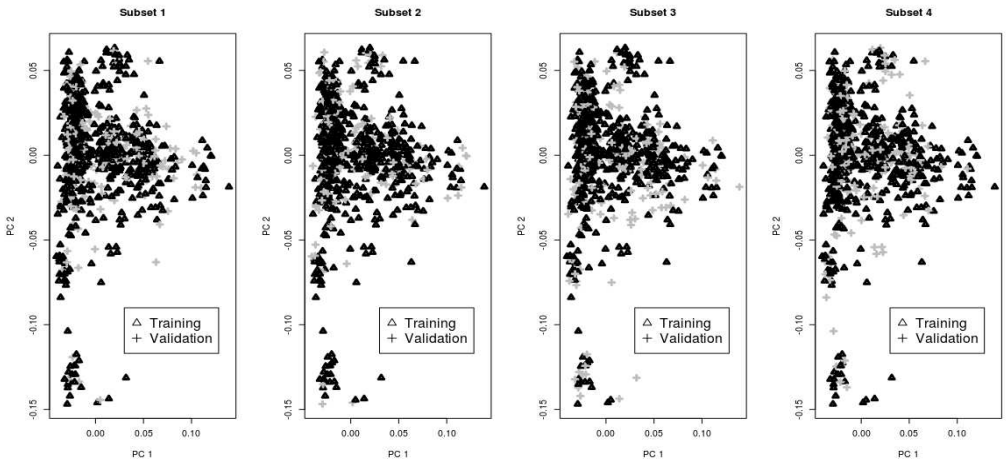

Figure 1 – Distribution of training and validation set in each cross-validation design made by principal components (PC1 and PC2) analyses based on the genomic matrix.

The estimated breeding value (EBV) and adjusted phenotype (Yc) were used as pseudo-phenotypes. The deregressed EBV was not considered as pseudo-phenotype once close to 50% of genotyped animals had unknown sire due to the presence of multiple sire mating system. The Yc was adjusted using an animal model considering the fixed effects of contemporary group (crop, farm and management group at yearling) and the covariate age at slaughter in each trait:

$$\mathbf{Y = Xb + Za + e}$$

where **Y** is a vector of phenotypic values of given quantitative traits, **b** is a vector of fixed effects and covariate, **a** is a vector of random animal effect with distribution $N \sim (0, A\sigma^2_a)$, **X** and **Z** are incidence matrixes of fixed and random effects, respectively, and **e** is the random residual vector with distribution $N \sim (0, I\sigma^2_e)$, where **A** is the relationship matrix, **I** is an identity matrix, $\boldsymbol{\sigma^2_a}$ is the additive genetic variance and $\boldsymbol{\sigma^2_e}$ is the residual variance.

The EBV was estimated based on BLUP method, using an animal model considering the random additive direct and residual effects, the fixed effects of contemporary group, and the covariate age at slaughter (linear). Single-trait analyses were performed:

$$\mathbf{Y = Xb + Za + e}$$

where **Y** is a vector of phenotypic values of given quantitative traits, **b** is a vector of fixed effects and covariate, **a** is a vector of random animal effect with distribution N ~ (0, $A\sigma^2_a$), **X** and **Z** are incidence matrixes of fixed and random effects, respectively, and **e** is the random residual vector with distribution N ~ (0, $I\sigma^2_e$), where **A** is the relationship matrix, **I** is an identity matrix, $\boldsymbol{\sigma^2_a}$ is the additive genetic variance and $\boldsymbol{\sigma^2_e}$ is the residual variance.

The general model for the genomic predictions can be expressed as follows:

$$\mathbf{Y = 1\,\mu + Xg + e}$$

where **Y** is the vector of pseudo-phenotypes (EBV or Yc); **1** is the vector of 1s; **μ** is the overall mean; **X** is the matrix (n x p) that consists of p SNPs for n animals; **g** is the random vector of SNP effects, and **e** is the random residual vector with distribution N ~ (0, $I\sigma^2_e$), where **I** is an identity matrix and $\boldsymbol{\sigma^2_e}$ is the residual variance. The genotypes were coded as 0, 1, 2 for genotypes AA, Aa (or aA) and aa, respectively.

A chain of 500,000 iterations, with a burn-in period of 80,000 iterations was used for Gibbs sampling, and all samples were stored in the GS3 software developed by Legarra et al. (2013). The prior distribution assigned to markers effects differs depending on the method (SNP-BLUP, BayesC or Bayesian Lasso), as explained below:

SNP-BLUP: The SNPs effects are estimated with BLUP *a priori* assuming a normal distribution and equal variance for all markers. The variance from the SNPs effects were obtained according to Legarra (2014):

$$\boldsymbol{\sigma^2_g} = \frac{\boldsymbol{\sigma^2_u}}{\mathbf{2}\sum \mathbf{q_j}(\mathbf{1} - \mathbf{q_j})}$$

where $\boldsymbol{\sigma^2_u}$ is the previous genetic variance, $\mathbf{q_j}$ is the allele frequency at a given marker **j**.

Bayesian LASSO: For this method, the marginal prior distribution for SNPs effects is a double exponential function (PARK & CASELA, 2008; CAMPOS et al., 2009; CAMPOS et al., 2013). The shape of SNP effects distribution determined by λ, which determines the variance of SNP effects, with a prior gamma distribution for λ^2.

BayesCπ: For this method, which used the π estimated from the analyzed data set, an additional variable is included (δ_i), which informs whether the marker has an effect (1) or not (0). The prior distribution of δ is binomial, with probability of π being zero (no effect). When the probability is 1-π, it is assumed that this portion of the markers with effect follows a normal distribution. In this method, it is assumed that variance is common to all SNPs, following a scaled inverse chi-squared, a priori distribution with v_a degrees of freedom and scale parameters S^2_a.

BayesC: This method is similar to the BayesCπ, but presents the assumption that π is fixed (KIZILKAYA et al., 2010; LEGARRA, 2014). In the present study, the π was fixed at zero.

For all methods, the DGV was predicted from the estimated SNPs effects using the following equation:

$$\mathbf{DGV} = \sum_{\mathbf{j}}^{\mathbf{n}} \mathbf{X_{ij}} \hat{\mathbf{g}}_\mathbf{i}$$

where **n** is the number of SNPs; $\mathbf{X_i}$ is the genotype of animal i for SNP j (coded as 0, 1 or 2), and $\hat{\mathbf{g}}_\mathbf{j}$ is the estimated SNP substitution effect for SNP j that was estimated from the training population.

The correlation coefficient between Yc or EBV and DGV were used to evaluate the prediction ability of the methods. The analyses that used Yc as response variable, the prediction accuracy was obtained by dividing the correlation between Yc and DGV by the square root of the heritability (h) of the trait, as described by Legarra et al. (2008). The linear regression coefficient of the pseudo-phenotype on DGV was considered to express the bias magnitude of DGV relative to the pseudo-phenotype. Values close to one are considered the most desirable. Both correlation and bias were used to evaluate and compare the prediction ability of the methods.

2.3 - Result and discussion

2.3.1 - Fatty acid profile

The descriptive statistics for composition of the most relevant individual SFA, MUFA and PUFA, and for the sum of the SFA, MUFA, PUFA, n-3, n-6, n-6/n-3 ratio, and PUFA/SFA ratio are presented in Table 1.

Table 1. Descriptive statistics for fatty acid composition (g/100g) in *Longissimus thoracis* muscle from Nelore cattle

Trait[a]	Chain Structure	Sample size	Mean	SD[b]
Myristic acid	C14:0	867	2.13	0.54
Palmitic acid	C16:0	867	21.03	2.49
Palmitoleic acid	C16:1	893	2.18	0.79
Stearic acid	C18:0	783	13.63	3.32
Myristoleic acid	C14:1	824	0.32	0.22
Elaidic acid	C18:1 n-9	483	2.90	5.07
Oleic acid	C18:1	934	17.60	14.77
Vaccenic acid	C18:1 n-7	878	15.05	15.33
Linoleic acid	C18:2 n-6	865	8.32	3.63
Conjugated Linoleic Acid (CLA)	C18:2 *cis*-9 *trans*-11	727	0.26	0.11
α-linolenic acid	C18:3 n-3	858	0.59	0.25
γ-linolenic acid	C18:3 n-6	569	0.08	0.08
Eicosatrienoic acid	C20:3 n-3	862	0.49	0.19
Docosahexaenoic acid	C22:6 n-3	865	0.95	0.39
Sum of saturated fatty acid (SFA)		868	40.66	6.12
Sum of monounsaturated fatty acid (MUFA)		868	37.55	8.05
Sum of polyunsaturated fatty acid (PUFA)		868	13.42	5.57
Sum of omega 3 (n-3)		868	3.81	1.55
Sum of omega 6 (n-6)		868	9.35	4.44
Ratio of n-6 and n-3 (n-6/n-3)		868	2.54	0.97
Ratio of PUFA and SFA (PUFA/SFA)		868	0.35	0.20
BF		1,564	4.02	2.7
IMF		1,812	0.82	0.42

[a] Concentration of fatty acids as a percentage of total fatty acids (FAME) quantified; BF: subcutaneous fat thickness (mm) measured between the 12th and 13th ribs; IMF: total intramuscular fat (%) in the *Longissimus thoracis* muscle; [b] Standard deviation.

Our results agreed with those reported by Kelly, Tume, Newman, and Thompson (2013) and Cesar et al. (2014) who also observed C16:0, C18:0 and C18:1 in the highest concentrations, however, in different proportions as ours (Table

1). The difference in FAs proportions observed by these authors could be due to the different degrees of carcass adipose tissue (WOOD & ENSER, 1997; PRADO et al., 2003), since lower fat deposition can result in higher PUFA and lower oleic acid deposition (RULE, 1997). According to Lawrie (2005), the individual SFAs predominant in cattle meat are C16:0, C14:0 and C18:0, as found in this study. The C14:0 and C16:0 are associated with an increase in circulating LDL cholesterol due to interference with hepatic LDL receptors (WOOLLETT et al., 1992; KATAN et al., 1994).

The MUFAs such as C18:1 and C18:1 n-7, and the PUFA such as linoleic were found in the highest concentrations in this study (Table 1). The C18:1 n-7 is a naturally occurring trans-fat found in red meat, and has been reported as having beneficial health effects on humans (LOCK et al., 2005; KELLY et al., 2013). Compared with other studies, the C18:2 n-6 concentration obtained in this study was higher (8.32%), since Prado et al. (2003) and Cesar et al. (2014) observed 3.74% and 1.60% for C18:2 n-6 concentration, respectively.

According to Wood and Enser (1997), a potential benefit of feeding diets rich in linolenic acid is that it could lead to an increased synthesis of long-chain PUFA such as eicosapentaenoic and docosahexaenoic acid, which are n-3 FAs involved in decreasing the blood thrombotic tendency. The n-3 concentration (3.81%) was higher than those reported by Cesar et al. (2014) (0.44%), Ekine-Dzivenu et al. (2014) (0.18%), and Prado et al. (2003) (5.39%). Rossato et al. (2010) showed that zebu breeds genetically have higher levels of higher n-3 FA than Angus meat. The n-6/n-3 ratio was lower than 4.84 found by Cesar et al. (2014), and higher than 1.58 found by Rossato et al. (2010). For human health, the optimal n-6/n-3 ratio ranges from 1 to 4 depending on the disease considered (SIMOPOULOS, 2002).

In the present study, the state of saturation was predominated by SFAs (40.66%), followed by the MUFAs (37.55%) and PUFAs (13.42%). Prado et al. (2003) reported similar results in Nelore breed: 43.93%, 42.33% and 12.08% for SFAs, MUFAs and PUFAs, respectively. However, the quantities reported by these authors were relatively high, and a slightly difference was observed between MUFA and SFA. Pitchford, Deland, Siebert, Malau-Aduliand, and Bottema (2002) and Cesar et al. (2014) also found similar concentrations for SFA (47%), 47.23% and 48.34% for

MUFA, in taurine and Nelore breeds, respectively. Beef and lamb meat normally have a low PUFA/SFA ratio due to their biohydrogenation of unsaturated FAs in the rumen and mean values may range largely depending on genetic and non-genetic factors (SMET et al., 2004).

Prado et al. (2003), Kelly et al. (2013), and Cesar et al. (2014) found a lower proportion of PUFA, 12.08%, 1.26%, and 2.87%, respectively, than the one obtained in the present study (13.42%). This difference is probably due to the high concentration of linoleic FA, as previously explained. Silva, Prado, Matsushita, and Souza (2002) working with crossbred heifers (European x zebu), found on MUFAs the most abundant FAs (40 to 55%) among all analyzed, with the greatest proportion for oleic. This difference is probably due to the experimental diets used in each study (SILVA et al., 2002). Studies have shown that in feedlot finishing systems, *Bos taurus taurus* meat presents lower percentages of SFA, higher percentages of MUFA, and similar levels of PUFAs compared to *Bos taurus indicus* meat (PERRY et al., 1998; MENEZES et al., 2009; ROSSATO et al., 2010; BRESSAN et al., 2011). According with Feitosa et al. (2017) who worked with the same data set used in this study, the mean and standard deviation values for shear force (5.17±1.4), intramuscular fat content (0.82±0.42%) and back fat thickness (4.02±2.7mm) indicated that the beef acceptability could compromised in some international markets. However, the Nelore beef has attributes that are beneficial to human health such as low intramuscular fat content and a beef fatty acid profile with high levels of the n-3 series and an adequate dietary quality based on the n-6/n-3 and PUFA/SFA ratios.

2.3.2 - Genomic predictive ability

Comparing the prediction methods using different pseudo-phenotypes for the SFA (Table 2), the Yc showed the best prediction ability. When comparing the prediction methods with the best pseudo-phenotype, the SNP-BLUP showed the best prediction ability for the myristic and palmitic FA, while the Bayesian methods were superior for stearic and sum of SFA.

Table 2. Accuracies of genomic predictions by different methods measured by Pearson's correlation between pseudo-phenotype and direct genomic breeding values ($r_{(Yi,DGV)}$) and standard error (SE) for beef saturated fatty acids of Nelore cattle

Fatty acid (g/100g)	Pseudo-phenotype	$r_{(Yi,DGV)}$[a] ± (SE)							
		SNP-BLUP		Bayesian LASSO		BayesC		BayesCπ	
C14:0	Yc	0.30	(0.03)	0.19	(0.07)	0.15	(0.08)	0.15	(0.10)
	EBV	0.20	(0.02)	0.16	(0.06)	0.10	(0.07)	0.16	(0.08)
C16:0	Yc	0.25	(0.06)	0.13	(0.06)	0.15	(0.03)	0.19	(0.10)
	EBV	0.14	(0.03)	0.07	(0.04)	0.03	(0.05)	0.09	(0.04)
C18:0	Yc	0.16	(0.14)	0.28	(0.03)	0.13	(0.13)	0.19	(0.15)
	EBV	0.05	(0.03)	0.07	(0.03)	-0.01	(0.04)	0.03	(0.04)
Sum of SFA	Yc	0.20	(0.19)	0.12	(0.07)	0.17	(0.11)	0.24	(0.12)
	EBV	0.17	(0.04)	0.04	(0.05)	0.10	(0.02)	0.09	(0.03)

[a] For the *Yc* as response variable, $r_{(yi,DGV)}$ was divided by the square root of heritability of the trait; *Yc* phenotype adjusted for fixed effects, *EBV* estimated breeding value, *SFA* saturated fatty acid.

When using different pseudo-phenotypes to compare MUFA (Table 3), the Yc showed the best prediction ability for the oleic and total sum of MUFA; with the exception for myristoleic, palmitoleic, and vaccenic FA. For the SNP-BLUP method, when the Yc was superior or close, it showed the best prediction ability; regarding the EBV as the best pseudo-phenotype for the myristoleic FA, the SNP-BLUP was superior to Bayesian methods.

Table 3. Accuracies of genomic predictions by different methods measured by Pearson's correlation between pseudo-phenotype and direct genomic breeding values ($r_{(Yi,DGV)}$) and standard error (SE) for beef monounsaturated fatty acids of Nelore cattle .

Fatty acid (g/100g)	Pseudo-phenotype	$r_{(Yi,DGV)}$[a] ± (SE)							
		SNP-BLUP		Bayesian LASSO		BayesC		BayesCπ	
C14:1	Yc	0.03	(0.03)	-0.02	(0.08)	0.08	(0.06)	-0.01	(0.06)
	EBV	0.42	(0.03)	0.02	(0.02)	0.10	(0.02)	0.05	(0.01)
C16:1	Yc	-0.23	(0.23)	-0.37	(0.13)	-0.54	(0.25)	-0.50	(0.33)
	EBV	0.03	(0.03)	-0.01	(0.06)	0.00	(0.04)	0.09	(0.01)
C18:1 n-9	Yc	0.12	(0.12)	0.11	(0.04)	0.13	(0.05)	0.10	(0.06)
	EBV	0.07	(0.04)	0.00	(0.03)	0.02	(0.06)	0.06	(0.01)
C18:1	Yc	0.33	(0.07)	0.34	(0.15)	0.33	(0.02)	0.32	(0.06)
	EBV	0.16	(0.05)	0.09	(0.04)	0.07	(0.05)	0.09	(0.04)
C18:1 n-7	Yc	0.14	(0.05)	0.04	(0.05)	-0.06	(0.08)	-0.11	(0.05)
	EBV	0.13	(0.04)	0.03	(0.03)	-0.01	(0.06)	0.06	(0.04)
Sum of MUFA	Yc	0.12	(0.03)	0.10	(0.02)	0.13	(0.05)	0.07	(0.04)
	EBV	0.07	(0.02)	0.10	(0.02)	0.06	(0.03)	0.05	(0.03)

[a] For the *Yc* as response variable, $r_{(yi,DGV)}$ was divided by the square root of heritability of the trait; *Yc* phenotype adjusted for fixed effects, *EBV* estimated breeding value, *MUFA* monounsaturated fatty acid.

The Yc for PUFA (Table 4) revealed similar prediction ability as those revealed by EBV for almost all FA, with an exception for α-linolenic acid and CLA in which the EBV was superior. This exception, however, must consider the reduced sample size, which might limit the accuracy. SNP-BLUP and Bayesian methods showed close results regarding the prediction ability for linoleic, γ-linolenic, docosahexaenoic, sum of n-6 and n-3, n-6/n-3 ratio, eicosatrienoic, PUFA/SFA ratio, and sum of PUFA; while the SNP-BLUP method showed better prediction ability for CLA and α-linolenic FA.

Table 4. Accuracies of genomic predictions measured by Pearson's correlation between pseudo-phenotype and direct genomic breeding values ($r_{(Yi,DGV)}$), and standard error (SE) for beef polyunsaturated fatty acids of Nelore cattle based on different methods

Fatty acid (g/100g)	Pseudo-phenotype	$r_{(Yi,DGV)}$[a] ± (SE)							
		SNP-BLUP		Bayesian LASSO		BayesC		BayesCπ	
C18:2 n-6	Yc	0.25	(0.10)	0.23	(0.06)	0.22	(0.06)	0.12	(0.11)
	EBV	0.21	(0.02)	0.13	(0.06)	0.11	(0.06)	0.11	(0.07)
C18:2 *cis*-9 *trans*-11	Yc	0.13	(0.06)	-0.11	(0.13)	-0.04	(0.09)	-0.07	(0.10)
	EBV	0.21	(0.02)	0.08	(0.04)	0.10	(0.01)	0.18	(0.03)
C18:3 n-3	Yc	-0.01	(0.09)	0.00	(0.05)	0.06	(0.07)	-0.03	(0.04)
	EBV	0.14	(0.01)	0.07	(0.05)	0.06	(0.03)	0.07	(0.05)
C18:3 n-6	Yc	-0.02	(0.04)	-0.05	(0.06)	0.10	(0.03)	0.09	(0.01)
	EBV	0.01	(0.01)	0.00	(0.05)	0.08	(0.03)	0.05	(0.04)
C20:3 n-3	Yc	-0.06	(0.12)	0.13	(0.06)	0.12	(0.04)	0.19	(0.08)
	EBV	0.12	(0.03)	0.06	(0.05)	0.09	(0.03)	0.10	(0.03)
C22:6 n-3	Yc	0.10	(0.08)	0.18	(0.11)	0.15	(0.13)	0.18	(0.12)
	EBV	0.36	(0.18)	0.36	(0.19)	0.33	(0.22)	0.31	(0.21)
Sum of n-3	Yc	0.12	(0.02)	0.24	(0.11)	0.11	(0.12)	0.25	(0.10)
	EBV	0.07	(0.06)	0.07	(0.06)	0.05	(0.07)	0.12	(0.05)
Sum of n-6	Yc	0.32	(0.09)	0.26	(0.07)	0.34	(0.07)	0.24	(0.08)
	EBV	0.22	(0.03)	0.14	(0.08)	0.22	(0.03)	0.15	(0.07)
n-6/n-3	Yc	-0.07	(0.12)	-0.02	(0.06)	-0.12	(0.15)	0.19	(0.06)
	EBV	0.11	(0.05)	-0.02	(0.01)	0.05	(0.05)	0.07	(0.05)
Sum of PUFA	Yc	0.50	(0.13)	0.45	(0.12)	0.56	(0.07)	0.48	(0.10)
	EBV	0.24	(0.03)	0.15	(0.08)	0.16	(0.07)	0.15	(0.09)
PUFA/SFA	Yc	0.28	(0.15)	0.17	(0.13)	0.21	(0.12)	0.13	(0.17)
	EBV	0.32	(0.14)	0.32	(0.15)	0.33	(0.17)	0.32	(0.15)

[a] For the *Yc* as response variable, $r_{(yi,DGV)}$ was divided by the square root of heritability of the trait, *Yc* phenotype adjusted for fixed effects, *EBV* estimated breeding value, *SFA* saturated fatty acid, *n-3* and *n-6* total of omega 3 and 6 fatty acids respectively, *n-6/n-3* ratio of omega 6 to omega 3 fatty acids, *PUFA* Polyunsaturated fatty acid, *PUFA/SFA* ratio of polyunsaturated to saturated fatty acid.

Overall, when using EBV in reduced samples size such as C14:0, C16:0, C14:1, C18:2 n-6, C18:2 cis-9 trans-11, and C18:3 n-3, the SNP-BLUP method showed superiority to Bayesian methods for almost all FA. On the other hand, when considering the Yc, the opposite was observed. Different from the result obtained in this study for Bayesian methods, Saatchi et al. (2013) observed high accuracies in Angus cattle for C14:0 and C16:0. Neves et al. (2014) disclosed that Lasso and BayesC methods were superior to SNP-BLUP method in growth traits for 685 Nelore animals, suggesting the segregation of major genes effect for the studied traits as the reason for the superiority of Bayesian methods.

The divergence between studies suggests that the difference within the methods is due to the genetic architecture of the trait i.e., the accuracy tends to increase as the model adjusts itself to the genetic architecture of the trait (LUND et al., 2009). For traits that are affected by moderate to major genes effect, higher accuracies can be reached through Bayesian methods (Neves et al., 2014). Traits that are controlled by many genes with small effects, the SNP-BLUP method shows better prediction ability (CLARK et al., 2011). Nonetheless, Daetwyler et al. (2010) in a simulation study proposed that the Bayesian method's superiority over the SNP-BLUP methods depends on the number of QTL for the trait. If the QTL number is higher than the effective number of chromosomal segments, the SNP-BLUP method shows better or similar prediction ability than Bayesian methods. In addition, the computational time displays an advantage of SNP-BLUP methods, Colombani et al. (2013) and Neves et al. (2014) figured out that Bayesian methods were less time effective.

These results demonstrated that the genomic prediction would lead to an increase in accuracy above that achieved with standard BLUP. Wiggans, Vanraden, and Cooper (2011) reported reliability gains for milk traits above parent average ranging in young bulls from 2.7 to 47.6 percentage units for Holsteins, 9.6 to 29.2 percentage units for Jerseys, and 3.0 to 25.8 percentage units for Brown Swiss. In beef cattle, Garrick (2011) stated that genomic prediction offers accuracies that exceed those of pedigree-based parent average of young selection candidates, and it can be equivalent to progeny tests based on up to 10 offspring.

In terms of magnitude of the observed results, Bolormaa et al. (2013) reported that although the prediction accuracy is still low in beef cattle compared with dairy cattle, this should not be a limiting, since genomic selection can improve traits which are difficult to measure, such as beef FA profile. Although the results presented here have a low to moderate accuracy, when considering the high cost of measurement and the difficulty of selecting animals for meat quality traits such as FA, the implementation of genomic selection in Nelore might be a viable alternative.

2.3.3 - Inflation/deflation of genomic prediction

By considering the Yc for SFA (Table 5), the regression coefficient estimates ($b_{(Yc,DGV)}$) for both the Bayesian methods as well as for the SNP-BLUP were, on average, below to one for all FA. When considering EBV, the Bayesian methods (LASSO and BayesCπ) showed a regression coefficient ($b_{(EBV,DGV)}$) close to one for C14:0, and lower to one for C16:0, C18:0 and sum of SFA, being inflated. The SNP-BLUP method showed ($b_{(EBV,DGV)}$) superior to one for sum of SFA, being deflated.

When considering the Yc for MUFA, the $b_{(Yc,DGV)}$ (Table 6) were lower to one for all considered FA and for all methods, being inflated. Considering EBV, $b_{(EBV,DGV)}$ estimate were inflated in all analyzed methods for C16:1, C18:1 n-9, C18:1 n-7, and sum of MUFA. Estimates were deflated for C14:1 using the SNP-BLUP method, and inflated for C18:1 using Bayesian methods.

The $b_{(Yc,DGV)}$ estimate for PUFA (Table 7) considering the Yc were, on average, lower to one when inflated; except for C18:2 *cis*-9 *trans*-11, C18:3 n-6, C20:3 n-3, and PUFA/SFA ratio in which values were higher than one, being deflated. Considering EBV, the $b_{(EBV,G)}$ estimate using SNP-BLUP method were close to one for C18:2 n-6, C18:2 *cis*-9 *trans*-11, C18:3 n-3, C20:3 n-3, C22:6 n-3, sum of n-3 and n-6, and n-6/n-3 ratio; and lower to one for C18:3 n-6, and superior to one for sum of PUFA. Using Bayesian methods, estimate were close to one for C18:2 *cis*-9 *trans*-11, C22:6 n-3, sum of n-3 and n-6, and PUFA; deflated for PUFA/SFA ratio, and inflated for C18:2 n-6, C18:3 n-3 and C18:3 n-6, and C20:3 n-3.

Table 5. Regression coefficient of the pseudo-phenotype on direct genomic breeding values ($b_{(Yi,DGV)}$) and standard error (SE) for beef saturated fatty acids of Nelore cattle based on different methods

Fatty acid (g/100)	Pseudo-phenotype	$b_{(Yi,DGV)}$ ± (SE)							
		SNP-BLUP		Bayesian LASSO		BayesC		BayesCπ	
C14:0	Yc	0.40	(0.04)	0.19	(0.10)	0.18	(0.10)	0.20	(0.11)
	EBV	0.47	(0.05)	0.99	(0.70)	0.30	(0.17)	0.82	(0.53)
C16:0	Yc	0.36	(0.12)	0.12	(0.05)	0.12	(0.05)	0.17	(0.06)
	EBV	0.56	(0.10)	0.38	(0.26)	0.17	(0.11)	0.33	(0.21)
C18:0	Yc	0.32	(0.09)	0.07	(0.02)	0.04	(0.02)	0.07	(0.02)
	EBV	0.24	(0.05)	0.01	(0.00)	0.01	(0.00)	0.03	(0.02)
Sum of SFA	Yc	0.17	(0.07)	0.10	(0.07)	0.10	(0.07)	0.15	(0.06)
	EBV	1.12	(0.24)	0.47	(0.47)	0.22	(0.11)	0.59	(0.37)

Yc phenotype adjusted for fixed effects, *EBV* estimated breeding value, *SFA* saturated fatty acid.

Table 6. Regression coefficient of the pseudo-phenotype on direct genomic breeding values ($b_{(Yi,DGV)}$) and standard error (SE) for beef monounsaturated fatty acids of Nelore cattle based on different methods

Fatty acid (g/100g)	Pseudo-phenotype	$b_{(Yi,DGV)}$ ± (SE)							
		SNP-BLUP		Bayesian LASSO		BayesC		BayesCπ	
C14:1	Yc	0.30	(0.11)	0.07	(0.02)	0.12	(0.03)	0.06	(0.02)
	EBV	1.65	(0.18)	0.01	(0.00)	0.03	(0.01)	0.02	(0.00)
C16:1	Yc	0.16	(0.11)	0.06	(0.02)	0.10	(0.04)	0.10	(0.05)
	EBV	0.55	(0.20)	0.44	(0.25)	0.08	(0.04)	0.33	(0.26)
C18:1 n-9	Yc	0.34	(0.06)	0.07	(0.02)	0.07	(0.03)	0.07	(0.03)
	EBV	0.68	(0.18)	0.02	(0.00)	0.03	(0.01)	0.03	(0.00)
C18:1	Yc	0.30	(0.10)	0.08	(0.07)	0.08	(0.02)	0.08	(0.04)
	EBV	3.43	(1.19)	1.74	(1.47)	0.55	(0.34)	1.07	(0.49)
C18:1 n-7	Yc	0.13	(0.04)	0.04	(0.02)	0.07	(0.03)	0.05	(0.02)
	EBV	0.77	(0.17)	0.02	(0.01)	0.01	(0.00)	0.02	(0.01)
Sum of MUFA	Yc	0.13	(0.03)	0.09	(0.04)	0.10	(0.04)	0.08	(0.04)
	EBV	0.37	(0.11)	0.38	(0.21)	0.15	(0.08)	0.33	(0.18)

Yc phenotype adjusted for fixed effects, *EBV* estimated breeding value, *MUFA* monounsaturated fatty acid.

Table 7. Regression coefficient of the pseudo-phenotype on direct genomic breeding values ($b_{(Yi,DGV)}$) and standard error (SE) for beef polyunsaturated fatty acids of Nelore cattle based on different methods

Fatty acid (g/100g)	Pseudo-phenotype	$b_{(Yi,DGV)}$ ± (SE)							
		SNP-BLUP		Bayesian LASSO		BayesC		BayesCπ	
C18:2 n-6	Yc	0.31	(0.14)	0.17	(0.07)	0.16	(0.07)	0.15	(0.07)
	EBV	1.13	(0.17)	0.72	(0.51)	0.30	(0.19)	0.61	(0.42)
C18:2 *cis*-9 *trans*-11	Yc	5.51	(2.14)	0.12	(0.03)	0.09	(0.03)	0.11	(0.03)
	EBV	1.59	(0.24)	0.44	(0.29)	0.17	(0.09)	0.79	(0.31)
C18:3 n-3	Yc	0.95	(0.38)	0.05	(0.02)	0.07	(0.02)	0.05	(0.01)
	EBV	0.83	(0.13)	0.51	(0.36)	0.16	(0.09)	0.44	(0.30)
C18:3 n-6	Yc	1.18	(1.04)	0.06	(0.04)	0.05	(0.02)	0.07	(0.03)
	EBV	0.07	(0.04)	0.04	(0.01)	0.05	(0.02)	0.08	(0.06)
C20:3 n-3	Yc	1.69	(0.30)	0.08	(0.03)	0.30	(0.23)	0.11	(0.04)
	EBV	0.83	(0.23)	0.56	(0.45)	0.22	(0.14)	0.58	(0.32)
C22:6 n-3	Yc	0.58	(0.31)	0.19	(0.11)	0.20	(0.10)	0.19	(0.11)
	EBV	1.59	(0.51)	1.40	(0.62)	0.66	(0.32)	1.19	(0.53)
Sum of n-3	Yc	0.14	(0.02)	0.13	(0.07)	0.09	(0.08)	0.14	(0.07)
	EBV	0.75	(0.55)	0.75	(0.55)	0.23	(0.17)	0.88	(0.43)
Sum of n-6	Yc	0.40	(0.13)	0.22	(0.09)	0.25	(0.07)	0.21	(0.09)
	EBV	1.11	(0.13)	0.76	(0.46)	1.11	(0.13)	0.60	(0.35)
n-6/n-3	Yc	0.18	(0.06)	0.04	(0.01)	0.10	(0.04)	0.07	(0.01)
	EBV	0.90	(0.24)	0.01	(0.00)	0.09	(0.09)	0.22	(0.20)
Sum of PUFA	Yc	0.38	(0.11)	0.26	(0.07)	0.33	(0.04)	0.28	(0.06)
	EBV	2.28	(0.28)	0.75	(0.44)	0.35	(0.20)	0.64	(0.36)
PUFA/SFA	Yc	2.65	(2.56)	0.15	(0.09)	0.15	(0.09)	0.16	(0.08)
	EBV	2.35	(0.61)	2.44	(0.69)	1.41	(0.42)	2.45	(0.70)

Yc phenotype adjusted for fixed effects, *EBV* estimated breeding value, *SFA* saturated fatty acid, *n-3* and *n-6* total of omega 3 and 6 fatty acids respectively, *n-6/n-3* ratio of omega 6 to omega 3 fatty acids, *PUFA* Polyunsaturated fatty acid, *PUFA/SFA* ratio of polyunsaturated to saturated fatty acid.

Overall, the SNP-BLUP method demonstrated a regression coefficient estimate closest to one than Bayesian methods, obtaining a less biased estimate, which favors its adoption in genetic selection for FA profile in Nelore meat. When the predictions are deflated and higher than one, in practice, the difference between progenies from selected animals are expected to be greater than those predicted by DGV, and the opposite occurs when the predictor is inflated. Considering pseudo-phenotype, the EBV exhibited the less biased regression coefficient estimate regarding the Yc. Different from our results, a resemblance between the Bayesian Ridge Regression model, BayesC, and Lasso were reported by Fernandes Júnior et al. (2016) in Nelore cattle for ribeye area, subcutaneous fat, and hot carcass weight.

The differences regarding the pseudo-phenotype are in agreement with the literature (BODDHIREDDY et al., 2014; MOROTA et al., 2014). Genomic selection studies for novel traits in beef cattle (SILVA et al., 2016; FERNANDES JÚNIOR et al., 2016), such as feed efficiency and beef quality traits, reported higher genomic prediction ability for adjusted phenotypic used as pseudo-phenotypes over EBV obtained from traditional BLUP. In beef cattle, the EBV obtained from BLUP model in general is less appropriated due to poor pedigree structure and small training population. These results obtained in this study were in accordance with Fernandes Júnior et al. (2016), whom indicated the Yc instead of EBV as pseudo-phenotype in genomic prediction for highly heritable traits, in spite of the lower biased observed when using EBV.

Overall, regarding the accuracies, the methods were similar and in agreement with the literature (MOSER et al. 2009; DE LOS CAMPOS et al., 2013; FERNANDES JÚNIOR et al., 2016). According to De los Campos et al. (2013), studies using real data do not always reveal relevant differences between methods, which can be attributed to the large number of regression coefficients that need to be inferred from a small number of samples ($n < p$). Another factor that could explain the similarity of results across the methods is the complex nature of the traits studied. According to Daetwyler et al. (2013), different methods tend to show similar predictive ability when the traits are affected by many small-effect loci.

Beef fat composition could be viewed in a more favorably standpoint for human health if effective approaches could be applied to decrease beef SFA content, while increasing the concentration of beneficial FA, such as PUFA, especially n-3 and C18:2 *cis*-9 *trans*-11. Thus, genomic information can be used to reduce SFA concentration in meat, mainly for C14:0 for being the most harmful to health, C16:0, and sum of SFA. In order to increase the concentration of MUFA, such as C18:1 and C18:1 n-7, as a result of its biological importance as precursors of PUFA and because of its importance on human health, the SNP-BLUP method is the most appropriate in this context. For n-3 acids, such as C20:3 n-3, the accuracies were low, however, its function in cell function regulation, decreased triglycerides blood levels, anti-inflammatory response, among others factors, need further studies to determine the most suitable method for genomic prediction.

Recently, the European Union established a new legislation (Regulation (EU) No 1169/2011) on the provision of food information to consumers. In this new regulation established that is mandatory specify information about food chemical composition, such as the amounts of fat saturates, monounsaturated, polyunsaturated, carbohydrate, sugars, protein and salt. Similarly, in United States, the Food Safety and Inspection Service (FSIS) developed a compliance guideline to help the industry determine which statements are permitted on the labeling of their products and the criteria for their use, particularly for omega fatty acids from animal sources. All these regulations aimed to give more detailed information to consumer about food chemical composition and potential impacts on human health. Moreover new and evolving food labelling legislation should protect the consumer from misleading claims about the health benefits of a food or any of its components. Although the beef fatty acid profile is not considered as selection criteria in beef cattle breeding programs, due to the high cost to obtain the phenotype and analyses' operating cost, is important that the breeders have alternative tools to improve the beef fatty acid composition in view of the greater demand of consumers.

Despite the prediction accuracies were not very high, the use of genomic information to predict genomic values for beef FA profile in breeding animals is a feasible alternative, with a reasonable cost, to contribute for meat quality improvement. In addition, for commercial herds the results of this study would give support to make better management decision within the farm in order to achieve different niche of markets. This would help the farmers to meet the requirements to participate in a special meat certification programs (prime beef cuts) that bonus for higher meat quality, for example beef fatty acid composition. Despite the large differences among the studied methods, the SNP-BLUP method is a worthwhile alternative for application in genomic evaluations on a large scale, considering the low computational requirement time and the similarity of the results obtained with the Bayesian methods.

2.4 - Conclusions

Genomic information can assist in improving fatty acid profile in Zebu animals, since the use of genomic information yielded genomic values for fatty acid profile with

accuracies ranging from low to moderate. None of the methods excelled in terms of accuracy, however the SNP-BLUP method allows obtaining less biased genomic evaluations. Despite the lowest bias observed for EBV, the adjusted phenotype is the preferred pseudo-phenotype considering the genomic prediction accuracies regarding the context of the present study.

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CHAPTER 3 - GENOMIC PREDICTION FOR BEEF FATTY ACID PROFILE IN NELORE CATTLE USING DIFFERENT PSEUDO-PHENOTYPES[b]

ABSTRACT - The objective of this study was to determine the best pseudo-phenotype phenotype adjusted for fixed effect (Yc), estimated breeding value (EBV) and estimated genomic breeding value (GEBV) for genomic prediction by SNP-BLUP method, using simulated and real data (saturated, monounsaturated, omega 3, omega 6, ratio of polyunsaturated and saturated and polyunsaturated fatty acid profile), in the *Longissimus thoracis* muscle of Nelore cattle finished in feedlot. The inclusion of the GEBV obtained by single step genomic BLUP (ssGBLUP) method as pseudo-phenotype in this research is innovator in genomic prediction, to answer one of the frequent problems when using the matrix derived from pedigree, by the mating system that uses multiple sires for many cattle breeders. 10,000 animals with phenotype and genotype, considering 50% of multiple sires in the pedigree, were simulated. A total of 937 Nelore bulls with phenotype for fatty acid profiles, were genotyped using the Illumina BovineHD BeadChip (Illumina, San Diego, CA) with 777,962 SNP. To compare the accuracy and bias of direct genomic value (DGV) for different pseudo-phenotypes, the correlations between DGV or true breeding value (TBV) and pseudo-phenotypes and regression of DGV or TBV on pseudo-phenotypes were calculated for real or simulated data, respectively. For simulated data, the correlations between DGV and TBV for high heritability trait were higher than those obtained with low heritability trait, the GEBV presented higher correlation than Yc and EBV. For real data, the correlations for fatty acids profile were low to medium for Yc and EBV as pseudo-phenotype and high for GEBV as pseudo-phenotype. The regression coefficient estimates for fatty acids, were on average lower, close and higher than one for Yc, EBV and GEBV, respectively. Genomic information can assist on the improvement of beef fatty acid profile in Nelore, once that the use of genomic information yielded genomic values for fatty acid profile with accuracies ranging from low to moderate. Notwithstanding the ssGBLUP procedure was not developed to deal with paternity uncertainty situations, the ssGBLUP model is an appropriate alternative to obtaining more reliable and less biased GEBVs as pseudo-phenotypes, in situations of missing pedigree due to high proportion of multiple sires, being more appropriate than the EBVs or adjusted phenotype to predict direct genomic values.

Keywords: Genomic prediction, lipid profile, Nelore, ssGBLUP

[b] Article submitted in the "Journal Animal of Science and Biotechnogy "

RESUMO – O objetivo desta pesquisa foi de determinar o melhor pseudo-fenótipo como o fenótipo ajustado aos efeitos fixos (Yc), velor genético estimado pelo método BLUP (EBV) e valor genético genômico estimado pelo método passo único genômico BLUP (ssGBLUP) para predizer os valores genômicos pelo método SNP-BLUP, em dados simulados e reais de perfil de ácidos graxos (saturados, monoinsaturados, omega 3, omega 6 e relação poliinsaturado e saturado) em músculo *Longissimus thoracis* de Nelore terminados em confinamento. A inclusão do GEBV obtido pelo método passo único genômico BLUP (ssGBLUP) como pseudofenótipo nesta pesquisa é inédita em predição genômica, para responder um dos problemas frequentes ao utilizar a matriz advinda da informação genealógica, pela maioria dos produtores de gado de corte utilizarem o sistema de acasalamento que utiliza reprodutores multiplos. 10.000 animais com fenótipo e genótipo, considerando 50% de reprodutores múltiplos no pedigree, foram considerados na simulação. Cerca de 937 touros Nelore com fenótipo para perfil de ácidos graxos, foram genotipados com um painel de 777.962 SNPs (Illumina BovineHD BeadChip). Calculou-se a correlação entre DGV ou TBV e pseudo-fenótipos para comparar a acurácia e o viés dos valores genômicos diretos para dados reais ou simulados, respectivamente. Para dados simulados, as acurácias para características de alta herdabildade foram maiores em relação às de baixa herdabilidade, o GEBV apresentou maior acurácia em relação ao Yc e o EBV. Para dados reais, as acurácias variaram baixa a média para o Yc e o EBV, e alta para o GEBV como pseudo-fenótipos. Os coeficientes de regressão, em média, foram menor, próximo e maior que 1 para o Yc, EBV e GEBV, respectivamente. A informação genômica pode ajudar a melhorar o perfil de ácidos graxos da carne em Nelore, uma vez que o uso de informações genômicas produziu valores genômicos para perfil ácidos graxos com acurácia variando de baixa a moderada magnitude. Apesar do método ssGBLUP não ter sido desenvolvido para situações de incerteza de paternidade, é uma alternativa apropriada para obter GEBVs como pseudo-fenótipos mais acurados, com menor viés em situações de pedigree incompleto, devido a alta proporção de reprodutores múltiplos, sendo melhores que o EBV ou Yc para predizer os valores genômicos diretos.

Palavras-chave: Nelore, perfil de ácidos graxos, predição genômica, ssGBLUP

3.1 - Introduction

There are different pseudo-phenotypes used in genomic predictions, being necessary to determine the ideal for each trait of interest. The inclusion of the genomic estimated breeding value (GEBV) obtained by single step genomic BLUP (ssGBLUP) method as pseudo-phenotype in this research is innovator in genomic prediction, to answer one of the frequent problems when using the matrix derived from pedigree, by the mating system that uses multiple sires for many cattle breeders.

There is a continuing and growing concern about excessive fat consumption and their impact on human health, especially those from animal sources. The high consumption of saturated fatty acids (SFA) is associated with high serum cholesterol and low-density lipoproteins levels (LDL), which are risk factors for the occurrence of cardiovascular diseases (KATAN et al., 1994). The beef fatty acid (FA) profile is a difficult and costly trait to measure, since it depends from a progeny test to evaluate candidates to selection. Nevertheless, the genomic selection has potential to increase the genetic gain for hard measure traits such as the beef FA profile (SAATCHI et al., 2013).

According to Berry et al. (2016), the development of accurate genomic evaluations is more difficult in beef populations than in dairy populations for several reasons. Some of those reasons may include the presence of multiple breeds, poor extent of phenotyping, lack of artificial insemination, and beef systems being generally a lower-margin business of poorer adopter of technology. In extensive beef cow-calf production systems, multiple service sire is the most common mating system. Despite the management advantages of this mating system, it does not allow the progeny paternity identification, increasing the occurrence of missing pedigree and, consequently, compromising the genetic evaluation reliability. Models that consider the uncertain paternity using genomic data are not frequently used in animal breeding programs.

The method that improve the relationship matrix, called single-step genomic BLUP (ssGBLUP) proposed by Legarra et al. (2009) and Misztal et al. (2009), consists in combine the pedigree (**A** matrix) and genomic information (**G** matrix) into

a single matrix (**H**) to predict the genomic estimated breeding value (GEBV). Recently, Tonussi et al. (2017) obtained evaluations up to 30% more accurate using ssGBLUP over traditional BLUP in a beef cattle simulated population with 50% of multiple sires in the pedigree. These authors also recommended the use of genomic information especially for situations of missing pedigree, where the ssGBLUP method is an appropriate alternative to obtain more reliable and less biased breeding values for young and genotyped animals with missing pedigree.

Commonly, the estimated breeding value (EBV), deregressed EBV (dEBV) and the adjusted phenotype for fixed effects, are pseudo-phenotypes used in genomic selection to estimate the marker effects (BODDHIREDDY et al., 2014; MOROTA et al., 2014). Some genomic selection studies in beef cattle on novel traits, such as feed efficiency and beef traits, reported higher genomic prediction ability when the adjusted phenotypic records were used as pseudo-phenotypes to train the marker effects compared to the EBV (SILVA et al., 2016; FERNANDES JÚNIOR et al., 2016). In beef cattle, the EBV obtained from BLUP model is less appropriated due to pedigree structure and small training population. According to Muñoz et al. (2011), improvements in BLUP EBV can be obtained simply by correcting errors in the pedigree or using more complex approaches, such as applying a realized relationship matrix (RRM) in the BLUP prediction as an alternative to the relationship matrix (**A**) based on expected values derived from the pedigree.

The genomic selection is still rarely applied in the beef cattle industry especially for phenotypes that are difficult or expensive to measure, such as beef FA profile, which is probably due to the lack of sufficiently large reference populations and unreliable pseudo-phenotypes. The objective of this study was to compare the predictive ability of SNP-BLUP model using different pseudo-phenotypes such as phenotype adjusted for fixed effects (Yc), estimated breeding value (EBV) and genomic estimated breeding value (GEBV) using simulated and real data for beef FA profile of Nelore cattle finished in feedlot.

3.2 - Material and methods

3.2.1 - Real Data

The phenotypes and genotypes were obtained from 937 Nelore steers finished in feedlot for a minimum period of 90 days and slaughtered with an average of 24 months of age. The animals belonged to eight different farms located in the Southeast, Northeast, and Midwest regions of Brazil, which participate in three beef cattle breeding programs (Nelore Qualitas, Paint and Delta Gen). In these breeding programs, animals are selected based on growth, finishing, and sexual precocity traits. Breeding seasons differed among these farms; therefore, calving seasons were concentrated from August to October in some farms and from November to January in others. Weaning was performed at seven months of average age. Animals were raised on grazing conditions using *Brachiaria sp.*, *Panicum sp.* Forages and had free access to mineral salt. After yearling, the breeding animals were selected and the remaining animals were kept in feedlot with forage: concentrate ratio ranging from 50:50 to 70:30, depending on the farm. In general, whole-plant corn or sorghum silage was used as high-quality forage; corn grains and/or sorghum, soybeans, soybean meal and sunflower seeds were used as protein concentrate.

The farmers used the live weight (between 500 and 550 kg) as criteria for slaughtering the animals. The slaughters were carried out in commercials slaughterhouses in accordance with the Brazilian Federal Inspection Service procedures. After 48 hours post mortem stored between 0 and 2°C, samples from 2.54 cm thick were removed from the *Longissimus thoracis* muscle, between the 12 and 13th ribs from each animal, were placed in plastic bags, and stored at -80°C until further analyses.

Phenotypes

The beef FAs were extracted using the method described by Folch et al. (1957) and the methyl esters were formed according to Kramer et al. (1997). The beef FA profile was performed at the Meat Science Laboratory (LCC) in the Department of Animal Nutrition and Production at Faculty of Veterinary Medicine and Animal Science, University of São Paulo, Pirassununga, São Paulo, Brazil.

The FAs were quantified using a gas chromatography (GC-2010 Plus - Shimadzu AOC 20i auto-injector) with a SP-2560 capillary column (100m × 0.25mm in diameter with 0.02mm thickness, Supelco, Bellefonte, PA). The initiating temperature was 70°C with gradual warming (13°C min^{-1}) up to 175°C, holding for 27 minutes, and later a further increase of 4°C.min^{-1} until 215°C was reached and held for 31 minutes. Hydrogen (H_2) was used as the gas flower with 40cm^3 s^{-1}. Fatty acids were identified by comparison of retention time of methyl esters of the samples with standards of FAs standard C4-C24 (F.A.M.E mix Sigma®), vaccenic acid: C18:1 t11 (V038-1G, Sigma®), CLA: C18:2 t10 c12 (UC-61M 100mg), CLA: C18:2 cis-9, trans-11 (UC- 60M 100mg), (Sigma®) e tricosanoic acid (Sigma®). Fatty acids were quantified by normalizing the area under the curve of methyl esters using Software GS solution 2.42. Fatty acids content were expressed in percentage of total FA methyl ester quantified.

Genotyping

Animals were genotyped using the Illumina BovineHD BeadChip (Illumina, San Diego, CA) with 777,962 SNPs. Quality control was performed excluding those SNPs markers with unknown genomic position, located on sex chromosomes, monomorphic and markers with minor allele frequency (MAF) less than 0.05, call rate less than 90%, and excess of heterozygosity. Samples with a call rate less than 90% were also excluded. After quality control, there were 868 samples (Table 1) and 470,007 SNPs left in the dataset for analyses.

3.2.2 - Simulation

Data

A pedigree with phenotypes and genotypes of 10,000 animals were simulated, considering 50% of multiple sires in the pedigree according to Tonussi et al. (2017). Regarding to phenotypes, two traits were simulated, one with high heritability (0.42), another with low heritability (0.13), with heritabilities estimates based on real data (LEMOS et al., 2016). Ten replicates were performed for each trait and results were averaged among replicates.

A historical population was created from generation zero to 2,020, with a constant size of 2,000 animals (from generation zero to 1,000) to produce different levels of linkage disequilibrium (LD). Therefore, there was a gradual reduction in the number of animals (from 2,000 to 600), producing a “bottleneck effect” and consequently, genetic drift and LD starting in the generation 1,001 to 2,020.

About 200 animals of the 600 animals from the latest generation of the historical population were selected (males and females equally distributed) for the expanded population, which had its effective size simulated based on the real population (BRITO et al., 2011). To simulate the expanded population, the mating system based on random union of gametes, the absence of selection, an exponential growth of the number of females, and an average of five progenies per dam were considered.

After the expansion process, 240 males and 6,000 females from the last generation were randomly selected based on expected breeding value, including the founder animals of selection population. This population was span over 10 generations and the selected males and females from each generation were randomly mated, generating a single product with equal probability of being a male or a female. The replacement rate of sires and dams was kept constant at 60% and 20%, respectively.

Genome and phenotype

The simulated genome presented a total length of 2,333 cM, 735,293 markers and 7,000 QTLs randomly distributed over 29 *Bos taurus taurus* autosomes chromossome (BTA). The length of the bovine genome was based on Base 4.6.1 (SNELLING et al., 2007), and was assumed that QTLs explain 100% of genetic variance.

The number of markers and QTLs per chromosome ranged from 12,931 to 46,495 and from 121 to 438, respectively. All markers were bi-allelic, mimicking SNPs present in the bovine commercial panels. For QTL, the amount of alleles per loci randomly ranged from 2 to 4. Minor allele frequencies (MAF) were assumed

equally for markers and QTL alleles. QTL allele effects were sampled from a gamma distribution with a shape parameter equal to 0.4 (HAYES & GODDARD, 2001).

Mutation rate of 10^{-5} for markers and QTLs in the historical populations was considered. A total of 335,000 markers (with MAF greater or equal to 0.02) and 1,000 QTL were randomly selected from the last generation of the historical population to generate genotypic data for the selection population. The phenotypes of the animals were computed as the sum of the QTL effects and an error term sampled from a normal distribution with zero mean and 0.88 genetic variance. For simulated data, 4,000 animals of the generations 7, 8 and 9 (with genotype and phenotype) were used as training population, and 1,000 animals of the last generation (10) were used as validation population.

3.2.3 – Pseudo-phenotypes

The adjusted phenotype (Yc), EBV and combining pedigree and genomic matrix (GEBV) were used as pseudo-phenotypes. The Yc pseudo-phenotype was adjusted using an animal model considering the fixed effects of contemporary group (year of birth, farm and management group at yearling) and the covariate age at slaughter in each trait:

$$\mathbf{Y = Xb + Za + e}$$

where **Y** is a vector of phenotypic values of given quantitative traits, **b** is a vector of fixed effects and covariate, **a** is a vector of random animal effect with distribution $N \sim (0, A\sigma^2_a)$, **X** and **Z** are incidence matrixes of fixed and random effects, respectively, and **e** is the random residual vector with distribution $N \sim (0, I\sigma^2_e)$, where **A** is the relationship matrix, **I** is an identity matrix, $\boldsymbol{\sigma^2_a}$ is the additive genetic variance and $\boldsymbol{\sigma^2_e}$ is the residual variance.

The EBV was estimated based on BLUP method, using an animal model considering the random additive direct and residual effects, the fixed effects of contemporary group, and the covariate age at slaughter (linear). Single-trait analyses were performed:

$$\mathbf{Y = Xb + Za + e}$$

where **Y** is a vector of phenotypic values of given quantitative traits, **b** is a vector of fixed effects and covariate, **a** is a vector of random animal effect with distribution N ~ $(0, A\sigma^2_a)$, **X** and **Z** are incidence matrixes of fixed and random effects, respectively, and **e** is the random residual vector with distribution N ~ $(0, I\sigma^2_e)$, where **A** is the relationship matrix, **I** is an identity matrix, $\boldsymbol{\sigma^2_a}$ is the additive genetic variance and $\boldsymbol{\sigma^2_e}$ is the residual variance. It is important to highlight that there were 1,894 animals in the pedigree file, which contained 322 sires and 1708 dams. There were 36% and 51% of animals with unknown sire in the pedigree file and in the dataset, respectively.

The GEBV was estimated using single-step genomic BLUP (ssGBLUP) method proposed by Misztal et al. (2009), where the inverse of the numerator based pedigree relationship matrix ($\mathbf{A^{-1}}$) was replaced by $\mathbf{H^{-1}}$, which combines pedigree and genomic information. Aguilar et al. (2010) decomposed $\mathbf{H^{-1}}$ as follows:

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

where $\mathbf{H^{-1}}$ is modified relationship matrix incorporating genomic information, $\mathbf{G^{-1}}$ is the inverse of the genomic relationship matrix and $\mathbf{A_{22}^{-1}}$ corresponds to the inverse of the numerator relationship matrix for genotyped animals. Genomic relationship matrix (**G**) was created according VanRaden (2008) and can be represented as follows:

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

where **M** is a matrix of marker alleles with **m** columns (**m** = total number of markers) and **n** rows (**n** = total number of genotyped individuals), and **P** is a matrix containing the frequency of the second allele ($\mathbf{p_j}$), expressed as $2\mathbf{p_j}$. $\mathbf{M}_{ij}$ was 0 if the genotype of individual **i** for SNP **j** was homozygous 11, was 1 if heterozygous, or 2 if the genotype was homozygous 22.

3.2.4 - Genomic prediction

To determine SNPs effects, the SNP-BLUP method was used. In this method, the SNPs effects were estimated with BLUP, *a priori* assuming a normal distribution and equal variance for all markers. The variances from the SNPs effects were obtained according to Legarra (2014):

$$\sigma_g^2 = \frac{\sigma_u^2}{2\sum q_j(1-q_j)}$$

where (σ_u^2) is the previous genetic variance, q_j is the allele frequency at a given marker **j**.

The DGV was predicted from the estimated SNPs effects using the following equation:

$$DGV = \sum_j^n X_{ij}\hat{g}_j$$

where **n** is the number of SNPs; X_i is the genotype of animal **i** for SNP **j** (coded as 0, 1 or 2), and $\hat{g}_j$ is the estimated SNP substitution effect for SNP **j** that was estimated from the training population.

The general model for the genomic predictions can be expressed in matrix notation as follows:

$$Y_p = 1\,\mu + Xg + e$$

where Y_p is the vector of pseudo-phenotypes (Yc, EBV or GEBV); **1** is the vector of 1s; **μ** is the overall mean; **X** is the matrix (n x p) that consists of **p** SNPs for **n** animals; **g** is the random vector of SNP effects, and **e** is the random residual vector which was normally distributed with mean zero and variance of $I\sigma^2_e$, where **I** is an identity matrix and σ^2_e is the residual matrix. The genotypes were coded as 0, 1, 2 for genotypes 11, 12 and 22, respectively. A chain of 500,000 iterations, with a burn-in period of 80,000 iterations was used for Gibbs sampling, and all samples were stored in the GS3 software developed by Legarra et al. (2013).

The correlation coefficient between pseudo-phenotypes (Yc, EBV or GEBV) with DGV and TBV, for real data and simulated data, respectively, it was used to evaluate and compare the accuracy of genomic prediction. For analyses that used Yc as response variable for real data, the prediction accuracy was obtained by dividing the correlation between Yc and DGV by the square root of the heritability (h) of the trait, as described by Legarra et al. (2008). The linear regression coefficient of the pseudo-phenotype on DGV for real data and TBV for simulated data was considered

to express the magnitude of inflation/deflation of regression coefficient. Values close to one are considered the most desirable. The results of accuracy and inflation/deflation for simulation data were the mean of the 10 replicates.

To evaluate the prediction ability of SNP-BLUP method for real data, the cross-validation methodology was used. The Figure 1 represents the analyzed subpopulations when determining the genomic values accuracies in each cross-validation design. For cross-validation, the population was randomly replicate into four groups of similar size in which three groups represents the training set (75% of overall population) and one represents the validation set (25% of overall population). To estimate the SNPs effects, a population with a known phenotype and genotype was used, denominated as training population. The validation population was used to predict the direct genomic value (DGV) based on the SNPs effects estimated from the training population. This process was repeated four times and each group was once considered to be the validation group. The ability to predict future phenotypes was the validation method chosen for simulated data. This method is based on Legarra et al. (2008), and predictive ability for animals without progeny and born in the last generation (10) was calculated as the correlation between TBV and DGV obtained with different pseudo-phenotypes (Yc, EBV or GEBV).

3.3 - Result and discussion

3.3.1 - Fatty acid profile

The descriptive statistics of the real data for composition of the sum of saturated fatty acid (SFA), monounsaturated fatty acid (MUFA), polyunsaturated fatty acid (PUFA), omega 3 (n-3), omega 6 (n-6) and polyunsaturated and saturated fatty acid ratio (PUFA/SFA) are presented in Table 1.

Table 1. Descriptive statistic for fatty acid profile (g/100g) in *Longissimus thoracis* muscle from Nelore cattle

Trait[a]	Mean	SD	σ^2_a	σ^2_e	h^2±SD
Sum of SFA	40.66	6.12	4.49	32.95	0.12±0.07
Sum of MUFA	37.55	8.05	1.05	46.64	0.02±0.15
Sum of PUFA	13.42	5.57	2.47	28.51	0.08±0.05
Sum of n-3	3.81	1.55	0.26	2.14	0.11±0.07
Sum of n-6	9.35	4.44	4.52	15.15	0.23±0.10
PUFA/SFA	0.35	0.20	0.003	0.028	0.07±0.05

[a] Concentration of fatty acids as a percentage of total fatty acids (FAME) quantified in g/100g. Standard deviation (SD); monounsaturated fatty acid (MUFA), polyunsaturated fatty acid (PUFA), omega 3 (n-3), omega 6 (n-6), Ratio of PUFA and SFA (PUFA/SFA), heritability (h^2); additive genetic variance (σ^2_a); residual variance (σ^2_e). Sample size: 868.

The n-3 concentration (3.81%) found in our study was lower than those reported by Prado et al. (2003) in of *Bos taurus indicus* and *Bos taurus indicus* x *Bos taurus taurus* crossbred steers finished in millet (*Pennisetum americanum L.*) or star grass (*Cynodon plectostachyus Pilger*) pasture systems, with mineral or mineral protein supplementation. Higher than those reported by Cesar et al. (2014) in Nelore raised in feedlots and Ekine-Dzivenu et al. (2014) in Angus and Charolaise based crossbred commercial steers, which reported n-3 concentration of 5.39%, 0.44% and 0.18%, respectively. Rossato et al. (2010) showed that zebu breeds have higher levels of n-3 FA than Angus beef and animals finished in pasture shows smaller percentage of cholesterol and higher levels of n-3 fatty acids than finished in feedlot.

In the present study, SFAs (40.66%) was predominant, followed by the MUFAs (37.55%) and PUFAs (13.42%). Prado et al. (2003) reported similar results for a Nelore beef, with 43.93%, 42.33% and 12.08% for SFAs, MUFAs and PUFAs, respectively. However, the quantities reported by these authors were relatively high, and a slightly difference was observed between MUFA and SFA. Pitchford et al. (2002) using taurine breeds and Cesar et al. (2014) using a Nelore population also found similar concentrations ranging from 47.00% to 47.05% for SFA, and from 47.23% to 48.34% for MUFA. Beef and lamb meat normally have a lower PUFA/SFA ratio than pork meat due to their biohydrogenation of unsaturated FAs in the rumen and mean values may range largely depending on genetic and non-genetic factors (SMET et al., 2004).

The proportion of PUFA (13.42%) was higher than reported by Prado et al. (2003), Kelly et al. (2013), and Cesar et al. (2014) with 12.08%, 1.26%, and 2.87%,

respectively. Silva et al. (2002) working with crossbred heifers (European x zebu), found on MUFAs the most abundant FAs (40 to 55%) among all analyzed, with the greatest proportion for oleic. This difference is probably due to the experimental diets used in each study (SILVA et al., 2002). Studies have shown that in feedlot finishing systems, *Bos taurus taurus* beef have lower percentages of SFA, higher percentages of MUFA, and similar levels of PUFAs compared to *Bos taurus indicus* meat (PERRY et al., 1998; MENEZES et al., 2009; ROSSATO et al., 2010; BRESSAN et al., 2011).

The heritabilities estimated by Lemos et al. (2016) (Table 1) for sum of SFA, MUFA, PUFA, n-3 and PUFA/SFA ratio were low, showing that the genetic additive component had only a small contribution to the phenotypic variation of these FAs in zebu cattle. However, moderate heritabilities were obtained for n-6. Cesar et al. (2014) and Ekine-Dzivenu et al. (2014) also estimated low heritability for SFAs and MUFAs and moderate values for omega 3 and omega 6. The estimates of variance components for beef FA composition that have been conducted in zebu breeds have been limited by the low number of records for these traits (CESAR et al., 2014).

3.3.2 - Genomic predictive ability

For simulated data (Table 2), the prediction abilities for the high heritability trait were higher than those obtained with low heritability trait. The bias was higher for Yc, therefore the predictions were not the same. For real data (Table 3), the pedigree BLUP prediction ability was higher than SNP-BLUP model when the EBV and Yc were used as pseudo-phenotype for sum of SFA, n-3 and PUFA/SFA, but lower for all FAs when GEBV was used as pseudo-phenotype. The prediction ability of genomic model using EBV as pseudo-phenotype for sum of SFA, MUFA, PUFA, n-6 and n-3 was lower than Yc. Wiggans et al. (2011) reported reliability gains for milk traits above parent average for Holstein, Jersey and Brown Swiss. In beef cattle, Garrick (2011) stated that genomic prediction offers accuracies that exceed those of pedigree-based parent average of young selection candidates, and it can be equivalent to progeny tests based on up to 10 offspring.

The results obtained in this study demonstrate that the accuracy of genomic prediction using GEBV of ssGBLUP method is better by correcting the pedigree structure. In the present study, the pedigree missing as consequence of unknown

sires probably limited the estimated EBV accuracies. For this reason, the genomic prediction ability based on adjusted phenotype was higher than those obtained based on EBVs. As expected, when the GEBV obtained by ssGBLUP was used, the prediction ability of DGV increased. Tonussi et al. (2017) worked with simulated and real data for age at first calving and adjusted weight at 550 days, and reported that selecting animals with EBV estimated in situations with missing pedigree can be unreliable and showed that the ssGBLUP method is more reliable for genetic evaluation in situations with missing pedigree information. According to Muñoz et al. (2011), better accuracy and less bias in EBV should improve the final accuracy of genomic selection predictions. Such improvements in genomic selection predictions are not due to genomic selection modeling itself, but rather to the reduced noise in the BLUP breeding value used as input.

3.3.3 - Inflaction/deflaction of genomic prediction

For simulated data, the regression coefficient estimates ($b_{(DGV,TBV)}$), were close to 1 for GEBV of high heritability trait and above of 1 for low heritability trait. The results are more biased for Yc and EBV (Table 2). For real data, the $b_{(DGV,Yi)}$ were on average lower, close and higher than one for Yc, EBV and GEBV, respectively, except for PUFA/SFA that presented values higher than one for all pseudo-phenotypes, being deflated (Table 3).

Table 2. Genomic prediction ability using simulated data and different pseudo-phenotypes under low and high heritability.

Heritability	**Pseudo-phenotype**	**Genomic prediction ability**			
		$r_{(DGV,TBV)}$	**± (SE)**	**$b_{(DGV,TBV)}$**	**± (SE)**
High (0.42)	Yc	0.18	0.01	0.06	0.01
	EBV	0.39	0.01	0.56	0.03
	GEBV	0.55	0.02	0.81	0.03
Low (0.13)	Yc	0.16	0.01	0.10	0.04
	EBV	0.34	0.01	1.39	0.07
	GEBV	0.53	0.02	1.73	0.05

Phenotype adjusted for fixed effects (Yc), estimated breeding value using pedigree (EBV), genomic estimated breeding value using pedigree and genomic information (GEBV); correlation between pseudo-phenotype and direct genomic breeding values ($r_{(DGV,TBV)}$), regression coefficient of the pseudo-phenotype on direct genomic breeding values ($b_{(DGV,TBV)}$) and standard error (SE).

Table 3. SNP-BLUP prediction ability of direct genomic value for real data of beef fatty acids based on different pseudo-phenotypes, direct accuracy BIF and pedigree BLUP prediction ability.

Fatty acid (g/100g)	Pseudo-phenotype	BIF Accuracy	Pedigree BLUP	SNP-BLUP Prediction ability	
				$r_{(Yi,DGV)}$ ± (SE)	$b_{(Yi,DGV)}$ ± (SE)
Sum of SFA	Yc			0.20 (0.19)	0.17 (0.07)
	EBV	0.06	0.30±0.04	0.17 (0.04)	1.12 (0.24)
	GEBV	0.08		0.54 (0.04)	1.67 (0.21)
Sum of MUFA	Yc			0.12 (0.03)	0.13 (0.03)
	EBV	0.01	0.11±0.04	0.07 (0.02)	0.37 (0.11)
	GEBV	0.02		0.34 (0.03)	1.39 (1.16)
Sum of n-3	Yc			0.12 (0.02)	0.14 (0.02)
	EBV	0.06	0.44±0.03	0.07 (0.06)	0.75 (0.55)
	GEBV	0.07		0.47 (0.02)	2.15 (0.07)
Sum of n-6	Yc			0.32 (0.09)	0.40 (0.13)
	EBV	0.12	0.31±0.05	0.22 (0.03)	1.11 (0.13)
	GEBV	0.14		0.47 (0.04)	1.85 (1.14)
Sum of PUFA	Yc			0.38 (0.11)	0.26 (0.07)
	EBV	0.04	0.25±0.19	0.24 (0.28)	0.75 (0.44)
	GEBV	0.05		0.45 (0.03)	3.51 (0.50)
PUFA/SFA	Yc			0.28 (0.15)	2.65 (2.56)
	EBV	0.05	0.41±0.19	0.32 (0.14)	2.35 (0.61)
	GEBV	0.06		0.45 (0.10)	2.61 (0.60)

Phenotype adjusted for fixed effects (Yc), estimated breeding value using pedigree (EBV), genomic estimated breeding value using pedigree and genomic information (GEBV); correlation between pseudo-phenotype and direct genomic breeding values ($r_{(DGV,TBV)}$), regression coefficient of the pseudo-phenotype on direct genomic breeding values ($b_{(DGV,TBV)}$) and standard error (SE). Beef Improvement Federation (BIF).

The Yc and EBV are essentially distinct in quantities, then, their ratios regarding the genetic signal and noise differ (DAETWYLER et al., 2013). As a consequence, the correlation between DGV derived from each one of these variables and the TBV tend to differ as well. This difference, which might represent an advantage for either one of these response variables, depends on the dataset used and its specific application (BODDHIREDDY et al., 2014). These results indicated that using GEBV instead of Yc or EBV as the pseudo-phenotype provided more accurate predictions.

Garrick et al. (2009) pointed out the importance of deregressing EBV and weighting information for genomic regression analyses. However, in the present study half of the animals in the training population have unknown sire, compromising the reliability of the deregressing process. The presence of animals with unknown sires due to the use of multiple sires is common in extensive beef cattle production systems, thus it is important to investigate the use of genomic data in uncertain paternity models aiming to increase the accuracy and to decrease bias in genetic evaluations. In these sense, Tonussi et al. (2017) showed that when large proportion of the pedigree is missing, the BLUP is not reliable, however, it is possible to increase prediction ability for selection candidates using ssGBLUP.

Through the application of ssGBLUP, it is possible to obtain more reliable genetic evaluations for young animals with missing pedigree, increasing the reliability of pseudo-phenotype to train the markers effects. To maximize the accuracy of genomic selection, Muñoz et al. (2011) recommended construct a realized relationship matrix (**G**-matrix) for the training population that should be used to correct the pedigree and to predict the BLUP breeding values.

Beef fat composition could be viewed in a more favorably standpoint for human health if effective approaches could be applied to decrease beef SFA content, while increasing the concentration of beneficial FA, such as PUFA. Thus, genomic information can be used to reduce SFA concentration in meat. In order to increase the concentration of MUFA, such as oleic and vaccenic, as a result of its biological importance as precursors of PUFA and because of its importance on human health, the GEBV pseudo-phenotype is the most appropriate in this context.

Fatty acid profile is not a selection criterion for beef cattle in Brazil, due to the high cost to obtain the phenotype as analyses' operating cost, and since there are no available phenotypes and breeding values for selection candidate. Despite the prediction accuracies were low to moderate, and considering that the beef FA profile is not used as a selection criterion, the use of genomic information to predict genomic values for meat FA profile is a feasible alternative, aiming to contribute to improve meat quality, and consequently consumer's health. It should be noted that the reason for the low accuracy of EBVs can be attributed on pedigree missing, then, in

situations with missing pedigree due to the use of multi-sire system, the GEBV as pseudo-phenotype is a worthwhile alternative for application in commercial genomic evaluations on a large scale.

In this study, the percentage of genotyped animals with unknown sires was about 50%, and the ssGBLUP model allows increasing the accuracy of pseudo-phenotype to train the markers, since it improves the unknown pedigree information. The poor data structure that did not match to the animal model to predict the EBV leads to decrease the prediction ability of DGV when the EBV was used as pseudo-phenotype. Fernandes Júnior et al. (2016) reported for the same population lower prediction ability of DGV when the EBV was used as pseudo-phenotype instead of Yc. This work gives the possibility of combining the ssGBLUP and multi-step method to develop genomic evaluation in herds with poor pedigree structure, allowing more reliable pseudo-phenotypes to train or estimate marker effects, increasing the prediction ability of genetic markers and DGV.

3.4 - Conclusions

Genomic information can assist in improving beef fatty acid profile in Zebu animals, since the use of genomic information yielded genomic values for fatty acid profile with accuracies ranging from low to moderate. The ssGBLUP model is an appropriate alternative to obtaining more reliable and less biased GEBVs as pseudo-phenotypes in situations of missing pedigree, due to high proportion of multiple sires, being more appropriate than the EBVs or adjusted phenotypes for fixed effect to predict direct genomic values.

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