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MODELOS E METODOLOGIAS PARA ESTIMAÇÃO DOS EFEITOS GENÉTICOS FIXOS EM UMA POPULAÇÃO MULTIRRACIAL ANGUS X NELORE

CLAUDIA DAMO BERTOLI
Eng^a Agr^a / UFSC
Mestre em Zootecnia / UFRGS

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CLÁUDIA DAMO BERTOLI
Engenheira Agrônoma e
Mestre em Zootecnia

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Pela Banca Examinadora

Homologado em: 06.05.2015
Por

JÚLIO OTÁVIO JARDIM BARCELLOS
Coordenador do Programa de
Pós-Graduação em Zootecnia

José Braccini Neto
JOSÉ BRACCINI NETO
PPG Zootecnia/UFRGS
Orientador

JAIME ARAÚJO COBUCI
PPG ZOOTECNIA-UFRGS

Arione Boligon
ARIONE AUGUSTI BOLIGON
UFPel - Pelotas/RS

PAULO ROBERTO NOGARA RORATO
UFSM - Santa Maria/RS

Vanerlei M. Roso
VANERLEI MOZAQUATRO ROSO
GenSys

Selbach
PEDRO ALBERTO SELBACH
Diretor da Faculdade de Agronomia

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"A mente que se abre a uma nova idéia,
jamais voltará ao tamanho original"
(Albert Einstein)

[1] MODELOS E METODOLOGIAS PARA ESTIMAÇÃO DOS EFEITOS GENÉTICOS FIXOS EM UMA POPULAÇÃO MULTIRRACIAL ANGUS X NELORE

Autor: Claudia Damo Bértoli
Orientador: José Braccini Neto
Co-orientador: Concepta McManus

RESUMO

Os objetivos deste trabalho foram estimar os efeitos genéticos fixos atuando sobre uma população sintética e testar diferentes modelos e metodologias neste processo de estimação. Os efeitos genéticos fixos testados foram os efeitos aditivos direto e materno de raça e não aditivos diretos e maternos de heterose, perdas epistáticas e complementariedade. Os modelos testados incluem alternada e conjuntamente todos estes efeitos. As metodologias de regressão de cumeeira e regressão por quadrados mínimos foram comparadas assim como dois métodos distintos para determinação do *ridge parameter*. Uma população sintética, envolvendo as raças Angus e Nelore foi utilizada. Foram utilizados 294.045 registros de desmame e 148.443 registros de sobreano de uma população sintética envolvendo as raças Angus e Nelore. Foram estudadas as seguintes características: ganho de peso do nascimento ao desmame (WG), escores de conformação (WC), precocidade (WP) e musculatura (WM) coletados ao desmame, ganho de peso do desmame ao sobreano (PG), escores fenotípicos de conformação (PC), precocidade (PP) e musculatura (PM) e perímetro escrotal (SC) coletados ao sobreano. Na maioria das análises, os efeitos genéticos fixos estimados foram estatisticamente significativos. O modelo completo, incluindo todos os efeitos genéticos fixos foi o mais indicado nas duas metodologias testadas. Na estimação por regressão de quadrados mínimos, o modelo mais parcimonioso foi o que incluiu apenas os efeitos aditivos de raça e não aditivos de heterose (dominância) e na estimação por regressão de cumeeira o mais parcimonioso foi o aquele que incluiu, além dos dois já referidos, os efeitos não aditivos de perdas epistáticas. As metodologias mostraram-se equivalentes, para os modelos que incluíram apenas efeito aditivo de raça e não aditivo de heterose. Todavia com a inclusão dos efeitos não aditivos de perdas epistáticas e/ou complementariedade, a regressão de cumeeira mostrou-se mais indicada até o momento em que os dados atingiram um determinado volume e estrutura, com grande parte das classes de composições raciais representadas na amostra e, a partir daí os modelos se mostraram equivalentes. Na comparação entre os métodos de determinação do *ridge parameter*, o mais indicado foi o método que identifica o menor valor possível que produz fatores de inflação de variância abaixo de 10 para todos os regressores estimados.

Palavras-chave: Bovinos de corte cruzados; complementariedade; efeitos genéticos; heterose; perdas epistáticas regressão de cumeeira;

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[2] MODELS AND METHODOLOGIES TO ESTIMATE FIXED GENETIC EFFECTS ESTIIMATION IN A CROSSBRED POPULATION ANGUS X NELORE

Author: Claudia Damo Bértoli
Advisor: José Braccini Neto
Co-Advisor: Concepta McManus

ABSTRACT

The objectives of this study were to estimate the fixed genetic effects acting on a synthetic population, as well as test different models and methodologies in this estimation process. The tested fixed genetic effects were the direct and maternal breed additive and direct and maternal heterosis, epistatic loss and complementarity non-additive effects The tested models include alternate and together all these effects. The ridge regression and least square regression methodologies were compared and were also compared two different methods for determining the ridge parameter to use in the ridge regression. A synthetic beef cattle population, involving Angus and Nellore in several breed combinations was used. 294,045 records at weaning and 148,443 records at yearling were used. The traits of weight gain from birth to weaning (WG), phenotypic scores of conformation (WC), precocity (WP) and muscling (WM) collected at weaning, weight gain from weaning to yearling (PG), phenotypic scores of conformation (PC), precocity (PP) and muscles (PM) collected at yearling and scrotal circumference (SC) were used in the analyzes. In most of analyzes, the estimated fixed genetic effects were statistically significant. The complete model, including all fixed genetic effects was the most suitable in the two tested methodologies. In the estimation by least squares regression, the most parsimonious model was the model that included only breed additive and non-additive heterosis (dominance) effects and in the estimation by ridge regression the most parsimonious model was that included, besides the breed additive and non-additive heterosis (dominance) effects, the non-additive epistatic loss effects. Comparing the two methodologies, for models that include only breed additive and non-additive heterosis effects, methodologies proved to be equivalent; with the inclusion of non-additive epistatic loss and / or complementarity effects, ridge regression was more indicated originally. After reached a certain volume and structure, with much of classes of breeds represented in the sample. Both least squares and ridge regression were equivalent. Comparing the methods for determining the ridge parameter, the best method was that which identifies the smallest possible value that produces the variance inflation factors below 10 for all estimated regressors.

Keywords: Complementarity; crossbred beef cattle; epistatic loss; genetic effects; heterosis; ridge regression.

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[2] Doctoral thesis in Animal Science, Faculdade de Agronomia, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil (109p.) February, 2015.

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aa - efeito genético direto aditivo de raça
am - efeito genético materno aditivo de raça
ha - efeito genético direto não aditivo de heterose (dominância)
hm - efeito genético materno não aditivo de heterose (dominância)
ea - efeito genético direto não aditivo de perdas epistáticas
em - efeito genético materno não aditivo de perdas epistáticas
ca - efeito genético direto não aditivo de complementariedade
cm - efeito genético materno não aditivo de complementariedade
G_a - Matriz de (co)variancia dos efeitos genéticos aditivos diretos
G_m - Matriz de (co)variancia dos efeitos genéticos aditivos maternos
G_{am} - Matriz de covariancia entre os efeitos genéticos aditivos diretos e maternos
Pe - Matriz de (co)variancia dos efeitos de ambiente permanente
R - Matriz de (co)variancia dos resíduos
σ_{a1}^2 - Variância genética do efeito aditivo direto da característica 1
σ_{a2}^2 - Variância genética do efeito aditivo direto da característica 2
σ_{a1a2} - Covariância genética entre os efeitos aditivos diretos da característica 1 e da característica 2
σ_{m1}^2 - Variância genética do efeito aditivo materno da característica 1
σ_{m2}^2 - Variância genética do efeito aditivo materno da característica 2
σ_{m1m2} - Covariância genética entre os efeitos aditivos maternos da característica 1 e da característica 2
σ_{a1m1} Covariância genética entre os efeitos aditivos direto e materno da característica 1
σ_{a2m2} Covariância genética entre os efeitos aditivos direto e materno da característica 2
σ_{a1m2} Covariância genética entre o efeito aditivo direto da característica 1 e o efeito materno da característica 2
σ_{p1}^2 - Variância do ambiente permanente da característica 1
σ_{p2}^2 - Variância do ambiente permanente da característica 2
σ_{p1p2} - Covariância entre o ambiente permanente da característica 1 e da característica 2
σ_{e1}^2 - Variância residual da característica 1
σ_{e2}^2 - Variância residual da característica 2
σ_{e1e2} - Covariância residual entre a característica 1 e a característica 2
RR - Metodologia de Regressão de cumeeira
R1 - Método 1 de escolha do "ridge parameter"
R2 - Método 2 de escolha do "ridge parameter"
LS - Metodologia de regressão por quadrados mínimos
WG - Ganho de peso do nascimento ao desmame
WC - Escore fenotípico de conformação ao desmame
WP - Escore fenotípico de precocidade ao desmame
WM - Escore fenotípico de musculatura ao desmame
PG - Ganho de peso do desmame ao sobreano
PC - Escore fenotípico de conformação ao sobreano
PP - Escore fenotípico de precocidade ao sobreano

PM - Escore fenotípico de musculatura ao sobreano
VIF - Fator de inflação da variância
CI - Índice de condição
AH - Modelo estatístico que considera os efeitos genéticos fixos aditivo de raça e não aditivo de heterose (dominância)
AC- Modelo estatístico que considera os efeitos genéticos fixos aditivo de raça e não aditivo de complementariedade
AE- Modelo estatístico que considera os efeitos genéticos fixos aditivo de raça e não aditivo de perdas epistáticas
ACH- Modelo estatístico que considera os efeitos genéticos fixos aditivo de raça e não aditivo de heterose (dominância) e complementariedade
ACE- Modelo estatístico que considera os efeitos genéticos fixos aditivo de raça e não aditivo de perdas epistáticas e complementariedade
AHE- Modelo estatístico que considera os efeitos genéticos fixos aditivo de raça e não aditivo de heterose (dominância), perdas epistáticas e complementariedade
AHEC/ACHE - Modelo estatístico que considera os efeitos genéticos fixos aditivo de raça e não aditivo de heterose (dominância), perdas epistáticas e complementariedade

CAPÍTULO I

INTRODUÇÃO

O grande benefício dos cruzamentos entre diferentes raças nos animais de produção inclui melhora na performance reprodutiva, aumento no ganho de peso e sensível diferença nas características de carcaça. Muitos pesquisadores, ao longo das últimas décadas tem se dedicado ao estudo desses cruzamentos, buscando as melhores formas de identificação e distinção dos efeitos ali existentes. Estes efeitos genéticos resultantes dos cruzamentos inter-raciais são tanto aleatórios (direto, materno, ambiente permanente) quanto fixos, aditivos (raça) ou não aditivos (heterose, perdas epistáticas, complementariedade entre raças).

O desafio do melhoramento genético de populações cruzadas reside na comparação justa entre reprodutores de distintas composições raciais para fins de seleção visando produção. Para que esta comparação seja realmente justa, uma avaliação genética multirracial incluindo as raças puras e as mais diversas composições raciais de animais sintéticos se torna necessáriaconforme proposto por Arnold et al. (1992) j. De lá para cá muitos avanços tem acontecido sem, no entanto, estas avaliações tenham se tornado corriqueiras na maioria dos programas de avaliação genética comerciais.

Uma análise multirracial envolvendo animais puros e cruzados exige a inclusão de uma série de efeitos tais como: efeito genético aditivo de raça e os efeitos genéticos não aditivos de heterose, perdas epistáticas e complementariedade, considerados tanto nos seus componentes diretos quanto maternos. Da mesma forma, o efeito genético aditivo para cada raça envolvida e sua habilidade, geral ou específica, de combinação deve ser considerada.

O efeito genético aditivo para cada raça envolvida e sua habilidade, geral ou específica, de combinação deve ser considerada. A simples inclusão do componente racial de cada raça envolvida pode ser um problema. A formação de grupos de raças geneticamente semelhantes têm sido usadas como alternativa. Já os efeitos genéticos não aditivos normalmente são incluídos como covariáveis no modelo estatístico. Os coeficientes utilizados como regressores para estas covariáveis são derivados de distintas combinações das composições raciais dos animais avaliados, de seus pais e avós.

Além da superparametrização, a inclusão de todos estes efeitos genéticos fixos (aditivo de raça, heterose, perdas epistáticas e complementariedade) como covariáveis do modelo, traz à tona um novo problema: a colinearidade ou multicolinearidade. Quando existe forte relação linear entre as covariáveis de um modelo de regressão, as estimativas obtidas pela tradicional metodologia dos quadrados mínimos tendem a ser instáveis, frequentemente apresentando grandes erros-padrão. Nestes casos, os coeficientes de regressão podem, frequentemente, cancelar uns aos outros. Além disso, estimativas com estas características podem levar a inferências errôneas e, consequentemente, afetar os rumos da seleção nos programas de melhoramento genético.

Muitos estudos propõem a regressão de cumeeira como alternativa para contornar a colinearidade. A regressão de cumeeira consiste na inclusão de um valor positivo na diagonal principal da matriz X'X, onde X é a matriz de incidência dos efeitos genéticos fixos para quebrar a colinearidade entre eles. Embora este método introduza um viés nas soluções, este pode ser compensado com a maior estabilidade nas estimativas dos valores genéticos e na redução dos seus erros-padrão.

O objetivo deste trabalho foi fazer uma análise comparativa entre diferentes modelos estatísticos incluindo os efeitos genéticos aditivos de raça e não aditivos de heterose, perdas epistáticas e complementariedade, estimados tanto sob a tradicional metodologia dos quadrados mínimos como sob a metodologia de regressão de cumeeira, buscando orientar futuras avaliações genéticas multirraciais.

REVISÃO BIBLIOGRÁFICA

Cruzamentos

O uso de animais cruzados vem, gradativamente, ganhando força na produção de carne bovina. As raças puras estão pouco a pouco dividindo seu espaço com populações multirraciais. Uma população multirracial é uma população composta por animais de raças puras e cruzados que acasalam entre si (Elzo & Wakeman, 1998). Estas populações são o produto dos Sistemas de Cruzamentos, amplamente usados em programas de melhoramento genético, tanto de plantas quanto de animais. Esses sistemas consistem em um programa de acasalamentos entre animais de distintas composições raciais, com o propósito de explorar as diferenças genéticas entre raças ou linhagens e/ou tirar vantagem da complementariedade entre elas para as diferentes características.(Cunningham e Connoly, 1989). As estratégias de cruzamentos podem tomar muitas formas, desde o cruzamento simples até a formação de populações sintéticas. (Cunninham e Connoly, 1989).

Melhoristas do mundo inteiro tem se utilizado dos programas de cruzamentos entre raças para tirar vantagem dos efeitos de heterose e da combinação de características de interesse das raças parentais na progênie, chamada de complementariedade racial (breed complementarity) (Weaber, 2005). Estes efeitos ocorrem nos cruzamentos em vários níveis de intensidade e, embora importantes, são frequentemente negligenciados nos programas de avaliação genética para melhoramento animal. Nos países de clima tropical e subtropical, os sistemas de cruzamentos são baseados na exploração de vários efeitos genéticos resultantes da diferença existente entra as raças zebuínas (*Bos indicus*) e taurinas (*Bos taurus*).

O grande benefício dos cruzamentos entre raças inclui melhora na performance de características de crescimento e de carcaça (Williams et al., 2010) e tem sido estudado por muitos pesquisadores ao longo da última década (Cardoso et al. 2008, Roso et al., 2005a,b; Carvalheiro et al. 2006; Dias et al., 2011). O desafio atual do melhoramento genético de populações cruzadas reside na comparação justa entre reprodutores de distintas composições raciais para fins de seleção visando produção. Para que esta comparação seja não viesada, uma avaliação genética multirracial incluindo indivíduos puros e cruzados no mesmo conjunto de dados é necessária. No século passado, Arnold et al.(1992) já propunham este tipo de análise.

Além da utilização de indivíduos puros e cruzados no mesmo banco de dados, a quantidade e estrutura desses dados são muito importantes e devem ser adequadas à avaliação genética (Hill, 2010). Base de informação adequada é necessária para dar suporte aos programas de avaliação genética multirracial. É importante ter representados diferentes grupos raciais (F1, F2, retrocruzamentos) para garantir acurácia suficiente (Cunninham e Connoly, 1989). Isto nem sempre é possível mas é importante lembrar que nenhum sistema de cruzamento pode prescindir de uma seleção cuidadosa, geração após geração (Olson, 1998)

A combinação de genes de diferentes raças pode levar a inúmeros efeitos além do efeito aditivo direto e materno de cada raça envolvida no cruzamento. Interações positivas dentro de um mesmo loco podem levar a ganhos por dominância (heterose) e interações entre alelos de locos diferentes ou perda de ligações favoráveis construídas pela seleção (perdas epistáticas). Há ainda o efeito multiplicativo (Cardoso et al., 2008) específico das raças envolvidas (complementariedade). As diferenças genéticas aditivas entre as raças, a escala dos efeitos de dominância que vão culminar em heterose e a extensão dos efeitos epistáticos precisam ser bem conhecidos para o sucesso da estratégia de cruzamentos escolhida. (Cunninham e Connoly, 1989). Se a epistasia puder ser ignorada,ou seja, se a pressuposição que que seu efeito é desprezível é verdadeira, então as estimativas dos efeitos aditivos de raça e de heterose podem atingir boa precisão, caso contrário, novos desenhos experimentais necessitam ser feitos.

Efeitos genéticos fixos

Em animais cruzados todas as formas de ação gênica e interações podem estar presentes. De acordo com VanRaden (2006), quando se trata de animais cruzados, se os efeitos não aditivos são subtraídos e só os efeitos aditivos são considerados, a seleção pode não ser ótima. Kinghorn (1987) sugere que onde o produto dos genes de importância é desconhecido e a herança é aparentemente poligênica, esta questão precisa ser analisada em nível de população, pela estimação dos parâmetros que se relacionam com a interação epistática dos genes. A interação epistática 2-locus pode ser de maior importância do que interações de ordem maior (Kinghorn, 1987).

Uma análise multirracial envolvendo animais puros e cruzados exige, portanto, a inclusão de uma série de efeitos genéticos fixos. Estes efeitos genéticos fixos são: efeito direto e materno aditivo de raça, direto e materno não aditivo de heterose (Williams et al,. 2010, Carvalheiro, et al., 2006; Cardoso et al., 2008; Kippert et al., 2008), perdas epistáticas (Dias et al.,2011; Cardoso et al., 2008; Carvalheiro et al., 2006) e complementariedade entre diferentes raças (Cardoso et al., 2008; Carvalheiro et al., 2006; Piccoli et al.et al., 2002). A inclusão de todos os efeitos simultaneamente pode, eventualmente, mostrar-se complexa. O que existe a seu favor é a evolução da informáticacomputacional e o conjunto de dados confiáveis, que com o passar das gerações, vai se acumulando junto aos programas comerciais de melhoramento avaliação genéticao.

Efeito aditivo de raça

O efeito genético aditivo para cada raça envolvida e sua habilidade, geral ou específica de combinação deve ser considerada. Quando a população multirracial compreende um número muito grande de raças envolvidas, este efeito pode se tornar problemático. Alternativas como formar grupos de raças geneticamente semelhantes tem sido usadas como alternativa (Dias et al. 2011).

O efeito aditivo de raça compreende os efeitos individuais de cada uma das raças envolvidas no cruzamento. A seleção natural e/ou artificial ocorrida em longo prazo dentro de cada raça aumentou a frequência de genes não alélicos que, juntos, produzem efeitos favoráveis extras (Fries *et al.*, 2002). Este efeito é considerado na maioria dos modelos que envolvem a avaliação de animais cruzados (Arthur et al., 1999; Piccoli et al., 2002; Abdel-Aziz et al., 2003; Demeke et al., 2003a,b; Pimentel et al., 2006; Carvalheiro, et al., 2006; Cardoso et al., 2008; Kippert et al., 2008; Vergara et al.,2008b; Cunha et al., 2009; Vergara et al., 2009; Williams et al. 2010; Bueno et al.,2011; Lema et al., 2011;). Quando este efeito não é incluído no modelo de avaliação genética, tabelas de fatores de correção podem e devem ser utilizadas para permitir comparação entre touros de diferentes raças (Elzo & Wakeman, 1998)

Heterose e dominância

Heterose pode ser definida como interação interracial intralocus entre alelos originários de diferentes raças. portanto o efeito de heterose estimado corresponde à média das interações entre as raças de todos as raças parentais disponíveis. (Vergara et al., 2009a). O efeito da heterose é devido, principalmente, aos efeitos de dominância dos genes e pode ser considerado como a recuperação da depressão por consanguinidade acumulada. Uma relação linear entre heterozigose e retenção da heterose foi relatada por Fries *et al.* (2000) e por Gregory *et al.*(1991). Este efeito é favorável para a maioria das características de interesse (VanRaden, 2006).

O efeito de heterose é incluído na grande maioria dos modelos de avaliação genética multirracial (Arthur et al., 1999; Piccoli et al., 2002; Demeke et al., 2003a,b; Carvalheiro et al., 2006; Pimentel et al., 2006; Cardoso et al., 2008; Vergara et al, 2009b; Bueno et al., 2011;). Programas de avaliação genética de populações bovinas sintéticas já utilizam estimação simultânea dos efeitos diretos e maternos de heterose nos Estados Unidos (Klei et al., 1996), Austrália (Johnston et al., 1999) e Brasil (Roso & Fries, 1998).

Efeitos de dominância e epistasia muitas vezes são estimados e interpretados de maneira conjunta, como sendo heterose(Arthur et al. 1999). Na verdade o efeito estimado aqui é um balanço dos efeitos positivos da heterose dos efeitos negativos das perdas epistáticas.

Perdas Epistáticas

Se a heterose é o benefício advindo da recuperação da depressão por consanguinidade presente em populações puras, as perdas epistáticas são o balanço negativo trazido por esses benefícios e que vai seguir agindo nas gerações seguintes (Fries et al., 2000c).

O efeito de perdas epistáticas compreende um desvio adicional do valor fenotípico, ocasionado pela combinação não aditiva, quando mais de um locus é considerado na análise (Falconer, 1986). Segundo Kinghorn (1987), perdas epistáticas são "efeitos negativos, em animais cruzados, resultantes da ação connjunta de genes, com funções diferentes, que não estão acostumados a interagir entre si". Para estimar os parâmetros de epistasia, ou testar modelos de epistasia com acurácia, grandes conjuntos de dados com boa estrutura são requeridos. (Kinghorn, 1987)

A inclusão dos efeitos de perdas epistáticas no modelo aditivo-dominante foi sugerido por Fries *et al.* (2000) e confirmado por Piccoli *et al.* (2002) com o objetivo de obter uma melhor explicação para a variação genética existente entre as distintas composições genéticas dos animais cruzados. O genótipo de um lócus pode influenciar o efeito genotípico de um segundo lócus e pode, eventualmente, inibir a expressão gênica deste segundo locos no fenótipo. Estudos recentes sugerem que o efeito das perdas epistáticas influenciam forte e negativamente os níveis de produção dos animais cruzados (Piccoli et al., 2002; Demeke et al., 2003a,b; Cardoso *et al.*, 2008, Lema *et al.*, 2011; Bueno et al.,2011) embora alguns pesquisadores optem por não incluir perdas epistáticas nos modelos utilizados, como Vergara *et al.* (2009b), Legarra *et al.* (2007) e Arthur *et al.* (1999)

Segundo Hill (2010), em populações com acasalamento aleatório é muito difícil estimar a variância epistática porque os coeficientes são muito pequenos e muito correlacionados com os componentes não epistáticos.

Complementariedade

O efeito não aditivo da combinação entre as diferentes raças envolvidas no cruzamento e que causa uma relação multiplicativa nas ações aditivas dos genes foi definida por Kinghorn (1993) como *profit heterosis*. Este efeito também foi denominado de *joint-additive effect* (Fries et al.,2000c) ou simplesmente complementariedade (Piccoli et al., 2002, Carvalheiro et al., 2006; Cardoso et al. 2008).

A inclusão do efeito de complementariedade no modelo de avaliação genética de bovinos sintéticos foi sugerida por Fries *et al.* (2000c) e seus resultados foram confirmados por Piccoli *et al.* (2002). Segundo Pimentel (2006), quando nos referimos a animais cruzados, criados em ambiente tropical, nós podemos considerar como se dois grupos de genes estivessem agindo sobre o desempenho desses animais. Um grupo relacionado às características de potencial de crescimento e outro grupo relacionado à adaptação destes animais ao meio ambiente em que estão inseridos. A relação multiplicativa entre seus efeitos, como demonstrado por Kinghorn(1993) em exemplo para bovinos leiteiros, pode ser interpretada como a complementariedade.

Muitos estudos que utilizam modelos para avaliação genética multirracial usam (Pimentel et al., 2006; Cardoso et al., 2008; Carvalheiro et al., 2006; Piccoli et al., 2002; Fries et al., 2000b,c) e outros tantos não incluem este efeito nos seus modelos. Piccoli *et al.* (2002) relataram que quando a complementariedade (interação multiplicativa entre os efeitos aditivos) é incluída no modelo a magnitude do efeito da heterose estimado é reduzido, indicando que sob modelos aditivo-dominantes a estimação da heterose pode incluir um componente aditivo não linear. Segundo Piccoli *et al.* (2002) este efeito se torna mais evidente quando o modelo também inclui o efeito de perdas epistáticas.

Modelos

De forma geral não existe um único modelo estatístico apropriado para todas as situações que envolvem a avaliação genética dos animais objetivando seleção. Os modelos que apresentam os melhores resultados do ponto de vista teórico, muitas vezes não são aplicáveis na estimação de parâmetros de cruzamentos em bovinos de corte (Queijo, 2011).

De acordo com Albuquerque & Pereira (2006), ainda existem diversas limitações e/ou dificuldades na aplicação dos modelos de avaliação genética multirraciais para os quais uma das alternativas seria o uso de fatores de ajuste previamente estimados. Miller (1996) sugeriu o *super-breed model*, proposto por Van Raden (1992), para avaliação de populações bovinas compostas de animais puros e cruzados, o qual possibilita incluir as variações genéticas epistática e de dominância entre e dentro de raças, bem como considerar endogamia. Roso *et al.* (2005a) detectaram problemas de multicolinearidade entre as variáveis preditoras. Roso *et al.*(2005b) utilizando regressão de cumeeira conseguiram reduzir estes efeitos nas estimativas dos efeitos aditivos utilizando um modelo complexo, considerando dominância e epistasia entre raças. Hoje muitos pesquisadores estão utilizando estes modelos em pesquisas (Cardoso *et al.*, 2004; Carvalheiro, 2006; Legrra *et al.* 2007;Cardoso *et al.*, 2008; Kippert *et al.*, 2008; Vergara et al. 2009a; Lopes *et al.*, 2010; Bueno *et al.*, 2011, Lema *et al.*, 2011). No Brasil os Programas Delta G (Hereford X Nelore) e NATURA (Angus X Nelore) utilizam os efeitos de dominancia na predição das DEPs para uso comercial (Piccoli *et al.*, 2015; Roso *et al.*, 2015).

Albuquerque & Pereira (2006), fazendo uma retrospectiva sobre a evolução dos modelos de avaliação genética concluíram que os desafios atuais são tão grandes quanto se apresentavam nas primeiras avaliações de animais, embora sejam diferentes. Na bovinocultura de corte, por exemplo, modelos cada vez mais complexos são necessários e precisam ser desenvolvidos, acompanhando a evolução dos métodos estatísticos e computacionais para tratamento dos dados oriundos de animais cruzados e/ou genômicos.

A predição dos valores genéticos dos animais é um componente fundamental dos programas modernos de melhoramento genético animal (Hill, 2010). Henderson (1950) propôs a metodologia BLUP (Best Linear Unbiased Prediction) e incorporou efeitos genéticos fixos e aleatórios num modelo misto. Com o avanço da computação o modelo animal passou a ser largamente utilizado na estimação dos valores genéticos para todas as características, permitindo soluções simultâneas para animais de diferentes idades, rebanhos, números de registro e número de parentes presentes na mesma análise (Hill, 2010). Todos os candidatos passam a ser diretamente comparáveis quando presentes na mesma análise.

Os modelos que estimam os efeitos aleatórios simultaneamente aos efeitos genéticos fixos ou aqueles que os estimam após ajuste dos dados para estes efeitos genéticos fixos, baseados principalmente na heterozigose esperada, são os modelos básicos mais comuns nos programas de melhoramento genético de populações multirraciais de bovinos de Corte. Modelos de estimação incluindo os efeitos genéticos fixos aditivo de raça e não aditivo de heterose, perdas epistáticas e complementariedade) simultaneamente aos efeitos aleatórios e ambientais tem sido usados em populações cruzadas no Brasil (Bueno et al, 2012; Lopes *et al.*, 2010; Cunha *et al.* 2009; Cardoso *et al.*, 2008; Kippert *et al.*, 2008; Carvalheiro *et al.* 2006; Pimentel *et al.*, 2006),na Africa (Theunissen *et al.*, 2013; Abdel-Aziz *et al.*, 2003; Schoeman et al., 2002), na Australia (Arthur *et al.*, 1999), no Canadá (Roso *et al.*, 2005a), na Colombia (Vergara *et al.*, 2009a,b), na Etiopia (Demeke *et al.*, 2003a,b), nos Estados Unidos (Williams et al., 2009; Elzo and Wakeman, 1998) e no Uruguai (Lema *et al.* 2011).

Estes autores concordam que os efeito direto aditivo de raça e o efeito de heterose são muito importantes e devem, necessariamente, estar presentes no modelo estatístico na avaliação genética de animais oriundos de populações multirraciais. Em relação aos efeitos de perdas epistáticas e complementariedade é quase consenso entre os autores, embora nem todos estes efeitos tenham sido usados em todos os estudos revidados. Em relação à complementariedade, esta parece ser importante, porem maiores estudos são necessários acerca deste efeito (Carvalheiro et al., 2006)

Os efeitos genéticos fixos (aditivo de raça e não aditivo de heterose, perdas epistáticas e complementariedade) normalmente são incluídos como covariáveis, onde os coeficientes utilizados como variáveis preditoas na regressão são todos derivados de distintas combinações das composições raciais dos animais incluídos na análise (Roso et al., 2005a,b; Cardoso, 2008; Carvalheiro, 2006; Dias et al., 2011). Esta origem comum dos regressores pode levar ao problema da colinearidade ou multicolinearidade (Roso et al. 2005b), exigindo escolha adequada da matodologia a ser utilizada na sua estimação.

Multicolinearidade

Como o principal objetivo dos sistemas de cruzamentos é tirar vantagem dos efeitos não aditivos entre as diferentes raças, obter estimativas confiáveis dos parâmetros envolvidos nos sistemas de cruzamentos e assim, estar apto a predizer a performance dos genótipos cruzados é um importante passo para o sucesso de um programa de cruzamentos. (Cardoso *et al.*, 2008).

A inclusão destes efeitos genéticos fixos como covariáveis pode trazer à tona o problema da colinearidade. Quando existe forte relação linear entre as covariáveis em um modelo de regressão, as estimativas obtidas pela tradicional metodologia dos quadrados mínimos tendem a ser instáveis, frequentemente apresentando grandes erros-padrão (Schebenberger et al, 2002). Nestes casos os coeficientes de regressão podem, frequentemente, cancelar uns aos outros (Roso et al., 2005b). Estimativas com estas características podem levar a inferências errôneas (Dias et al., 2011) e, consequentemente, afetar os rumos da seleção nos programas de melhoramento genético. A colinearidade existente entre as variáveis preditoras dos efeitos fixos também tem sido alvo de muitos estudos científicos (Roso et al., 2005b; Dias, et al., 2011; Petrini et al.,2012; Schoeman et al., 2002).

Quando se usa modelos não aditivos, a composição racial do indivíduo, de seus pais e avós é utilizada para estimar todos os coeficientes (direto e materno aditivo de raça e não aditivo de heterose, perdas epistáticas e complementariedade). Possível colinearidade pode estar presente entre todos os estimadores, uma vez que a composição racial de cada indivíduo possui a restrição de somar a 1 (Roso et al. 2005b). Somando-se a isso existe o fato de que a composição racial de um indivíduo é igual à média da composição racial de seus pais, aumentando ainda mais a possibilidade de multicolinearidade. Na prática, a mesma informação é usada para predizer diferentes efeitos, vistos a partir de distintas perspectivas.

Metodologias

Numa análise de regressão múltipla, multicolinearidade existe quando uma ou mais variáveis expressam uma combinação linear com as outras variáveis usadas no mesmo modelo (Schebenberger & Pierce, 2002). Na regressão multipla, as colunas de X quase nunca são totalmente ortogonais e dependências exatas entre as colunas também raramente existem. (Schabenberger & Pierce, 2002). Para estimar esta colinearidade, correlações entre os pares de variáveis podem ser estimadas, mas esta informação nem sempre é suficiente para indicar uma situação de colinearidade. Altas correlações entre pares de variáveis podem indicar multicolinearidade, mas não são indicadores absolutos (Roso et al., 2005b). Quanto maior a colinearidade, maiores serão os erros padrões e mais amplos os intervalos de confiança (Roso et al. 2005b). O Cálculo dos fatores de inflação da variância (FIV) oferece um diagnóstico alternativo, simples e eficiente, para detecção da colinearidade. Quando colinearidade é encontrada, uma das opções é deletar uma ou mais variáveis que estão provocando esta colinearidade, já que esta condição gera estimativas instáveis e elevados erros padrão (Schabenberger & Pierce, 2002), outra opção é o uso da regressão de cumeeira ("ridge regression") (Schabenberger & Pierce, 2002).

Petrini et al. (2012), Dias et al. (2011), Cardoso et al. (2008, 2004), Roso et al. (2005a), Abdel-Aziz et al. (2003), Schoeman et al. (2002), Arthur et al. (1999) estudaram o problema da colinearidade na estimação dos efeitos genéticos fixos. Estes autores concluíram que as variáveis preditoras destes efeitos apresentam algum grau de colinearidade que pode e deve ser superado. A regressão de cumeeira foi originalmente proposta por Hoerk e Kennard (1970) para superar os problemas causados pela colinearidade. Com a escolha adequada do *ridge parameter* , a regressão de cumeeira produz estimativas mais precisas dos coeficientes de regressão porque suas variâncias e quadrado médio do erro (QME) são menores do que aquelas produzidas pelo método dos quadrados mínimos.Muitos estudos propõem a regressão de cumeeira como alternativa para contornar a colinearidade (Dias et al., 2011; Petrini et al., 2012; Carvalheiro et al., 2006; Cardoso et al. 2008; Roso et al. 2005b).

O modelo usual para uma regressão multipla é representado por y = X *b* + e. Soluções para *b* são obtidas resolvendo-se $\hat{b}=(X'X)^{-1} X'y$. Na regressão de cumeeira (RC) um parâmetro k é adicionado à diagonal da matriz X'X, causando uma redução na variância das estimativas. Assim, a RC tom a forma $\hat{b}_k=(X'X + K)^{-1} X'y$, sendo $K = diag(k_1, k_2,...,k_{p'})$, ki >0. As RC foram aplicadas na forma padronizada, usando-se a matriz de correlações e, depois da estimação, foram transformadas à forma original e apresentadas desta forma. Para transformar $\hat{b}(i)$ a forma origina;: $\hat{b}(i) = \hat{b}(i) * (SSyy/SSxx(i))$, onde SSyy e SSxx(i) são as raízes quadradas das somas de quadrados de y e x(i), respectivamente. Este procedimento é feito para eliminar o efeito de escala em que as variáveis preditoras são expressas e também para eliminar correlação entre a constante e as variáveis preditoras incluídas no modelo linear. Este método, no entanto propõe uma escolha empírica dos valores de K (Dias et al. 2011). Os valores de K devem ser grandes o suficiente para quebrar as relações lineares existentes entre as covariáveis, e pequenos o suficiente para produzir o menor viés possível. (Schabenberger & Pierce, 2002)

HIPOTESES e OBJETIVOS

Hipóteses

a) Os efeitos genéticos fixos (aditivos de raça e não aditivos de heterose, perdas epistáticas e complementariedade) são importantes na avaliação genética multirracial;

b) Existe multicolinearidade entre os estimadores dos efeitos genéticos fixos num modelo de avaliação genética multirracial;

c) A metodologia da Regressão de Cumeeira (*ridge regression*) é a mais adequada para a estimação dos valores genéticos fixos numa população genética multirracial.

Objetivos

a) Estimar os efeitos genéticos fixos (aditivo de raça, heterose, perdas epistáticas e complementariedade) utilizando a metodologia dos quadrados mínimos;

b) Estimar os efeitos genéticos fixos (aditivo de raça, heterose, perdas epistáticas e complementariedade) utilizando a metodologia da regressão de cumeeira;

c) Comparar diferentes modelos estatísticos na estimação dos efeitos genéticos fixos;

d) Testar a ocorrência de colinearidade entre os estimadores dos efeitos genéticos fixos;

e) Comparar a metodologia da regressão de cumeeira com a regressão de quadrados mínimos na estimação dos efeitos genéticos fixos e,

f) Testar dois métodos de determinação do parâmetro de cumeeira a serem utilizados na estimação dos efeitos genéticos fixos.

[3]CAPÍTULO II

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[3] Artigo redigido de acordo com as normas do periódico *Livestock Science*

Modeling breed additive and non-additive genetic effects using a Angus x Nellore crossbred population

Claudia Damo Bertoli[a,b,*], Jose Braccini Neto[b,f], Connie McManus[c], Jaime Araujo Cobuci[b], Elisandra Lurdes Kern[b], Mario Luiz Piccoli[b,d], Flavio Schenkel[e], Vanerlei Roso[d]

[a] Instituto Federal Catarinense Campus Camboriu IFC-CC address: Rua Joaquim Garcia, s/n centro, Caixa Postal 2016, CEP 88.340-055 Camboriu - SC - Brazil Tel: +55 47 2104-0800 e-mail: cdbertoli@ifc-camboriu.edu.br

[b] Universidade Federal do Rio Grande do Sul - UFRGS Departamento de Zootecnia address: Avenida Bento Gonçalves, 7712 agronomia CEP 91.509-900 Porto Alegre - RS - Brazil Tel: +55 51 3308-6048

[c] Universidade de Brasília - UnB address: Campus Universitário Darcy Ribeiro, CEP 70.910-900 Brasília - DF - Brazil Tel: +55 61 3107-3300

[d] GenSys Consultores Associados address: Rua Guilherme Aves, 170/304 Jardim botânico CEP 90.680-000 Porto Alegre - RS - Brazil Tel: +55 51 3330-6804

[e] University of Guelph - UofG, CGIL - Centre of Genetic Improvement of Livestock address: 50, Stone Road East N1G 2W1 Guelph ON Canada Tel: +1 519 824 4120 *58650

[f] CNPq fellow

[*] Corresponding author at: Rua Rio Amazonas, 3477 Rio Pequeno, Caixa Postal 2139 CEP 88340-000 Camboriu - SC - Brazil Tel: +55 51 9751-3086/+55 47 9977-3086; fax: 55 47 2104-0800 e-mail address: cdbertoli@gmail.com

Abstract

The objectives of this study were to estimate fixed genetic (both additive and non-additive) effects and test different non-additive models. These effects included direct and maternal cumulative breed additive effects, direct and maternal complementarity (or profit heterosis), direct and maternal heterosis (dominance) and direct and maternal epistatic loss non-additive effects. A large crossbred Angus x Nellore population with approximately 300,000 records for weaning gain (WG) and 150,000 records for post-weaning gain (PG) was used. Phenotypic scores for weaning (WC) and post-weaning (PC) conformation, weaning (WP) and post-weaning (PP) precocity, weaning (WM) and post-weaning (PM) muscling and scrotal circumference (SC) were also used. All models included the fixed contemporary group effect and random animal, maternal and permanent environment effects. Each model was tested against all other models for all nine traits using the likelihood ratio test. The complete model, including all additive and non-additive effects and the model without complementarity, were seen to be the best options to analyze this crossbred population. However, least squares may not be the best methodology due to possible collinearity among estimators that may inflate the variance. In the complete model most effects were statistically significant ($P<0.01$) for weaning traits, except for direct and maternal breed additive effects and direct complementarity effect for WM. For post-weaning traits, the direct complementarity effect for phenotypic scores (PC, PP and PM) and the maternal heterosis effect for PG, PC, PM, were not statistically significant. For scrotal circumference the maternal complementarity, direct and maternal heterosis and maternal epistatic loss effects were not statistically significant. All other effects were statistically significant ($P<0.01$). For the model without complementarity, the direct breed additive effect for PG and PP was not statistically significant, including the maternal breed additive effect for WC, WD, PP and PM and maternal heterosis, direct and maternal epistatic loss effects for SC. Breed additive direct effect was mostly positive for weaning traits and negative for post-weaning and SC. The breed additive maternal effect for SC and maternal complementarity effect for WG were negative. Direct and maternal epistatic loss effects were negative for all traits, except for PG. We conclude that the fixed genetic effects are mostly significant, thus it is important to include them in the model when evaluating crossbreed animals and the models including breed additive effects, heterosis and epistatic loss with or without complementarity were the more appropriate.

Keywords: epistatic loss, heterosis, non-additive genetic effects, complementarity, crossbreed beef cattle

1.Introduction

Widely used in tropical and sub-tropical climate countries, crossbreeding systems are based on the exploration of various genetic effects resulting from existing differences between breeds. Among these effects are the breed additive effect and the non-additive effects of the combination of the involved breeds (joint additive effect), as well as heterosis and epistatic loss effects.

The breed additive effect comprehends the individual effects of each of the involved breeds; as long-term selection within a breed increased frequencies of non-allelic genes that jointly produce favorable extra effects (Fries *et al.et al.*, 2002). The non-additive effect of the combination of breeds involved in the crossbreeding, that causes a multiplicative relation among the additive actions was defined by Kinghorn (1993) as "profit heterosis". The heterosis effect is mainly due to the dominance effects on the genes and can be considered as the recovery from the depression due to accumulated consanguinity. A linear relationship between heterozygosis and heterosis retention has been found (Fries *et al.et al.*, 2000; Gregory *et al.et al.*, 1991). The epistatic loss effect comprehends an additional deviation from the genotypic value occasioned by the non-additive combination when more than one locus is considered in the analysis (Falconer, 1996). According to VanRaden (2006), talking about crossbred animals, "If non-additive effects are subtracted and only additive effects are reported, selection may not be optimal".

The models that estimate simultaneously additive and heterosis effects or estimate additive effects after the adjustment of the data for heterosis based on the expected heterozygosis are the most common basic models of multiracial populations breeding programs for beef cattle. These models have been used in crossbred populations in Brazil (Lopes *et al.et al.*, 2010; Cunha *et al.et al.* 2009; Cardoso *et al.et al.*, 2008; Kippert *et al.et al.*, 2008; Carvalheiro *et al.et al.* 2006; Pimentel *et al.et al.*, 2006), Africa (Theunissen *et al.et al.*, 2013; Abdel-Aziz *et al.et al.*, 2003), Australia (Arthur *et al.et al.*, 1999), Canada (Roso *et al.et al.*, 2005a), Colombia (Vergara *et al.et al.*, 2009a,b), Ethiopia (Demeke *et al.et al.*, 2003a,b), USA (Elzo and Wakeman, 1998) and Uruguay (Lema *et al.et al.* 2011).

The inclusion of complementarity effect in the model was suggested by Fries *et al.et al.* (2000) and reaffirmed by Piccoli *et al.et al.* (2002). According to Pimentel (2006), when referring to crossbred animals in a tropical environment, we can consider that two groups of genes were acting, one related to the growth potential and the other to adaptation. The multiplicative relation among their effects could be interpreted as complementarity. A large number of studies do not consider complementarity as an important effect, but Piccoli *et al.et al.* (2002) found that the magnitude of heterosis estimates is reduced when the complementarity (additive*additive interactions) is included in the model, indicating that under the additive-dominance model the heterosis estimation may be due to a non-linear additive effect. According to these authors this effect becomes more evident when the model also includes an epistatic loss effect.

The inclusion of the epistatic loss effect in the additive-dominant model was also suggested by Fries *et al.et al.* (2000) and reaffirmed by Piccoli *et al.et al.* (2002) with the objective of achieving a better explanation of the existing genetic variation among different breed compositions. The genotype at a locus can influence the genotype effect of a second locus and may inhibit gene expression of the second locus in the phenotype. Recent studies suggest that the epistatic loss effect strongly and negatively influenced crossbred animals´ levels of production (Cardoso *et al.et al.*, 2008, Lema *et al.et al.*, 2011), although some researchers choose do not include epistasis in the models, such as Vergara *et al.et al.* (2009b), Legarra *et al.et al.* (2007) and Arthur *et al.et al.* (1999).

As the main objective of crossbreeding systems is taking advantage from non-additive genetic effects among breeds, obtaining reliable estimates of the parameters involved in crossbreeding systems and thus being able to predict the performance of the crossed genotypes is an important step for the successful development of a breeding program (Cardoso *et al.et al.*, 2008).

The main objective of this study was to test different additive and non-additive genetic models. We also aim to estimate the fixed genetic effects (cumulative breed direct and maternal additive effects and complementarity (or profit heterosis), heterosis and epistatic loss direct and maternal non-additive effects), involving crosses between Angus and Nellore beef cattle breeds.

2. Materials and methods

2.1 Data

Data from different breed compositions resulting from crosses between Angus and Nellore cattle was used. This data came from more than 200 herds distributed in the Brazilian states of Rio Grande do Sul, Paraná, São Paulo, Mato Grosso do Sul, Mato Grosso and Goiás and also from Paraguay. All herds were participants of "Programa Natura de Melhoramento Genético de Bovinos" (Natura Cattle Breeding Program).

Table 1 presents the total number of animals and the distribution of observations throw coefficients used to estimate the fixed genetic effects and the percentage of the total number of observations.

2.2 Predictor variables of fixed genetic effects

2.2.1 Breed additive effect

The contribution of Nellore genes in the genetic composition of the animal (**aa**) and their dams (**am**) were used to estimate the direct and maternal genetic effect of breed, respectively. To avoid dependence in incidence matrix columns, only the Nellore coefficient was used, giving an estimation of a deviation from the Angus breed performance.

2.2.2 Complementarity

The coefficients proposed by Kinghorn (1993) and used by Fries *et al.et al.* (2000), Piccoli *et al.et al.* (2002), Cardoso *et al.et al.* (2008) were used to estimate the complementarity effects. The prediction variables of direct complementarity (**ca**) coefficient is described as **ca** = **aa***(1.0-**aa**) and the maternal complementarity (**cm**) coefficient is described as **cm** = **am***(1.0-**am**) where **aa** is the Nellore fraction of the animal breed and **am** is the Nellore fraction of the dam breed.

2.2.3 Heterosis effect

To estimate the direct and maternal heterosis effects, the heterozygosity coefficients **ha** and **hm** were used as described by Bertoli (1991) and Schenkel (1993), also used by Cardoso *et al.* (2008,2004), Pimentel *et al.* (2006) and Roso *et al.* (2005b). These coefficients are given by **ha** =

$(1-\sum_{i=1}^{2}\ (Sire\ breed_i\ *\ Dam\ breed_i))$ and **hm** = $(1-\sum_{i=1}^{2}\ (Maternal\ Grand\ Sire\ breed_i\ *\ Maternal\ Grand\ Dam\ breed_i))$ where i=1 refers to Angus breed proportion and i=2 refers to Nellore breed proportion. When the breed composition of a cow was not known (all products had known breed composition) the cow was considered as *inter se* mating.

2.2.4 Epistatic loss effect

To estimate the direct and maternal epistatic loss effects, the epistazygosity coefficients **ea** and **em** were used as proposed by Fries *et al.* (2002,2000) and also used by Cardoso *et al.* (2008), Pimentel *et al.* (2006), Carvalheiro *et al.* (2006) and Roso *et al.* (2005a,b). These coefficients are given by **ea**= ½ [Hs + Hd] and **em**= ½ [Hmgs + Hmgd], where Hs is the sire's heterozygosities, Hd is the dam's heterozygosities, Hmgs is the maternal grand sire heterozygosities and Hmgd is the maternal grand dam heterozygosities. When the breed composition of a cow was not known (all products had known breed composition) the cow was considered as *inter se* mating.

2.3 *Traits*

Nine traits were used in this analysis: weaning gain (WG), post-weaning gain (PG), phenotypic scores of conformation (WC), precocity (WP) and muscling (WM) taken at weaning, phenotypic scores of conformation (PC), precocity (PP) and muscling (PM) at post-weaning as well as scrotal circumference (SC) adjusted for animal weight and age. The phenotypic score for each trait is given on a five-point scale, where one is the worst, and five is the best score for each management group. The number of observations, means and standard deviations of each trait are presented in Table 2.

2.4 Statistical Analysis

2.4.1 Genotypic models

The general model is described by equation (1). The pair-traits WG-PG, WC-PC, WP-PP, WM-PM and WG-SC were analysed in a two-trait analysis using this model with the systematic inclusion of fixed genetic terms, in order to compare models and effects.

$$\mathbf{y = X\beta + W\gamma + Z\alpha + \varepsilon} \qquad \mathbf{(1)}$$

where **y** is the vector of observations of trait 1 and trait 2; **β** is the vector of fixed effects of contemporary group, which is formed by herd, birth year, birth season sex, manage group and evaluation date; **γ** is the vector of fixed genetic effects; **α** is the vector of random direct, maternal and permanent environmental effects and **ε** is the vector of random residual effects. Incidence matrices X, W and Z relate records to fixed environmental effects, to fixed genetic effects and to random direct and maternal additive genetic and permanent environment effects, respectively. Data was pre-corrected for fixed effects of animal age, dam age and birth date (julian).

The vectors of random effects **α** and **ε** were assumed to have (co)variance =

V(**α**)= $\begin{bmatrix} A\otimes G_a & A\otimes G_{am} & 0 \\ A\otimes G_{am} & A\otimes G_m & 0 \\ 0 & 0 & I\otimes Pe \end{bmatrix}$ and V(**ε**) = I⊗R. A is the additive numerator relationship matrix among animals and I is the identity matrix; $G_a= \begin{bmatrix} \sigma^2_{a1} & \sigma_{a1a2} \\ \sigma_{a1a2} & \sigma^2_{a2} \end{bmatrix}$, $G_m= \begin{bmatrix} \sigma^2_{m1} & \sigma_{m1m2} \\ \sigma_{m1m2} & \sigma^2_{m2} \end{bmatrix}$, $G_{am}= \begin{bmatrix} \sigma_{a1m1} & \sigma_{a1m2} \\ \sigma_{a2m1} & \sigma_{a2m2} \end{bmatrix}$, $Pe= \begin{bmatrix} \sigma^2_{p1} & \sigma_{p1p2} \\ \sigma_{p1p2} & \sigma^2_{p2} \end{bmatrix}$ and $R=\begin{bmatrix} \sigma^2_{e1} & \sigma_{e1e2} \\ \sigma_{e1e2} & \sigma^2_{e2} \end{bmatrix}$ where σ^2 refers to variance and σ refers to covariance; ***a*** refers to direct additive genetic, ***m*** to maternal additive genetic ***p*** to permanent environmental effects due to dam and **e** to residual; ***1*** refers to the first and ***2*** to the second trait on a two-trait analysis.

The complete general model above (1) was analyzed and also with reductions. The unique difference among compared models was in **γ** vector, which includes different fixed genetic effects. The considered effects for each tested model are presented in Table 3. In total, eight models were analyzed for each trait using the least squares methodology to estimate the fixed genetic effects in a two-trait analysis. Software for solving model (1) was provided by GenSys Consultores Associados, using Fortran 95.

The Likelihood Ratio, as described by Regazzi and Silva (2004), was used to compare the models for each model pair.

2.4.2. The (co)variance components

The (co)variance components were previously estimated using model (1), including all effects (fixed effects of environment, fixed genetic effects, random direct, maternal and permanent environmental effects and residual). The Restricted Maximum Likelihood (REML) method with the DMU (Madsen & Jensen, 2000) software was used. The convergence criterion was 10^{-12}.

2.4.3 Connectedness analysis

A connectedness analysis between contemporary groups was carried out according to Roso *et al.* (2004), using the total number of direct genetic links between contemporary groups due to any common ancestors. Contemporary groups with more than two calves and with at least five direct links were considered connected and retained for analysis. Roso *et al.* (2004) found that as the degree of connectedness among test groups decreases, the accuracy of comparisons of EBVs of bulls in different test groups also decreases. As one of the final objectives of a genetic evaluation is to obtain accurate EBVs, we tested the connectedness, using only animals of connected contemporary groups in this analysis. The number of animals and contemporary groups for each trait before and after the connectedness analysis is presented in Table 4.

2.4.4 Collinearity diagnosis

Principal components (PC), condition index (CI) and variance inflation factor (VIF) were used to perform a collinearity diagnosis. CI was obtained for each eigenvalue by computing $CI_i=\sqrt{\frac{\lambda_{max}}{\lambda_i}}$, where λ_{max} is the largest eigenvalue and λ_i is the i^{th} eigenvalue of the correlation matrix. The condition number (k) is the condition index of the highest value. Values of k between 10 and 30may indicate problems of collinearity. (Belsley, 1991) VIF was given by VIF = 1/(1-R_i^2), where R_i is the determination coefficient. (Schabenberger & Pierce, 2002).Usually values larger than 10 suggests that multicollinearity may be causing estimation problem. (Chatterjee *et. al*., 2000)

3. Results and Discussion

3.1 The models

The significance of the contrasts of the models against reductions is presented in table 5. Of the 198 realized comparisons (22 between each two of the eight models, for each of the nine analyzed traits), using the Likelihood ratio test and testing under a significance level of P<0.001, 40 comparisons (20%) were not significant. Of these, 45% were for scrotal circumference. The nullity hypothesis was rejected, indicating that for each of the 158 significant comparisons the tested models presented a significant difference in at least one of the considered parameters.

All models tested against reduced **A, AC and AE** models, presented significant differences except for SC, showing that for all other traits these models are not the best models to use to crossbreed animals.

The **AH** reduction model did not show significant difference from **ACH** for most traits, but did with **ACE**, **AHE** and **ACHE** models. If **AH** and **ACH** are not truly different, we may suppose that **ca** and/or **cm** are not really important to these traits. Lopes *et al.* (2010), testing different models to estimate genetic effects in Angus x Nellore crosses, found that the "joint additive effect does not substantially improve the adjustment". Carvalheiro *et al.* (2006), studying Hereford-Nellore crosses, suggest that complementarity seems to be important but should be further investigated to better comprehend the effect and how to model it.

The comparison of **ACHE/ACE** did not present any significance and **ACHE/AHE** presented non-significant contrasts for most number of traits. Observing **ACHE/ACE** we might suppose that **ha** or **hm** were not important to improve the adjustment of the tested models, thus the models are equivalent. However, if we consider the significance of the contrast **ACH**/**AC** a possible confounding may exist when **ha**/**hm** or **ea**/**em** were not included in the model. According to VanRaden (2006) "Breed differences contain additive, dominance, and epistatic effects that are confounded if only two breeds are considered...". When using simpler models, joint additive and epistatic effects appear to be mixed in the heterosis effect (Pimentel *et al.* 2006).

For weaning traits, the determination coefficient (R^2) (not shown) was highest and the mean square error (MSE) was lower for the **ACE** model and for post weaning traits the **AHE** model had the highest R^2 and lowest MSE.

Although **ACHE** did not differ statistically from **ACE** and **AHE** for most traits, the **ACE** model produced very high magnitude of the estimates. These high estimates hinder the biological interpretation and lead us to assume that this is not the best model to use. The **ACHE** and **AHE** models seem more parsimonious to use with crossbred animals.

A wide variety of forms of interactions may be manifested in a crossbred animal, often estimated as a single component, called heterosis. This estimated heterosis value is, actually, the liquid balance of all the genes interactions that are present in the animal, herded from different breeds. Models that include non-additive effects can be more precise, but also more confusing. Although genetic interactions are complicated terms to extract from models, they can provide useful predictions if used carefully. Breeders must continue selecting for additive merit, but can also improve non-additive merit, considering these interactions in breeding programs where crossbred animals are used (VanRaden, 2006).

Bueno *et al.* (2011), studying epistasis on genetic evaluation models, concluded that simpler models used to evaluate bovine composites might wrongly identify various additive and non-additive effects as a heterosis effect. Breed additive, heterosis and epistatic loss effects, as well as direct and maternal effects, should be included in models to evaluate crossbreed beef cattle. (Bueno *et al.*, 2012; Lema *et al.*, 2011; Cunha *et al.*, 2009; Cardoso *et al.*, 2008; Kippert *et al.*, 2008; Carvalheiro *et al.*, 2006)

Complementarity effects are more controversial. Cardoso *et al.* (2008) and Piccoli *et al.* (2002) found that they are as important as the other non-additive effects; however, Lopes *et al.* (2010) concluded "The inclusion of joint additive effects does not substantially improve the adjustment promoted by the analysis models, besides inserting a bias attributed to multicollinearity". Carvalheiro *et al.* (2006) argue that complementarity seems important but should be further investigated.

3.1.1 Collinearity analysis

Correlation between predictor variables

The correlation between the coefficients used for the estimation of the fixed genetic effects for WG and PG are presented in table 6.

In total, 46% of the correlations between the pairs for WG and 50% for PG, presented values superior to 0.5, indicating medium to high correlations between the pairs. This high correlation may indicate multicollinearity between the coefficients; however, the coefficient pairs must not be the only verified factor as the existing relationship between three or more coefficients can also be interfering in this multicollinearity

For all analyzed traits (WG, WC, WP, WM, PG, PC, PP, PM and SC), the highest correlation was found between the coefficients for maternal complementarity and maternal heterosis, followed by the correlation of maternal and direct epistatic loss with maternal complementarity. This high correlation might be the reason why significant differences were not detected between the **ACH/AH** and **ACHE/ACE** reductions**.**

When complementarity is removed from the model (not shown), the highest correlation is between maternal heterosis and direct epistatic loss, keeping values around 0.85 for all traits. This high correlation may result from data structure, which cause a possible linear dependence (multicollinearity) involving the predictors.

When we remove the maternal component of heterosis from the analysis of PG, PC and PM (maternal heterosis was not significant for these traits) the highest correlation remains between complementarity and epistatic loss, with very close values.

Principal Components and Conditional Index

The first principal component indicates a possible collinearity between the prediction variables of direct (**ca**) and maternal complementarity (**cm**), maternal heterosis (**hm**), direct (**ea**) and maternal (**em**) epistatic loss estimates. These estimates may be confounded for these traits. The second principal component shows that the breed direct (**aa**) and maternal (**am**) additive effect, direct heterosis (**ha**) and direct complementarity (**ca**) effect opposes to the maternal complementarity (**cm**), maternal heterosis (**hm**) and direct (**ea**) and maternal (**em**) epistatic loss effects, showing again a possible confounding between these estimators (Figure 1).

When there is no collinearity, the eigenvalues, condition index and condition numbers are all one. With increasing collinearity, eigenvalues are both larger and smaller than one (eigenvalue close to zero indicates multicollinearity problem) and the condition index and number will increase (Schabenberger & Pierce, 2002). According to Schabenberger & Pierce (2002), if the value of the condition number of the matrix is lower than the upper threshold of 30, this indicates problems of multicollinearity. The highest condition index we found was 21.2493 for WG. The other CIs were 21.0631 for WC, 20.4443 for WP, 20.8205 for WM, 24.4637 for PG, 22.8341 for PC, 21.9954 for PP, 22.3479 for PM and 28.5690 for SC. Lema *et al.* (2011) also used the threshold of 30. They found condition number of 28.3 and concluded that collinearity was not a problem.

Multicollinearity can occur when one or more variables are dependent on others present in the same model. When using non-additive models, we are using breed composition (individual, parents and grandparents) to estimate all coefficients (breed direct, complementarity, heterosis and epistatic loss). High correlations between variable pairs may be indicative of multicollinearity (Roso *et al.*, 2005b). The higher the collinearity, the higher the standard errors and, wider the confidence intervals. The *t* statistics tend to be very small in this case. When multicollinearity is present, it is therefore difficult to reject the null hypothesis (Schabenberger and Pierce, 2002).

Variance inflation factor

The variance inflation factor (VIF) indicates the variance inflation of each regression coefficient compared with an orthogonal situation. Usually values above 10 for VIF suggest that multicollinearity may be causing problems in the estimation (Schabenberger & Pierce, 2002).

The variance inflation factor (VIF) analysis for the models **ACHE**, **AHE** and **ACE** are presented in table 7.

The VIF shows that the estimates had their variance inflate up to 110 times (SC) when compared to an orthogonal condition (VIF=1) for the model **ACHE**. Roso *et al.* (2005b) suggested the use of ridge regression to solve the problem of multicollinearity; however, Cardoso *et al.* (2008), comparing the least squares and ridge regression methodologies, showed that, although the most consistent results were generated by the ridge regression technique, the estimates of genotypic effects, with and without the use of this technique, generate similar predicted values, and this occurred for all tested traits.

This possible collinearity can be partially explained as all estimators are based on the breed composition of individuals, which is equal to the average of the breed composition of their parents. In practice, we are using the same information to predict different effects, seen from different perspectives.

For the **ACE** model, except PP, all other traits presented FIV higher than ten for maternal complementarity and higher FIV for direct and maternal epistatic loss than **AHE** model. For the **AHE** and **ACH** models, only SC produced a FIV higher than 10. The **AC, AH, AE** and **A** models did not present any FIV above ten. These results may indicate that the greatest problem for collinearity is complementarity, as **cm** always showed the highest values.

3.2 Estimates of fixed genetic effects

Estimates of fixed genetic effects, obtained as a deviation from Angus, are presented in Table 8.

All regression coefficients for WG and WM are statistically significant (P<0.01), as were most coefficients for the other traits (WC, WP, PG, PC, PP, PM). Scrotal circumference presented 30% of the total statistically non-significant coefficients. Among the non-significant effects, there were some maternal components for post-weaning traits, which were not expected to be significant. Contrary to this, the non-significance of the direct and maternal breed additive and direct complementarity effects for WM (models **ACHE**, **ACH** and **AHE**) was not expected nor was the direct breed additive effect for PG (model **AHE**) and for PP (models **ACE** and **AHE**).

The breed additive effect was estimated as a deviation of Nellore from Angus. The direct breed additive effect (**aa**) was positive for weaning traits and negative for post-weaning traits and SC for most of the tested models, showing that as the Nellore (*B. indicus*) gene proportion increases, the general weaning growth rate increases and the general post-weaning growth rate decreases. For **A**, **AC** and **AE** models, **aa** was negative for all traits. The positive or negative effect does not mean that the animals are heavier or lighter; it is just the gene effect. The final animal weight will be a balance of all involved effects. Negative values were reported for weaning weight for Nellore (Lopes *et al.*, 2010) and positive for Brahman (Elzo and Wakeman, 1998), both as deviation from Angus. A positive value of **aa** for weaning weight was reported by Lema *et al.* (2011) and negative values for average pre-weaning daily gain were reported by Cardoso *et al.* (2008) and for pre-weaning gain by Carvalheiro *et al.* (2006). These effects considered Nellore as a deviation from Hereford. Kippert *et al.* (2008) studying 205 day and 550 day weights found negative values for both periods, weaning and post-weaning, even though neither the complementarity nor epistatic loss effects were considered. Cardoso *et al.* (2008), studying Nellore x Hereford crosses also found negative values of **aa** for all traits (WC, WP, WM, PC, PP, PM and SC).

The maternal breed additive effect (**am**) was positive for most of models and traits except for SC, showing that as the Nellore genes proportion increase the calf performance also increase, but with a small scrotal circumference. Negative values of **am** for WC (model **ACE**), WP (models **ACHE**, **ACE** and **AHE**) and WM (models **ACE** and **AHE**) may indicate poorer performance in conformation, precocity and muscling at weaning for the Nellore genes. We did not find literature testing these models with these traits. Positive values of **am** for 205 day and 550 day weights were reported by Kippert *et al.* (2008) and for weaning weight by Lopes *et al.* (2010). Lema *et al.* (2011), using a model without a complementarity effect, found strongly negative values for Nellore breed as a deviation from Hereford. They suggest their environment was less restricted, explaining the better performance for the British breed compared to Zebu. All models presented negative values of **am** for SC. Cardoso *et al.*(2008), studying crosses between Hereford and Nellore found negative values of **am** only for post-weaning precocity.

Complementarity can be considered as what Kinghorn (1993) called "profit heterosis". If we consider this effect as the joint action of two gene pools, as suggested by Pimentel *et al.* (2006), these results can be interpreted as additive interaction between two different traits, independent of dominance (heterosis) or epistasis. When we consider a tropical or a temperate environment, the change in performance when we move the genetic composition from 0.00 to 0.25 *Bos indicus* is not necessarily equivalent for the move from 0.75 to 1.00. What we are considering here is a quadratic effect between two breeds as suggested by Kinghorn (1993). The complementarity coefficient reaches its maximum value at ½ Angus ½ Nellore animals, which presents a complementarity coefficient of 0.25. According to Cardoso *et al.* (2008), if for a trait such as weaning gain, **am** is the additive effect due to the Nellore dam maternal instinct (defense and calf care), heat and parasites tolerance and ability to digest food with low nutritional value and turn it into milk with high solids, while **(1-am)** represents the maternal breed additive effect due to high feed intake and high conversion rate from the Angus breed. Thus **cm** (=**am***(1,0-**am**)) represents an extra effect due to both gene pools (Cardoso *et al.*, 2008). This may explain the significance for this effect for these two specific breeds.

Direct complementarity (**ca**) presented positive values for models **ACHE**, **ACE** and **AC,** but negative values for weaning and post weaning phenotypic scores using the **ACH** model (WC, WP, WM, PC, PP, PM). These negative values may imply that Nellore cows, although producing heavier calves may produce less harmonious calves in terms of conformation, precocity and musculature, both at weaning and post weaning. For the **ACHE** model, **ca** was not statistically significant for WM, PC, PP and PM. Cardoso *et al.* (2008) found negative values for all weaning traits and SC and positive values for post-weaning traits for Hereford x Nellore crosses. Carvalheiro *et al.* (2006) reported negative values for pre-weaning gain (-65.38(3.78)) for an equivalent model, also with Hereford x Nellore crosses. Lopes *et al.* (2010) reported a value of 21.82 for direct complementarity for weaning weight of Angus x Nellore crosses.

Maternal complementarity (**cm**) presented the highest magnitude effect for all traits and also the highest standard errors, followed by direct complementarity. These coefficients presented the highest FIV, especially for SC. For the **ACHE** model, **am** was 36.70 for WG and -12.82 for PG. Carvalheiro *et al.* (2006) reported a value of 61.38 for pre-weaning gain for Hereford X Nellore crosses when estimating **am** with ordinary least squares methodology and 11.94 when using ridge regression methodology. They assume that multicollinearity can cause these high values that have a difficult biological interpretation (Carvalheiro *et al.*, 2006). **cm** ranged from 1.0 to 1.3 for weaning and 0.4 to 0.7 for post-weaning phenotypic scores with the **ACHE** model. Similar values (between 0.78 and 1.47 for WC, WP and WM) were reported by Cardoso *et al.* (2008) for Hereford x Nellore crosses. For Angus x Nellore crosses, Lopes *et al.* (2010) reported negative values for **cm** (-45.52 for weaning weight). It is difficult to find results for the complementarity effect for many traits in the literature, but it seems that the presented values are very high. Perhaps with other estimation methodology, as is the case of Carvalheiro *et al.* (2006) and Cardoso *et al.* (2008) who used ridge regression, these values would be smaller and more reliable.

Unlike the complementarity, heterosis is widely studied and interest is increasing in epistatic loss . Lopes *et al.* (2010), Vergara *et al.* (2009b), Kippert *et al.* (2008), Elzo and Wakeman (1998) estimated heterosis and/or epistatic loss in Angus x Nellore or Angus x Brahman or Angus X Zebu crosses; Lema *et al.* (2011), Cardoso *et al.* (2008), Carvalheiro *et al.* (2006), Pimentel *et al.* (2006), Piccoli *et al.* (2002), Arthur *et al.* (1999) worked on heterosis and/or epistatic loss with Hereford x Nellore or Hereford x Brahman crosses and Bueno *et al.* (2011), Roso *et al.* (2015a), Demeke *et al.* (2003a,b) and Abdel-Aziz *et al.* (2003) studied heterosis and/or epistasis with another crossbreed cattle. These authors also tested different models and/or methodologies to estimate non-additive genetic effects. The range for direct and maternal heterosis effects is wide and usually positive. When estimates of heterosis effect are negative, it usually has a very low magnitude. For epistatic loss, the estimates frequently changed from negative to positive.

The direct heterosis effect (**ha**) was positive and statistically significant for all traits, except for SC, in **ACHE** and **ACH**. When complementarity or epistatic loss were included in the model, but not both (models **AHE** and **ACH**), estimated values of **ha** remained close one to each other, but when compared to the **ACHE** model, the estimated values of **ha** are around half the previous value. It is possible that the estimates for complementarity or epistasis decrease heterosis estimates, because when the model does not include complementarity and/or epistatic loss effects, heterosis estimates were much higher. In the same manner, when the model does not include heterosis, complementarity effects increased significantly. This probably refers to what Dickerson (1973) commented as recombination effects between joint gametes which may be confounded with heterosis effects. These effects are then estimated as heterosis or complementarity, if the complementarity is included in the model, and represent the sum of all interactions for each locus and among every gene that affects the trait.

Maternal heterosis was not statistically significant for SC in all tested models. For the **ACHE** model**, hm** was not statistically significant for most post-weaning traits (PG, PC and PM). For all other situations, **hm** was statistically significant. **ha** was positive for all models and traits except for PG in the **ACH**, **AHE** and **AH** models**.** Lema *et al.* (2011), Lopes *et al.* (2010), Cardoso *et al.* (2008) and Kippert *et al.* (2008) found positive values for direct and maternal heterosis and greater values for **hm** than **ha**.

Epistatic effects are understood as interaction of genes at different loci. When breeds were formed, benefic interactions between genes were selected and produced linkage disequilibrium among them. When breeds are crossed, these interactions may be broken. Crossbred animals may be out of harmony and epistasis, if important, is a negative effect (Kinghorn, 1993). Recombination loss is a measure to attempt to all deviations from linear association of heterosis with degree of heterozigosity (Dickerson, 1973) and “epistatic loss” is “proportional to the probability that two non-allelic genes in the diploid individual are from different breeds”(Kinghorn, 1980). What we are estimating here are the interactions between non-allelic genes due to crossbred mating.

Estimates for direct epistatic loss effect were negative and statistically significant for all traits, except for weaning traits in the **AE** model and SC in the **AHE** model. The estimate for the maternal component of epistatic loss effect for post-weaning gain was positive and negative for all other traits and models. The epistatic loss effect for scrotal circumference was statistically significant ($P<0.05$) only for the **AE** model. Cardoso *et al.* (2008) studying Hereford x Nellore crosses, found positive estimates to epistatic loss for all weaning traits and negative values for post-weaning traits, as found here in the **AE** model. Lema *et al.* (2011) found negative effects for direct and positive for maternal components for all traits. The negative epistatic loss effect may be explained as the broken positive interaction, if they exist.

Even if most full models are significantly different from their reduced versions and the most tested effects are significant, when we look at the rank of animal EBVs, we find 70 % of coincidence in the first 10% for all tested models.

4. Conclusion

Considering the high significance of most contrasts between models and their reduced versions we conclude that the best models are ACHE and AHE. ACHE includes all effects and they were mostly significant but this model has many effects with extremely high estimated values, which may have been caused by a collinearity of the predictor variable. We suggest further studies around collinearity in the specific case of this model, perhaps using the ridge regression methodology can solve this. AHE model proved extremely interesting, especially with regard to minor estimated standard errors for the effects of heterosis and epistasis compared with the ACHE model with FIV lower than ten for all traits, except SC. The fixed genetic effects of breed, complementarity, heterosis and epistatic loss effects are really acting behind the models. If the interaction between different alleles effectively exists, even if their magnitudes are unstable, we must include them in the models to evaluate crossbred animals, under a risk of selection bias. The results depend on the breeds and environment where the animals are maintained. The results presented here are from Angus x Nellore crosses, reared on extensive pastures in South America.

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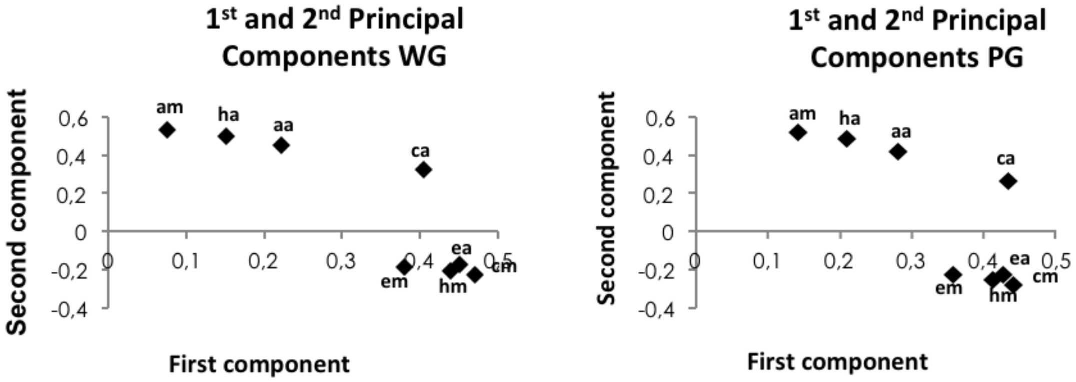

aa: direct breed additive effect, **ca,** direct complementarity effect, **ha:** direct heterosis effect, **ea:** direct epistatic loss effect **am:** maternal breed additive effect, **cm:** maternal complementarity effect, **hm:** maternal heterosis effect, **em**: maternal epistatic loss effect

Figure 1. First and second principal components for weaning gain (WG) and post-weaning gain (PG) traits.

Table 1
Absolute and relative frequencies of observations among coefficients of fixed genetic effects, grouped in classes of 0.125, ranging from zero to one.

Classes	aa	am	ca	cm	ha	hm	ea	em
0.000	27135 (9.5)	37561 (13.2)	27135 (9.5)	89677 (31.4)	27107 (9.5)	89598 (31.4)	54852 (19.2)	103209 (36.2)
0.125	522 (0.2)	145 (0.1)	1013 (0.4)	200 (0.1)	17 (0.0)	3 (0.0)	35 (0.0)	6 (0.0)
0.250	7140 (2.5)	2385 (0.8)	257161 (90.1)	195431 (68.5)	731 (0.3)	98 (0.0)	66553 (23.3)	23795 (8.3)
0.375	118626 (41.6)	84046 (29.5)			3110 (1.1)	24370 (8.5)	9924 (3.5)	26693 (9.4)
0.500	84259 (29.5)	65641 (23.0)			136291 (47.8)	132697 (46.5)	120060 (42.1)	121670 (42.6)
0,625	11868 (4.2)	8575 (3.0)			43545 (15.3)	9490 (3.3)	20810 (7.3)	6273 (2.2)
0.750	33676 (11.8)	34416 (12.1)			36052 (12.6)	14284 (5.0)	12576 (4.4)	3527 (1.2)
0.875	2050 (0.7)	420 (0.1)			3120 (1.1)	232 (0.1)	494 (0.2)	130 (0.0)
1.000	32 (0.0)	52120 (18.3)			35335 (12.4)	14538 (5.1)	6 (0.0)	5 (0.0)
Total	285,309 (100.00)	285,309 (100.00)	285,309 (100.00)	285,309 (100.00)	285,309 (100.00)	285,309 (100.00)	285,309 (100.00)	285,309 (100.00)

aa, am, ca, cm, ha, hm, ea, em: coefficients used to estimate direct and maternal breed additive genetic effects, direct and maternal complementarity, heterosis and epistatic loss non-additive genetic effects, respectively. Classes include fractions equal or smaller than the mentioned value. Percentages in parentheses were expressed as relative frequencies.

Table 2
Number of observations (N), means and standard deviation (SD) of analysed traits

Trait		N	Mean	SD
WG	**(Kg)**	294,045	152.92	16.96
WC	**(score)**	288,182	3.42	0.68
WP	**(score)**	276,264	3.44	0.72
WM	**(score)**	286,350	3.32	0.72
PG	**(Kg)**	148,443	83.36	13.61
PC	**(score)**	149,091	2.53	0.66
PP	**(score)**	141,188	2.74	0.73
PM	**(score)**	147,392	2.52	0.70
SC	**(cm)**	46,269	29.17	1.65

WG: weaning gain; WC: visual score of conformation; WP: visual score of precocity and WM: visual score of muscling taken at weaning; PC: visual score of conformation; PP: visual score of precocity and PM: visual score of muscling taken at post-weaning; SC: scrotal circumference

Table 3

Predictor variables of fixed genetic effects included in the genotypic models considered in this study

Model	**aa**	**am**	**ca**	**cm**	**ha**	**hm**	**ea**	**em**
A	x	x						
AC	x	x	x	x				
AH	x	x			x	x		
AE	x	x					x	x
ACH	x	x	x	x	x	x		
ACE	x	x	x	x			x	x
AHE	x	x			x	x	x	x
ACHE	x	x	x	x	x	x	x	x

aa, am, ca, cm, ha, hm, ea, em: direct and maternal breed additive genetic effects, direct and maternal complementarity non-additive genetic effects, direct and maternal heterosis non-additive genetic effects, direct and maternal epistatic loss non-additive genetic effects, respectively

Table 4
Number of animals (A) and contemporary groups (CG) used in the analysis.

Trait		Weight Gain		Conformation		Precocity		Muscling		Scrotal Circumference	
		TOTAL	CONNEC (%)	TOTAL	CONNEC (%)	TOTAL	CONNEC (%)	TOTAL	CONNEC (%)	TOTAL	CONNEC (%)
A	W	294,045	284,628 (97)	288,182	279,582 (97)	276,264	268,333 (97)	286,350	277,734 (97)		
	PW	148,443	138,102 (93)	149,091	144,264 (98)	141,188	136,802 (97)	147,392	142,580 (97)	46,269	40,092 (87)
CG	W	9,242	6,615 (72)	8,840	6,433 (73)	8,312	6,011 (72)	8,807	6,398 (73)		
	PW	11,398	7,044 (62)	3,535	2,496 (71)	3,304	2,318 (70)	3,506	2,471 (70)	4,222	2,445 (58)

W: weaning phenotypes; **PW**: post-weaning phenotypes; **CONNEC.(%):** number (and percentage) of animals(A) / contemporary groups(CG) connected to the analyzed data.

Table 5
Significance of the models tested against each possible reduced model

model	**AC**	**AH**	**AE**	**ACH**	**ACE**	**AHE**	**ACHE**	**ACH**	**ACE**	**AHE**	**ACHE**	**ACH**	**ACE**	**AHE**	**ACHE**	**ACH**	**ACE**	**AHE**	**ACHE**	**ACHE**	**ACHE**	**ACHE**
reduction	**A**	**A**	**A**	**A**	**A**	**A**	**A**	**AC**	**AC**	**AC**	**AC**	**AH**	**AH**	**AH**	**AH**	**AE**	**AE**	**AE**	**AE**	**ACH**	**ACE**	**AHE**
trait																						
WG	***	***	***	***	***	***	***	***	***	***	***	ns	***	***	***	***	***	***	***	***	ns	ns
WC	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	ns	***
WP	***	***	***	***	***	***	***	***	***	***	***	ns	***	***	***	***	***	***	***	***	ns	ns
WM	***	***	***	***	***	***	***	***	***	***	***	**	***	***	***	***	***	***	***	***	ns	***
PG	***	***	***	***	***	***	***	***	***	***	***	ns	***	***	***	***	***	***	***	***	ns	ns
PC	***	***	***	***	***	***	***	***	***	***	***	**	***	***	***	***	***	***	***	***	ns	ns
PP	***	***	***	***	***	***	***	***	***	***	***	ns	***	ns	***	***	***	***	***	***	ns	***
PM	***	***	***	***	***	***	***	***	***	***	***	ns	ns	ns	ns	***	***	***	***	***	ns	ns
SC	***	**	**	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

*** P<0.001; ** P< 0.01; **ns**: statistically non significant; **A:** model including only the breed additive (direct and maternal) effect; **AC:** model including the breed additive (direct and maternal) and complementarity (direct and maternal) effects; **AH:** model including the breed additive (direct and maternal) and heterosis (direct and maternal) effects; **AE:** model including the breed additive (direct and maternal) and epistatic loss (individual and maternal) effects; **ACH:** model including the breed additive (direct and maternal), complementarity (individual and maternal) and heterosis (individual and maternal) effects; **ACE:** model including the breed additive (direct and maternal), complementarity (direct and maternal) and epistatic loss (direct and maternal) effects; **AHE:** model including the breed additive (direct and maternal), heterosis (direct and maternal) and epistatic loss effects (direct and maternal) and the complete model **ACHE:** the breed additive (direct and maternal), complementarity (direct and maternal), heterosis (direct and maternal) and epistatic loss (direct and maternal) effects.

Table 6

Correlation between the coefficients used for estimating of fixed genetic effects. Weaning gain below and post-weaning gain above diagonal.

	aa	**am**	**ca**	**cm**	**ha**	**Hm**	**ea**	**em**
aa	1	0.7552	0.7172	0.1195	0.6607	0.1165	0.2652	0.0884
am	0.7435	1	0.5577	-0.1375	0.7379	-0.1200	-0.1077	-0.1281
ca	0.6726	0.5298	1	0.5073	0.7559	0.4548	0.5513	0.4241
cm	0.0724	-0.1810	0.4774	1	-0.0052	0.9013	0.8373	0.8362
ha	0.6015	0.6970	0.7288	-0.0323	1	-0.0025	-0.0425	-0.0012
hm	0.0711	-0.1628	0.4247	0.8998	-0.0242	1	0.8760	0.5367
ea	0.2210	-0.1416	0.5259	0.8305	-0.0792	0.8719	1	0.5630
em	0.0521	-0.1610	0.4000	0.8339	-0.0248	0.5345	0.5540	1

aa, am, ca, cm, ha, hm, ea, em: direct and maternal breed additive effect, direct and maternal complementarity, heterosis and epistatic loss non-additive effects, respectively.

Table 7
Variance inflation factor (VIF) estimated (**ACHE, AHE** and **ACE** models)

model ACHE

	WG	WC	WP	WM	PG	PC	PP	PM	SC
aa	3.544	3.593	3.455	3.503	4.174	4.024	3.823	3.853	6.054
am	3.712	3.892	4.024	3.844	4.030	4.323	4.854	4.230	4.773
ca	13.730	13.935	13.815	13.355	21.228	19.661	19.140	18.183	22.848
cm	69.093	67.611	62.564	66.808	86.393	75.271	68.870	74.077	110.851
ha	8.896	8.886	8.460	8.672	13.638	12.444	11.416	11.911	13.541
hm	36.929	36.343	34.335	36.021	45.887	41.392	38.361	40.770	51.637
ea	13.924	14.158	13.918	13.975	18.166	17.214	16.603	16.795	21.906
em	17.169	16.908	15.957	16.755	20.864	18.359	17.366	18.199	28.671

model AHE

	WG	WC	WP	WM	PG	PC	PP	PM	SC
aa	3,544	3,592	3,454	3,502	4,165	4,010	3,798	3,837	6,053
am	3,481	3,606	3,659	3,561	3,775	3,993	4,317	3,902	4,415
ha	2,216	2,285	2,370	2,249	2,568	2,596	2,839	2,521	3,421
hm	5,124	5,172	5,073	5,132	5,383	5,301	5,177	5,218	6,661
ea	6,330	6,380	6,250	6,313	7,012	6,784	6,586	6,655	10,394
em	1,496	1,491	1,453	1,481	1,511	1,474	1,448	1,459	1,705

model ACE

	WG	WC	WP	WM	PG	PC	PP	PM	SC
aa	3,465	3,502	3,369	3,414	4,008	3,865	3,675	3,699	5,686
am	3,672	3,849	3,980	3,802	3,960	4,254	4,781	4,164	4,588
ca	3,399	3,561	3,840	3,441	3,973	4,080	4,728	3,831	5,716
cm	10,189	10,147	9,704	10,032	10,926	10,329	9,781	10,147	15,204
ea	5,745	5,764	5,726	5,689	6,341	6,124	6,134	5,988	9,462
em	4,501	4,477	4,291	4,439	4,673	4,467	4,278	4,418	5,917

aa, am, ca, cm, ha, hm, ea, em: direct and maternal breed additive genetic effects, direct and maternal complementarity non-additive genetic effects, direct and maternal heterosis non-additive genetic effects, direct and maternal epistatic loss non-additive genetic effects, respectively; **WG**: weaning gain; **PG**: post-weaning gain; **WC**: weaning conformation; **PC**: post-weaning conformation; **WP**: weaning precocity; **PP** post-weaning precocity; **WM**: weaning muscling; **PM**: post-weaning muscling; **SC**: scrotal circumference adjusted to age.

Table 8

Estimates of breed additive and non-additive genetic effects of pre and post-weaning traits obtained as a deviation from Angus.

	ACHE	ACH	ACE	AHE	AC	AH	AE	A
WG								
aa	1,405 (0,323) **	1,881 (0,302) **	4,776 (0,319) **	4,429 (0,323) **	-1,504 (0,295) **	1,810 (0,271) **	-5,551 (0,295) **	-2,535 (0,257) **
am	2,111 (0,195) **	4,322 (0,183) **	1,513 (0,194) **	2,957 (0,189) **	6,085 (0,172) **	4,238 (0,181) **	6,970 (0,172) **	4,739 (0,152) **
ca	16,269 (1,605) **	3,350 (1,079) **	58,021 (0,798) **		40,823 (0,768) **			
cm	36,701 (2,339) **	5,190 (0,747) **	90,059 (0,898) **		27,964 (0,395) **			
ha	8,079 (0,365) **	14,437 (0,245) **		11,356 (0,182) **		14,573 (0,174) **		
hm	3,872 (0,665) **	15,026 (0,251) **		21,465 (0,248) **		16,346 (0,116) **		
ea	-3,821 (0,541) **		-20,403 (0,347) **	-10,531 (0,365) **			8,096 (0,194) **	
em	-11,616 (0,559) **		-24,588 (0,286) **	-3,070 (0,165) **			-5,002 (0,163) **	
PG								
aa	-1,090 (0,405) **	-4,681 (0,371) **	-1,115 (0,397) **	-0,172 (0,405) ns	-10,265 (0,362) **	-3,038 (0,326) **	0,638 (0,357) ns	-6,705 (0,303) **
am	1,892 (0,235) **	2,529 (0,217) **	1,457 (0,232) **	1,373 (0,227) **	6,577 (0,202) **	2,468 (0,214) **	4,734 (0,204) **	11,593 (0,179) **
ca	21,586 (2,204) **	17,294 (1,365) **	55,084 (0,953) **		52,577 (0,919) **			
cm	-12,820 (3,018) **	-6,783 (0,889) **	-6,212 (1,073) **		-28,680 (0,467) **			
ha	6,112 (0,522) **	12,215 (0,321) **		13,145 (0,227) **		14,567 (0,216) **		
hm	0,594 (0,858) ns	-5,025 (0,293) **		-2,627 (0,294) **		-5,610 (0,135) **		
ea	-8,452 (0,706) **		-15,337 (0,417) **	-5,886 (0,438) **			-13,226 (0,227) **	
em	1,496 (0,714) *		-1,854 (0,338) **	-0,510 (0,192) **			-1,097 (0,190) **	
WC								
aa	0,107 (0,014) **	0,126 (0,013) **	0,241 (0,013) **	0,224 (0,014) **	-0,002 (0,012) ns	0,087 (0,011) **	-0,099 (0,012) **	-0,030 (0,011) **
am	0,023 (0,008) **	0,091 (0,008) **	-0,011 (0,008) ns	0,004 (0,008) ns	0,160 (0,007) **	0,069 (0,008) **	0,122 (0,007) **	0,099 (0,006) **
ca	0,376 (0,067) **	-0,399 (0,045) **	1,490 (0,034) **		0,819 (0,033) **			
cm	1,310 (0,097) **	0,160 (0,031) **	2,808 (0,037) **		0,725 (0,017) **			
ha	0,222 (0,015) **	0,471 (0,010) **		0,251 (0,008) **		0,406 (0,007) **		
hm	0,091 (0,028) **	0,418 (0,010) **		0,677 (0,010) **		0,427 (0,005) **		
ea	-0,229 (0,023) **		-0,737 (0,014) **	-0,524 (0,015) **			0,150 (0,008) **	
em	-0,423 (0,023) **		-0,779 (0,012) **	-0,131 (0,007) **			-0,178 (0,007) **	
PC								
aa	-0,123 (0,019) **	-0,185 (0,018) **	-0,062 (0,019) **	-0,046 (0,019) *	-0,412 (0,017) **	-0,270 (0,016) **	-0,261 (0,018) **	-0,371 (0,015) **
am	0,142 (0,012) **	0,215 (0,011) **	0,126 (0,012) **	0,130 (0,012) **	0,360 (0,010) **	0,214 (0,011) **	0,284 (0,010) **	0,415 (0,009) **
ca	0,190 (0,106) ns	-0,918 (0,066) **	1,526 (0,048) **		0,955 (0,046) **			
cm	0,665 (0,139) **	0,084 (0,043) ns	1,425 (0,051) **		-0,195 (0,024) **			
ha	0,336 (0,025) **	0,648 (0,015) **		0,385 (0,011) **		0,526 (0,011) **		
hm	0,027 (0,040) ns	0,113 (0,014) **		0,346 (0,014) **		0,077 (0,007) **		
ea	-0,326 (0,034) **		-0,788 (0,020) **	-0,529 (0,021) **			-0,204 (0,011) **	
em	-0,235 (0,033) **		-0,467 (0,016) **	-0,089 (0,009) **			-0,100 (0,009) **	
WP								
aa	0,036 (0,015) *	0,029 (0,014) *	0,189 (0,014) **	0,170 (0,015) **	-0,092 (0,013) **	-0,005 (0,012) ns	-0,146 (0,014) **	-0,099 (0,012) **
am	-0,045 (0,010) **	0,023 (0,009) *	-0,105 (0,009) **	-0,087 (0,009) **	0,084 (0,008) **	0,005 (0,009) ns	0,038 (0,008) **	0,038 (0,007) **
ca	0,180 (0,073) *	-0,914 (0,049) **	1,144 (0,039) **		0,311 (0,037) **			
cm	1,063 (0,103) **	-0,191 (0,034) **	3,149 (0,041) **		0,635 (0,019) **			
ha	0,196 (0,016) **	0,483 (0,011) **		0,170 (0,009) **		0,388 (0,008) **		
hm	0,200 (0,030) **	0,528 (0,011) **		0,770 (0,011) **		0,442 (0,005) **		
ea	-0,305 (0,025) **		-0,858 (0,016) **	-0,709 (0,017) **			0,116 (0,009) **	
em	-0,432 (0,025) **		-0,919 (0,013) **	-0,216 (0,007) **			-0,261 (0,007) **	
PP								
aa	-0,122 (0,022) **	-0,195 (0,020) **	0,000 (0,021) ns	-0,020 (0,022) ns	-0,442 (0,020) **	-0,289 (0,018) **	-0,227 (0,020) **	-0,394 (0,017) **
am	0,042 (0,015) **	0,111 (0,014) **	-0,015 (0,015) ns	0,002 (0,014) ns	0,290 (0,013) **	0,118 (0,014) **	0,192 (0,012) **	0,385 (0,010) **
ca	0,187 (0,120) ns	-1,189 (0,075) **	1,873 (0,060) **		0,974 (0,056) **			
cm	0,402 (0,155) **	-0,153 (0,050) **	1,728 (0,058) **		-0,379 (0,030) **			
ha	0,406 (0,027) **	0,782 (0,017) **		0,456 (0,014) **		0,636 (0,013) **		
hm	0,113 (0,044) *	0,164 (0,015) **		0,386 (0,016) **		0,059 (0,008) **		
ea	-0,410 (0,038) **		-1,028 (0,023) **	-0,658 (0,024) **			-0,290 (0,012) **	
em	-0,225 (0,037) **		-0,607 (0,018) **	-0,148 (0,011) **			-0,156 (0,010) **	
WM								
aa	0,017 (0,014) ns	0,011 (0,013) ns	0,151 (0,014) **	0,125 (0,014) **	-0,092 (0,013) **	-0,030 (0,012) *	-0,199 (0,013) **	-0,109 (0,011) **
am	0,005 (0,009) ns	0,082 (0,008) **	-0,027 (0,009) **	-0,016 (0,009) ns	0,134 (0,008) **	0,056 (0,008) **	0,092 (0,008) **	0,048 (0,007) **
ca	0,089 (0,071) ns	-0,882 (0,048) **	0,886 (0,036) **		0,174 (0,035) **			
cm	1,248 (0,102) **	0,130 (0,033) **	3,211 (0,040) **		0,931 (0,018) **			
ha	0,178 (0,016) **	0,415 (0,011) **		0,131 (0,008) **		0,314 (0,008) **		
hm	0,161 (0,029) **	0,496 (0,011) **		0,771 (0,011) **		0,481 (0,005) **		
ea	-0,222 (0,024) **		-0,741 (0,015) **	-0,611 (0,016) **			0,213 (0,009) **	
em	-0,409 (0,024) **		-0,851 (0,013) **	-0,146 (0,007) **			-0,191 (0,007) **	
PM								
aa	-0,206 (0,021) **	-0,267 (0,019) **	-0,144 (0,021) **	-0,158 (0,021) **	-0,461 (0,019) **	-0,335 (0,017) **	-0,293 (0,019) **	-0,414 (0,016) **
am	0,042 (0,013) **	0,093 (0,012) **	0,014 (0,013) ns	0,022 (0,013) ns	0,225 (0,011) **	0,091 (0,012) **	0,160 (0,011) **	0,286 (0,010) **
ca	0,092 (0,115) ns	-0,836 (0,072) **	1,421 (0,053) **		0,851 (0,050) **			
cm	0,551 (0,150) **	0,026 (0,047) ns	1,264 (0,056) **		-0,245 (0,026) **			
ha	0,333 (0,027) **	0,596 (0,017) **		0,368 (0,012) **		0,488 (0,012) **		
hm	0,007 (0,043) ns	0,092 (0,015) **		0,272 (0,015) **		0,049 (0,007) **		
ea	-0,261 (0,036) **		-0,738 (0,022) **	-0,443 (0,023) **			-0,204 (0,012) **	
em	-0,202 (0,036) **		-0,426 (0,017) **	-0,088 (0,010) **			-0,093 (0,010) **	
SC								
aa	-1,589 (0,121) **	-1,909 (0,107) **	-1,649 (0,117) **	-1,648 (0,121) **	-2,010 (0,105) **	-1,846 (0,087) **	-1,776 (0,095) **	-1,864 (0,073) **
am	-0,889 (0,062) **	-0,938 (0,052) **	-0,904 (0,060) **	-0,949 (0,059) **	-0,984 (0,046) **	-0,993 (0,051) **	-0,943 (0,051) **	-0,875 (0,042) **
ca	1,187 (0,489) *	1,156 (0,337) **	1,039 (0,245) **		1,736 (0,236) **			
cm	-0,345 (0,797) ns	-0,566 (0,215) **	0,219 (0,295) ns		-0,623 (0,109) **			
ha	-0,092 (0,114) ns	0,048 (0,078) ns		0,151 (0,057) **		0,250 (0,055) **		
hm	0,197 (0,222) ns	0,055 (0,074) ns		0,095 (0,080) ns		-0,014 (0,034) ns		
ea	-0,367 (0,175) *		-0,269 (0,115) *	-0,198 (0,121) ns			-0,142 (0,059) *	
em	-0,037 (0,194) ns		-0,172 (0,088) ns	-0,082 (0,047) ns			-0,098 (0,047) *	

** P<0,01; * P<0.05; ns: statistically non significant; **aa, am, ca, cm, ha, hm, ea, em**: direct and maternal breed additive genetic effects, direct and maternal complementarity, heterosis and epistatic loss non-additive genetic effects, respectively. **WG, WC, WP, WM**: weaning gain, conformation, precocity, muscling respectively; **PG, PC, PP, PM**: post-weaning gain, conformation, precocity, muscling respectively; **SC**: Scrotal circumference; standard error are in parenthesis.

[4]CAPÍTULO III

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[4] Artigo redigido de acordo com as normas do periódico *Livestock Science*

Modeling non-additive genetic effects using Ridge Regression for an Angus-Nellore crossbred population

Claudia Damo Bertoli[a,b,*], José Braccini Neto[b,f], Concepta McMannus[c], Jaime Araújo Cobuci[b], Gabriel Soares Campos[b], Mario Luiz Piccoli[b,d], Flavio Schenkel[e], Vanerlei Roso[d]

[a] Instituto Federal Catarinense Campus Camboriu IFC-CC address: Rua Joaquim Garcia, s/n centro, Caixa Postal 2016, CEP 88.340-055 Camboriu - SC - Brazil Tel: +55 47 2104-0800 e-mail: cdbertoli@ifc-camboriu.edu.br
[b] Universidade Federal do Rio Grande do Sul - UFRGS Departamento de Zootecnia address: Avenida Bento Gonçalves, 7712 agronomia CEP 91.509-900 Porto Alegre - RS - Brazil Tel: +55 51 3308-6048
[c] Universidade de Brasília - UnB address: Campus Universitário Darcy Ribeiro, CEP 70.910-900 Brasília - DF - Brazil Tel: +55 61 3107-3300
[d] GenSys Consultores Associados address: Rua Guilherme Aves, 170/304 Jardim botânico CEP 90.680-000 Porto Alegre - RS - Brazil Tel: +55 51 3330-6804
[e] University of Guelph - UofG, CGIL - Centre of Genetic Improvement of Livestock address: 50, Stone Road East N1G 2W1 Guelph ON Canada Tel: +1 519 824 4120 *58650
[f] CNPq fellow
[*] Corresponding author at: Rua Rio Amazonas, 3477 Rio Pequeno, Caixa Postal 2139 CEP 88340-000 Camboriu - SC - Brazil Tel: +55 51 9751-3086/+55 47 9977-3086; fax: 55 47 2104-0800 e-mail address: cdbertoli@gmail.com

Abstract

The objectives of this study were to estimate fixed genetic effects (both additive and non additive) and test different non-additive models using Ridge Regression. The direct and maternal cumulative breed additive effects, as well as breed complementarity, heterosis (dominance) and epistatic loss direct and maternal non-additive effects were studied. A large crossbred Angus X Nellore population, with 294,045 records for weaning gain (WG) and 148,443 records for post-weaning gain (PG) was used. Phenotypic scores for weaning (WC) and post-weaning (PC) conformation, weaning (WP) and post-weaning (PP) precocity, weaning (WM) and post-weaning (PM) muscling and scrotal circumference (SC) were also used. All models included fixed contemporary group effect and random animal, maternal and permanent environment effects. All models were compared for all nine traits using the likelihood ratio test. The model including all fixed genetic effects (breed additive, complementarity, heterosis and epistatic loss non-additive effects, both direct and maternal) the best option to analyze this crossbred population using ridge regression methodology. The ridge regression methodology was efficient to control the collinearity among prediction variables of fixed genetic effects. For SC, only the direct and maternal additive effects were statistically significant ($P<0.01$). For the complete model, all effects were statistically significant ($P<0.01$) for weaning traits, except the direct breed additive effects for WP and WM; direct complementarity effect for WP, WM, PP and PM and maternal epistatic loss for PG. Direct breed additive effect was positive for weaning traits and negative for post-weaning. Maternal breed additive effect was negative for SC and WP. Direct complementarity and heterosis were positive for all traits and maternal complementarity and heterosis were also positive for all traits, except for PG. Direct and maternal epistatic loss effects were negative for all traits. We conclude that the fixed genetic effects are mostly significant. Thus it is important to include them in the model when evaluating crossbred animals and the model which includes breed additive effects, complementarity, heterosis and epistatic loss was more appropriate and the model with only breed additive and heterosis more parsimonious.

Keywords: complementarity, crossbred beef cattle, epistatic loss, fixed genetic effects, heterosis,

1.Introduction

Breeders worldwide have used breeding programs to take advantage of the beneficial effects of heterosis and to combine strengths of parental breeds, called "breed complementarity" (Weaber, 2005). These effects occur in crossbred animals at various levels of intensity and, although important, are frequently neglected in genetic evaluation breeding programs.

The estimation of fixed genetic effects (additive breed and non-additive heterosis, epistatic loss and complementarity) has been the subject of many studies around the world: Brazil (Bueno et al, 2012; Lopes et al., 2010; Cardoso et al., 2008; Kippert et al., 2008; Carvalheiro et al., 2006), Australia (Arthur et al., 1999), Colombia (Vergara et al., 2009), Ethiopia (Demeke et al., 2003a,b), South Africa (Schoeman et al., 2002), United States (Williams et al., 2009; Elzo & Wakeman, 1998) and Uruguay (Lema et al., 2011). Besides the estimation of these effects, collinearity has been studied among the predictors of effects.

When considering non-additive models, we are using breed composition of individual, parents and grandparents to estimate all coefficients (breed direct, complementarity, heterosis and epistatic loss). Possible collinearity can be present as all estimators are based on the breed composition of individuals, which is equal to the average of the breed composition of their parents. In practice, the same information is used to predict different effects seen from different perspectives.

In a multiple regression analysis, multicollinearity exists when one or more variables express linear combination with the other variables used in the same analysis. In multiple regression, the columns of X are almost never orthogonal and exact dependencies among the columns also rarely exist (Schabenberger & Pierce, 2002). In order to estimate this collinearity, the pairwise correlations can be estimated but this information is not always sufficient to indicate the condition of collinearity. High correlations between variable pairs may be indicative of multicollinearity (Roso *et al.*, 2005b). The higher the collinearity, the higher the standard errors and wider the confidence intervals will be. Variance Inflation Factor (VIF) calculations offer an alternative diagnosis of collinearity, that is simple and efficient. When collinearity is found, one option is to delete one or more variables that are causing this collinearity, since this condition generates unstable least squares estimates with large standard errors, another option is to use ridge regression (Schabenberger & Pierce, 2002).

Arthur et al. (1999) , Schoeman et al. (2002), Abdel-Aziz et al. (2003), Cardoso et al. (2004, 2008), Roso et al. (2005a), Dias et al. (2011) and Petrini et al. (2012) studied the problem of multicollinearity in the estimation of the fixed genetic effects. These authors conclude that these effects have some degree of collinearity that can and must be overcome. Most authors have pointed out the ridge regression as the best solution to estimate fixed genetic effects (Schoeman et al., 2002; Roso et al., 2005b; Cardoso et al., 2008; Dias et al., 2011).

In addition to the methodology, the authors are in agreement that the additive effect of breed and the effects of heterosis are important and must be present in the statistical models used for genetic evaluation of animals in breeding programs. As far non-additive effects of breed complementarity and epistatic loss, there is almost a consensus among the authors. Not all of these effects are used in all the studies.

The main objective of this study was to test different additive and non-additive genetic models under ridge regression. We also aimed to estimate the fixed genetic effects (direct and maternal cumulative breed, complementarity (or profit heterosis), heterosis and epistatic loss), involving crosses between Angus and Nellore beef cattle breeds.

2. Materials and methods

2.1 Data

Data from different breed compositions, resulting from crosses between Angus and Nellore cattle, was used. This data came from more than 200 herds distributed in the Brazilian states of Rio Grande do Sul, Paraná, São Paulo, Mato Grosso do Sul, Mato Grosso and Goiás and also from Paraguay. All herds were participants of "Programa Natura de Melhoramento Genético de Bovinos" (Natura Cattle Breeding Program). (Table 1)

2.2 Predictor variables of fixed genetic effects

2.2.1 Breed additive effect

The contribution of Nellore genes in the genetic composition of the animal (**aa**) and their dams (**am**) were used to estimate the direct and maternal genetic effect of breed, respectively. To avoid dependence in incidence matrix columns, only the Nellore coefficient was used, giving an estimation of the deviation from the Angus breed performance.

2.2.2 Breed complementarity

The coefficients proposed by Kinghorn (1993) and also used by Fries *et al.* (2000), Piccoli *et al.* (2002), Cardoso *et al.* (2008) were used to estimate the breed complementarity effects. The predictor variable of direct complementarity (**ca**) coefficient is described as **ca** = **aa***(1.0-**aa**) and the maternal complementarity (**cm**) coefficient is described as **cm** = **am***(1.0-**am**) where **aa** is the Nellore fraction of the animal breed and **am** is the Nellore fraction of the dam breed composition.

2.2.3 Heterosis effect

To estimate the direct and maternal heterosis effects, the heterozigosity coefficients ha and hm were used as described by Bertoli (1991) and Schenkel (1993), also used by Cardoso et al. (2008), Pimentel et al. (2006) and Roso et al. (2005b). These coefficients are given by **ha** = $(1 - \sum_{i=1}^{2}(Sire\ breed_i * Dam\ breed_i))$ and **hm** = $(1 - \sum_{i=1}^{2}(Maternal\ Grand\ Sire\ breed_i\ *\ Maternal\ Grand\ Dam\ breed_i))$ where i=1 refers to Angus breed proportion and i=2 refers to Nellore breed proportion. When the breed composition of a cow was not known (all products had known breed composition), the cow was considered to be inter se mating.

2.2.4 Epistatic loss effect

To estimate the direct and maternal epistatic loss effects, the epistazygosity coefficients **ea** and **em** were used, as proposed by Fries *et al.* (2000,2002) and also used by Cardoso *et al.* (2008), Pimentel *et al.* (2006), Carvalheiro *et al.* (2006) and Roso *et al.* (2005a,b). These coefficients are given by **ea**= ½ [Hs + Hd] and **em**= ½ [Hmgs + Hmgd], where Hs is the sire's heterozygosis, Hd is the dam's heterozygosis, Hmgs is the maternal grand sire heterozygosis and Hmgd is the maternal grand dam heterozygosis. When the breed composition of a cow was not known (all products had known breed composition), the cow was considered to be *inter se* mating.

2.3 *Traits*

Nine traits were used in this analysis: weaning gain (WG), post-weaning gain

(PG), phenotypic scores of conformation (WC), precocity (WP) and muscling (WM) taken at weaning; phenotypic scores of conformation (PC), precocity (PP) and muscling (PM) taken at post-weaning as well as scrotal circumference at yearling (SC). The phenotypic score for each trait is given on a five-point scale, where one is the worst, and five is the best score for each management group. The number of observations, means and standard deviations of each trait are presented in Table 2.

2.4 Statistical Analysis

2.4.1 Genotypic models

The general model is described by equation (1). The pair-traits WG-PG, WC-PC, WP-PP, WM-PM and WG-SC were analysed in a two-trait analysis using this model with the systematic inclusion of fixed genetic terms, in order to compare models and effects.

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{W}\boldsymbol{\gamma} + \mathbf{Z}\boldsymbol{\alpha} + \boldsymbol{\varepsilon} \qquad \mathbf{(1)}$$

where $\mathbf{y}$ is the vector of observations of trait 1 and trait 2; $\boldsymbol{\beta}$ is the vector of fixed effects of environment, which includes contemporary group (all traits were pre-adjusted for fixed effects of animal age, dam age and birth date (julian), except SC, that was pre adjusted for age and weight); $\boldsymbol{\gamma}$ is the vector of fixed genetic effects; $\boldsymbol{\alpha}$ is the vector of random direct, maternal and permanent environmental effects of the dam and $\boldsymbol{\varepsilon}$ is the vector of random residual effects. Incidence matrices **X**, **W** and **Z** relate records to fixed effects, to fixed genetic effects and to random direct and maternal additive genetic and permanent environment effects, respectively.

The vectors of random effect $\boldsymbol{\alpha}$ and $\boldsymbol{\varepsilon}$ were assumed to have (co)variance = $\mathbf{V}(\boldsymbol{\alpha}) = \begin{bmatrix} \mathbf{A}\otimes\boldsymbol{G_a} & \mathbf{A}\otimes\boldsymbol{G_{am}} & 0 \\ \mathbf{A}\otimes\boldsymbol{G_{am}} & \mathbf{A}\otimes\boldsymbol{G_m} & 0 \\ 0 & 0 & \mathbf{I}\otimes\mathbf{Pe} \end{bmatrix}$ and $\mathbf{V}(\boldsymbol{\varepsilon}) = \mathbf{I}\otimes\mathbf{R}$. A is the additive numerator relationship matrix among animals and **I** is the identity matrix; $\mathbf{G_a} = \begin{bmatrix} \sigma^2_{a1} & \sigma_{a1a2} \\ \sigma_{a1a2} & \sigma^2_{a2} \end{bmatrix}$, $\mathbf{G_m} = \begin{bmatrix} \sigma^2_{m1} & \sigma_{m1m2} \\ \sigma_{m1m2} & \sigma^2_{m2} \end{bmatrix}$, $\mathbf{G_{am}} = \begin{bmatrix} \sigma_{a1m1} & \sigma_{a1m2} \\ \sigma_{a2m1} & \sigma_{a2m2} \end{bmatrix}$, $\mathbf{Pe} = \begin{bmatrix} \sigma^2_{p1} & \sigma_{p1p2} \\ \sigma_{p1p2} & \sigma^2_{p2} \end{bmatrix}$ and $\mathbf{R} = \begin{bmatrix} \sigma^2_{e1} & \sigma_{e1e2} \\ \sigma_{e1e2} & \sigma^2_{e2} \end{bmatrix}$ where σ^2 refers to variance and σ refers to covariance; ***a*** refers to direct additive genetic, ***m*** to maternal additive genetic ***p*** to permanent environmental effects and **e** to residual; ***1*** refers to the first and ***2*** to the second trait on a two-trait analysis.

The general model above (1) was analyzed complete and with reductions. The only difference among compared models was in $\boldsymbol{\gamma}$ vector, which includes different fixed genetic effects. The considered effects for each tested model is presented in table 3. In total, eight models were analyzed for each trait.

The models described above were analyzed using ridge regression (RR) in a two-trait analysis. To compare these models, we used the Likelihood Ratio as described by Regazzi and Silva (2004) for each model pair.

In the present study, the RR analysis were carried out in the standardized form of the model, using the correlation matrix. After estimation the estimates were transformed to the original scale and were presented in this way.

2.4.2 *Ridge regression*

Collinearity analysis

To identify the possible causes of the collinearity we calculated the variance inflation factor (VIF). VIF was given by VIF = $1/(1-R_i^2)$, where R_i is the coefficient of determination. (Schabenberger & Pierce, 2002). To verify collinearity, as well as using the VIF, we calculated the Pearson correlation between the estimates of fixed genetic effects.

The ridge parameter

The ridge regression methodology is "an **ad-hoc** regression method to combat collinearity. The ridge regression estimator allows for some bias in order to break the collinearity and thus reduce the mean square error compared to Ordinary Least Squares. The user must choose the ridge parameter, a small number by which to shrink the least squares estimates" (Schabenberger & Pierce, 2002). The ridge regression estimator consists of adding a small positive number - the ridge parameter (k) - on the diagonal of the **W'W** matrix in order to break the relationship between the columns of the **W'W**. There is not a clear rule to choose k so it must be determined empirically (Dias et al., 2011).

To perform the ridge regression analysis, a diagonal matrix **K** is added to the **W'W** matrix. The values of the non-negative diagonal elements of K (k_1, k_2,..., k_i) were adapted from Roso et al. (2005b) and estimated as $k_i = \theta * (VIF_i/VIF_{max})^{½}$, where *i* is the i^{th} element of the diagonal matrix **K**, VIF_i is the variance inflation factor of the i^{th} predictor variable and VIFmax is the maximum value of all VIF_i. The magnitude of the elements k_i will be proportional to the variance inflation factor of each predictor variable.

To choose the value of θ, the bootstrap procedure, originally proposed by Efron (1979) and described by Roso (2005b) in R2 method, was performed. This is an iterative process, with the value of θ ranging from 0.000 to1.000 with increments of 0.002. For each value of θ, ten bootstrap samples were used to estimate all effects of the model (1) as well as VIF. For each value of θ, an average of FIV, obtained with the ten bootstrap samples, was calculated. From there, two procedures guided the choice of the value of θ: the factors of inflation of variance and the visual evaluation of the range of estimates, obtained for each value of θ.

2.4.3. The (co)variance components

The (co)variance components were estimated (Table 4) using model (1), including all effects (fixed effects of environment, fixed genetic effects, random direct, maternal and permanent environmental effects and residual). The Restricted Maximum Likelihood (REML) method and the DMU (Madsen & Jensen, 2000) software were used. The convergence criterion was 10^{-12}.

2.4.4 Connectedness analysis

Roso *et al.* (2004) found that as the degree of connectedness among test groups decreases, the accuracy of comparisons of EBVs of bulls in different test groups also decreases. As one of the final objectives of a genetic evaluation is to obtain accurate EBVs, we tested the connectedness, using only connected animals and contemporary groups in this analysis. A connectedness analysis between contemporary groups was carried out according to Roso *et al.* (2004). The total number of direct genetic links between contemporary groups due to any common ancestors was used. Contemporary groups with more than two calves and with at least five direct links were considered connected and retained for analysis. (Table 5)

3. Results and Discussion

3.1 Collinearity analysis

3.1.1 Correlation among predictor variables

The predictor variable (estimators) of maternal complementarity was strongly correlated with maternal heterosis (Table 6) and direct and maternal epistatic loss as well, maternal heterosis was strongly correlated with direct epistatic loss (Table 6a). The highest correlation between pairwise estimates, using the **ACHE** model, was between direct complementarity and direct heterosis, followed by the correlation between maternal complementarity and maternal epistatic loss. These results were similar for all tested traits (Table 6b).

According to Cunningham and Connoly (1989), cited by Roso et al. (2005a) high correlation between estimates can jeopardize the accuracy of estimated genetic values of the analysis. Large pairwise correlations may indicate collinearity but are not a necessary condition for it (Schabenberger & Pierce, 2002).

When the complementarity was not considered, using the **AHE** model, the highest correlation was between maternal heterosis and direct epistatic loss (-0.7733 for WG / -0.7775 for PG), followed by the correlation between direct and maternal breed additive (-0.5867 for WG / PG is -0.5679). When the heterosis was not considered, using the **ACE** model, the highest correlations were between maternal complementary and maternal epistatic loss (-0.6953 for WG / PG is -0.6931), followed by maternal complementarity and direct epistatic loss (-0.6567 for WG / -0.6604 for PG). When the epistatic loss was not considered, in the **ACH** model, the highest correlations were between maternal complementarity and maternal heterosis (-0.7418 for WG / PG is -0.7343), followed by the correlation between direct complementarity and direct heterosis (-0.6180 for WG / PG is -0.6320). Most of the simple correlations between estimates were negative (65%). Schoeman et al. (2002) also reported negative correlations between breed additive effects, direct and maternal, arguing they involve mutually exclusive proportions, not being independent.

Although the magnitude of pairwise correlations between prediction variables are high, this was not the only indicator of collinearity as the interrelations among three or more variables can also result in a high degree of collinearity (Roso et al., 2005b). Regarding the correlation between the coefficients used for the estimation (estimators) of fixed genetic effects, 46% showed values above 0.5. Thus, it was observed that after using the method of ridge regression, correlation between the estimates remains relatively low, only 25% presented values below 0.5.

3.1.2 Variance inflation factor

Variance inflation factor (VIF) indicates the variance inflation of each regression coefficient compared with an orthogonal situation. Usually values above ten for VIF suggest that multicollinearity may be causing problems in the estimation. (Schabenberger & Pierce, 2002). The VIF obtained using ACHE model and θ=0.06 are presented in Table 7. These values are around 10 for all tested traits, except for SC. Although creating a bias when using ridge regression, this bias may be more preferable than high VIF (when θ=0.00, corresponding to least squares (LS) estimators. In the LS, the VIFs reached values of 110 (not shown)). High VIF can generate unstable estimates (Schabenberger & Pierce, 2002). As the final objective of this estimation is obtaining genetic values for animal selection, stable estimates with low standard errors are preferable (Dias et al.,2011).

Considering all traits, VIFs are larger for the effects of maternal complementarity, followed by the effect of direct complementarity. Relating to traits, the higher values of VIFs always are presented by scrotal circumference. SC has much less data in comparison to the other traits. This affect the structure of correlation among prediction variables The post-weaning traits present intermediate VIFs and the lower VIFs are presented by weaning traits. When the used model excludes complementarity (**AHE**), epistatic loss effect presents the highest VIF to all traits. Weaning traits still present the lowest VIFs (3.87 for WG), followed by post-weaning traits (4.14 for PG). Scrotal circumference presents the highest VIF (5.15) when using this model.

3.1.3 Ridge Parameter

The visual (graphical) evaluation was proposed by Freund & Littell (2000) and also suggested by Schabenberger & Pierce (2002) The estimates of the fixed genetic effects of model ACHE for each value of θ are presented in Figure 1 The results indicate that with θ between 0.060 and 0.100, all estimates for all traits tend to stabilize. According to Schabenberger & Pierce (2002), stabilization is not necessary when the ridge trace becomes a flat line. They also said that the inexperienced users tend to choose a ridge parameter that is too large.

Concerning VIF, the lower value of θ, whose average bootstrap samples generated VIF below ten for all fixed genetic effects, was between 0.060 and 0.066. The studies of Piccoli et al. (2002) and Cardoso et al. (2008) used θ=0.06 to calculate k in their analysis and Carvalheiro (2006) used values where all VIF became lower than ten. For this analysis, the chosen value of θ was 0.06. With this value, a new analysis was performed, containing the complete set of data, for the estimation of all effects according to the model(1), for all traits

3.2 The models

Of the 198 comparisons, 22 were between two of the models, for each of the nine analyzed traits, using the Likelihood ratio test. Most of these comparisons

(91.4%) were statistically significant. The nullity hypothesis indicates that, for each of the 17 non-significant comparisons between the tested models, there is no significant difference in, at least, one of the considered parameters. The contrasts that show significant differences are all comparing the full model (**ACHE**) with any reduction, for all tested traits (Table 8).

The **ACHE** model was statistically different from the three closest reductions (**ACH**, **ACE** and **AHE**). This means that the complete model differs statistically in, at least, one effect for each of the three comparisons made. Carvalheiro et al. (2006) also found that the inclusion of complementary and epistasis in the genetic evaluation of crossbred animals "... seems to be important but should be further investigated... ". The results presented in table 8 indicate that the full model (**ACHE**) is the most suitable for use in the estimation of the fixed genetic effects, using the ridge regression methodology.

The comparison between the **AH** model and the **ACH**, **ACE** and **AHE** models, for most traits, was not statistically significant, suggesting that this model (**AH**) could be considered a more parsimonious model to use. Carvalheiro et al. (2006), testing similar models, confirmed results in the literature (Arthur et al (1999;. Demeke at al 2003), that models that include only the additive and dominance effects are not enough and that the epistatic loss effect, if important, should be included in the model. Pimentel et al. (2006) suggest that the effects of epistasis can remain embedded in the heterosis effects when the estimation is made with simpler models.

AH model could be used as an alternative when the amount or the structure of data does not allow the use of more complex models.

3.3 Fixed genetic effects estimates

Estimates of fixed genetic effects with all used models are presented in Table 9. The values of **aa**, **am**, **hm** and **ha** vary little between the estimates made by the **AH** model and the **ACHE** model as well, as the standard errors in the **AH** model tend to be smaller. For SC, only the direct and maternal breed additive effects were statistically significant. Considering all the tested models, the effects of **ca**, **cm**, **ha**, **hm**, **ea** and **em** were statistically not different from zero ($p>0.05$) for SC. Cardoso et al. (2008) reported significant values for **ca** and **ea**. They did not test maternal components for SC.

The direct breed additive effect accounts for the increase (or decrease) due to the expected increase the proportion of Nellore genes in the breed composition of the animal. Williams et al. (2009), using published results, presented negative values for posterior means of **aa** in weaning and post weaning gain for the Brahman breed. All estimates of breed additive effect are negative for all traits. Except in the **AE** model, which is positive for PG. The estimates of breed additive effect show that Nellore genes decrease the phenotype value of each trait. This does not mean a lower final weight, as the final weight is given by the sum of all involved effects in animal performance. When comparing the **ACHE** model with the **AH** model, generally, **aa** estimates were higher for the **AH** model and displayed lower standard errors. The positive effect of **aa** for WG in the **AHE** model is in accordance with the values obtained by Arthur et al. (1999) and Abdel-Aziz et al. (2003), who obtained positive estimates for weaning weight in crossed Brahman animals; however, contrasts with those values obtained by Carvalheiro et al. (2006), Pimentel et al. (2006), and Cardoso et al. (2008), who found negative effects of **aa** for weaning weight and average daily gain, working with Hereford x Nellore animals. Kippert et al. (2008) found negative values for direct breed additive effect of Nellore crossed with Angus for weaning weight, yearling weight and post weaning gain but positive values for weaning gain.

The maternal breed additive effect was positive for all models and traits at weaning and post-weaning, except for WP in the **ACHE** and the **AHE** models. These results show advantage of Nellore dam when compared to Angus dam. Cardoso et al. (2008), Carvalheiro et al. (2006) and Pimentel et al. (2006) also found positive effects in Nellore x Hereford crosses. Arthur et al. (1999), working with Brangus found positive effects for Brahman when the climate is temperate and negative effects when the climate is subtropical. Vergara et al. (2009) found positive values for weaning weight in zebu animals. Kippert et al. (2008) found similar values to our findings and argues that Nellore cow has greater maternal ability and/or better adaptation to the environment in which they operate.

Under the full model (**ACHE**), the traits of precocity and musculature were statistically not different from zero ($P<0.05$) for the effect of direct complementarity. From this result, we can suggest that there is no extra gain, beyond linear, for these traits when Nellore and Angus are crossed. The WG trait showed high and positive values for **ca** and **cm**; PG had positive values for **ca** and negative values for **cm** for all tested models, showing that the proportion of Nellore genes in the dam leads to weight loss in the post weaning period. Carvalheiro et al. (2006) and Cardoso et al. (2008) found negative values for **ca** and Carvalheiro et al. (2006) found positive values for **cm** in weaning weight gain.

The effect of direct heterosis was positive and statistically significant for all tested models and for all traits except SC. Carvalheiro et al. (2006), studying Nellore X Hereford crossbred animals, also found positive and significant effects for weaning gain, but found much higher values (14.78 ± 0.52), obtained with equivalent model and methodology. Cardoso et al. (2008), studying WC, WP, WM, PC, PP and PM in Nellore crosses with Hereford, found positive and statistically significant values for **ha**. The values found by Cardoso et al. (2008) are lower compared to our findings, except for PC, whose estimated effect of **ha** was higher in comparison to this work. Kippert et al. (2006), in Nellore x Angus crosses, also found positive and statistically significant values for **ha** in weaning and post-weaning weight.

Similar to the **cm** effect, the **hm** effect was negative only for PG in all tested models. The values obtained for **ha** and **hm** for all models were of similar magnitude, showing a slight tendency to increase as the terms were removed from the model. The lower standard errors were obtained with the **AH** model, followed by models **AHE**, **ACH** and **ACHE**. Carvalheiro et al. (2006) estimated the effect of **hm** to the trait of WG at 12.77Kg, nearly double the value estimated in this work. Abdel-Aziz et al. (2003), Kippert et al. (2006), Pimentel et al. (2006), Cardoso et al. (2008) and Vergara et al. (2009) also found positive and statistically significant **hm** effects. Positive heterosis confirms that the crossbred dams will be better mothers with respect to the purebred dams. The higher the cow heterosis, the greater the pre-weaning development of the calf will be.

The estimate of **ea** and **em** effects in the **ACHE**, **ACE** and **AHE** models were negative for all traits, except for WG in the **AHE** model. The coefficients of epistatic loss can provide estimates of the recombination losses that occurred as a result of crossbred systems, that will undo the favorable connections that settled in the process of pure bred formation (Fries et al., 2000), as well as in the natural and/or artificial breed selection processes over the generations. This leads us to expect negative values for this effect. However, Cardoso et al. (2008) found positive values for **ea** in weaning traits, and Carvalheiro et al. (2006) found no statistical significance in **ea** nor **em** for WG in an equivalent model and methodology. The **em** effect was not significant for PG in the **ACHE** and the **ACE** models. Under the **AE** model, weaning traits presented positive **ea** estimates. It is likely that theses effects will present embedded values of the effects that are not included in the model.

4. Conclusion

Two of the tested models were suitable for use in crossbred population breeding programs, with respect to fixed genetic effects: **ACHE** and **AH**. The **ACHE** model, that estimates the fixed genetic effects of direct and maternal breed additive, complementarity, heterosis and epistatic loss non-additive effect is complete and accounts for all tested effects. The **AH** model, that includes only the direct and maternal breed additive and direct and maternal heterosis non-additive effects is the more parsimonious, and could be used when the structure or amount of data does not permit the use of **ACHE**. The breed additive, complementarity, heterosis and epistatic loss non-additive effects affects the performance at weaning and post weaning gain, conformation, precocity and muscling at weaning and post weaning, and should be included in genetic evaluation of crossbred populations. Scrotal circumference does not present the complementarity, heterosis or epistatic loss, direct or maternal effects in its expression.

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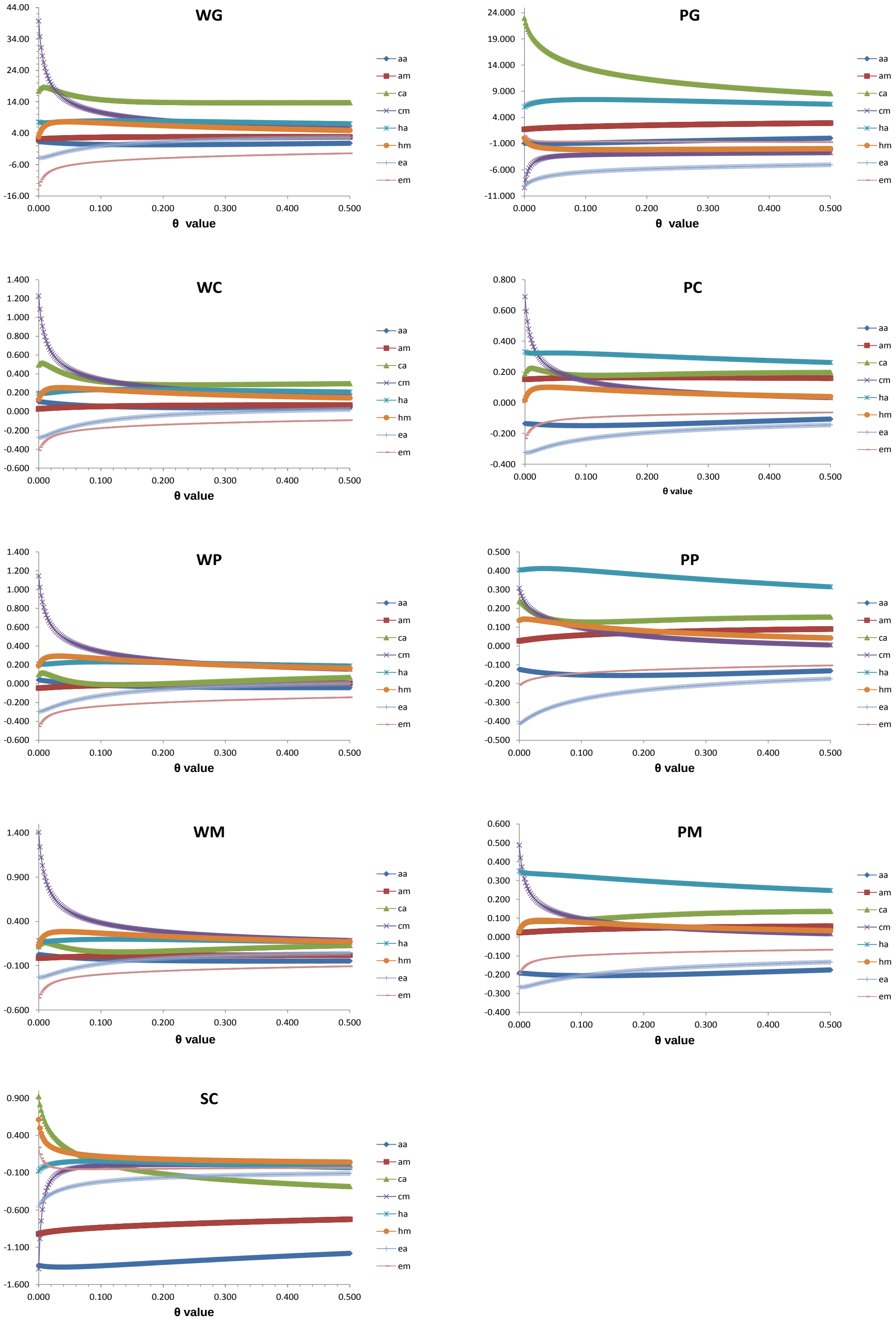

Figure 1 - Estimation values of direct (**aa**) and maternal (**am**) breed additive, direct (**ca**) and maternal (**cm**) complementarity, direct (**ha**) and maternal (**hm**) heterosis and direct (**ea**) and maternal (**em**) epistatic loss non-additive effects for gain (WG), conformation (WC), precocity (WP), muscling (WM) at weaning, gain (PG), conformation (PC), precocity (PP), muscling (PM) and Scrotal circumference (SC) at post weaning with ACHE model, using different θ values for calculating the ridge parameter.

Table 1
Distribution of animals, according to sire and dam breed composition, presented as percentage of Nellore (N).

		Dams									
		Angus	**1/8N**	**2/8N**	**3/8N**	**4/8N**	**5/8N**	**6/8N**	**7/8N**	**Nellore**	**Total**
Sires	Angus	27,795	96	698	3,164	6,219	4,048	20,243	194	28,330	90,787
	1/8N	52	5	24	10	71	0	2	0	17	181
	2/8N	85	206	760	1434	6780	163	3,520	1	502	13,451
	3/8N	1,305	371	2,238	78,159	43,194	2,690	6,061	148	18,713	152,879
	4/8N	47	125	96	687	4,066	218	1,587	28	5947	12,801
	5/8N	1,170	0	14	443	1,046	1,186	1,084	21	1,053	6017
	6/8N	8,668	4	5	697	466	181	285	3	185	10,494
	7/8N	0	0	0	0	5	0	0	0	13	18
	Nellore	241	31	52	1,341	4,726	236	738	51	1	7,417
	Total	39,363	838	3,887	85,935	66,573	8,722	33,520	446	54,761	294,045

Every class included fractions equal or smaller than the mentioned values.

Table 2
Number of observations (N), means and standard deviation (SD) of analysed traits

Trait		N	Mean	SD
WG	**(Kg)**	294,045	152.92	16.96
WC	**(score)**	288,182	3.42	0.68
WP	**(score)**	276,264	3.44	0.72
WM	**(score)**	286,350	3.32	0.72
PG	**(Kg)**	148,443	83.36	13.61
PC	**(score)**	149,091	2.53	0.66
PP	**(score)**	141,188	2.74	0.73
PM	**(score)**	147,392	2.52	0.70
SC	**(cm)**	46,269	29.17	1.65

WG: weaning gain; WC: visual score of conformation; WP: visual score of precocity and WM: visual score of muscling taken at weaning; PC: visual score of conformation; PP: visual score of precocity and PM: visual score of muscling taken at post-weaning; SC: scrotal circumference

Table 3
Fixed genetic effects included in the genotypic models considered in this study

	Effects included on **γ**							
Model	**aa**	**am**	**ca**	**cm**	**ha**	**hm**	**ea**	**em**
A	★	★						
AC	★	★	★	★				
AH	★	★			★	★		
AE	★	★					★	★
ACH	★	★	★	★	★	★		
ACE	★	★	★	★			★	★
AHE	★	★			★	★	★	★
ACHE	★	★	★	★	★	★	★	★

aa, am, ca, cm, ha, hm, ea, em: direct and maternal breed additive effect, direct and maternal complementarity, heterosis and epistatic loss non-additive effects, respectively.

Table 4

Additive, permanent environment and residual (co)variances – Superior triangular of G, Pe and R matrices.

	WG-PG (SE)	WC-PC (SE)	WP-PP (SE)	WM-PM (SE)	WG-SC (SE)
Superior Triangular of G					
a1 a1	89,316 (5,207)	0,139 (0,008)	0,156 (0,010)	0,141 (0,009)	93,556 (5,379)
a1 a2	9,609 (3,503)	0,104 (0,007)	0,127 (0,009)	0,119 (0,008)	4,564 (1,245)
a1 m1	-25,680 (3,412)	-0,043 (0,006)	-0,045 (0,006)	-0,037 (0,006)	-27,951 (3,463)
a1 m2	6,442 (2,540)	-0,039 (0,005)	-0,015 (0,006)	-0,019 (0,006)	-1,648 (0,883)
a2 a2	47,864 (3,945)	0,132 (0,009)	0,185 (0,012)	0,159 (0,011)	4,125 (0,347)
a2 m1	20,891 (2,641)	-0,014 (0,005)	-0,018 (0,006)	-0,017 (0,005)	-1,277 (1,219)
a2 m2	-11,614 (2,260)	-0,036 (0,005)	-0,027 (0,006)	-0,026 (0,006)	-1,394 (0,285)
m1 m1	50,019 (3,874)	0,069 (0,006)	0,054 (0,007)	0,056 (0,007)	47,004 (3,893)
m1 m2	-13,839 (2,202)	0,036 (0,005)	0,017 (0,004)	0,026 (0,005)	1,624 (0,786)
m2 m2	8,486 (1,999)	0,033 (0,005)	0,017 (0,005)	0,024 (0,005)	1,013 (0,255)
Superior Triangular of Pe					
p1 p1	97,470 (2,558)	0,118 (0,004)	0,118 (0,004)	0,122 (0,005)	101,206 (2,605)
p1 p2	-21,655 (1,495)	0,044 (0,003)	0,031 (0,003)	0,033 (0,003)	2,982 (0,490)
p2 p2	7,201 (1,542)	0,020 (0,004)	0,015 (0,005)	0,009 (0,005)	0,236 (0,143)
Superior Triangular of R					
r1 r1	252,058 (3,550)	0,527 (0,006)	0,625 (0,007)	0,633 (0,006)	249,341 (3,651)
r1 r2	-37,607 (2,454)	0,128 (0,005)	0,137 (0,006)	0,150 (0,006)	8,550 (0,825)
r2 r2	219,202 (2,870)	0,516 (0,006)	0,634 (0,009)	0,622 (0,008)	3,691 (0,226)

G: genetic additive (co)variance matrix; Pe: Permanent environment (co)variance matrix; R: residual (co)variance matrix; a1: trait 1 on two-trait analysis; a2: trait 2 on two-trait analysis; m1: maternal effect of trait 1; m2: maternal effect of trait 2; p1: phenotype of trait 1; p2: phenotype of trait 2; r1: residual effect of trait 1; r2: residual effect of trait 2; WG-PG: weaning gain as trait 1 and post-weaning gain as trait 2; WC-PC: weaning conformation as trait 1 and post-weaning conformation as trait 2;WP-PP: weaning precocity as trait 1 and post-weaning precocity as trait 2; WM-PM: weaning muscling as trait 1 and post-weaning muscling as trait 2; WG-SC: weaning gain as trait 1 and scrotal circumference as trait 2;SE: standard error.

Table 5
Number of animals (A) and contemporary groups (CG) used in the analysis.

Trait		**Weight Gain**		**Conformation**		**Precocity**		**Muscling**		**Scrotal Circumference**	
		TOTAL	CONNEC (%)	TOTAL	CONNEC (%)	TOTAL	CONNEC (%)	TOTAL	CONNEC (%)	TOTAL	CONNEC (%)
A	W	294,045	285,309 (97)	288,182	280,199 (97)	276,264	268,757 (97)	286,350	278,349 (97)		
	PW	148,443	138,139 (93)	146,493	144,264 (98)	141,188	138,126 (98)	147,392	144,032 (98)	45,288	40,092 (88)
CG	W	9,242	6,646 (72)	8,840	6,461 (73)	8,312	6,036 (73)	8,807	6,426 (73)		
	PW	11,398	7,048 (62)	3,529	2,496 (71)	3,304	2,353 (71)	3,506	2,508 (72)	3,770	2,445 (65)

W: weaning phenotypes; PW: post-weaning phenotypes; CONNEC.(%): number (and percentage) of animals/contemporary groups connected to the analyzed data.

Table 6

Pearson correlation among predictor variables (a) and estimates (b) of fixed genetic effects, obtained using the **ACHE** model. Weaning gain is presented below and post-weaning gain above diagonal.

a - Pearson correlation among predictor variables

	aa	am	ca	cm	ha	Hm	ea	em
aa		0.7552	0.7172	0.1195	0.6607	0.1165	0.2652	0.0884
am	0.7435		0.5577	-0.1375	0.7379	-0.1200	-0.1077	-0.1281
ca	0.6726	0.5298		0.5073	0.7559	0.4548	0.5513	0.4241
cm	0.0724	-0.1810	0.4774		-0.0052	0.9013	0.8373	0.8362
ha	0.6015	0.6970	0.7288	-0.0323		-0.0025	-0.0425	-0.0012
hm	0.0711	-0.1628	0.4247	0.8998	-0.0242		0.8760	0.5367
ea	0.2210	-0.1416	0.5259	0.8305	-0.0792	0.8719		0.5630
em	0.0521	-0.1610	0.4000	0.8339	-0.0248	0.5345	0.5540	

b - Pearson correlação among estimates obtained by ridge regression

	aa	am	ca	cm	ha	hm	ea	em
aa		-0,5810	-0,0953	0,0655	-0,1060	0,1834	-0,3592	-0,0235
am	-0,5858		-0,1604	-0,0160	-0,0985	-0,0892	0,2993	0,1141
ca	-0,1058	-0,1841		-0,0783	-0,7928	0,1968	-0,6025	-0,2022
cm	0,0607	-0,0077	-0,0800		0,0472	-0,6562	-0,0810	-0,7590
ha	-0,0722	-0,0911	-0,7763	0,0488		-0,2435	0,6003	0,1340
hm	0,1594	-0,0698	0,2160	-0,6557	-0,2641		-0,5058	0,4173
ea	-0,3218	0,2820	-0,5973	-0,0795	0,5910	-0,5144		0,1211
em	-0,0250	0,1167	-0,1856	-0,7590	0,1179	0,4096	0,1119	

aa, am, ca, cm, ha, hm, ea, em: direct and maternal breed additive effect, direct and maternal complementarity effect, direct and maternal heterosis effect and direct and maternal epistatic loss effect, respectively.

Table 7

Ridge parameter (k) obtained with θ=0.06 and corresponding variance inflation factor (VIF) estimated for model **ACHE**

	i	k_i	WG	k_i	WC	k_i	WP	k_i	WM	k_i	PG	k_i	PC	k_i	PP	k_i	PM	k_i	SC
aa	1	0,014	3,17	0,014	3,20	0,014	3,09	0,014	3,12	0,014	3,63	0,014	3,49	0,014	3,33	0,014	3,35	0,014	4,91
am	2	0,014	3,33	0,014	3,46	0,015	3,55	0,014	3,43	0,014	3,55	0,014	3,77	0,016	4,13	0,014	3,70	0,012	3,88
ca	3	0,027	7,65	0,027	7,69	0,028	7,60	0,027	7,48	0,027	9,31	0,031	8,83	0,032	8,73	0,030	8,49	0,027	10,66
cm	4	0,060	10,31	0,060	10,27	0,060	10,08	0,060	10,24	0,060	10,63	0,060	10,36	0,060	10,17	0,060	10,32	0,060	11,24
ha	5	0,022	5,16	0,022	5,12	0,022	4,92	0,022	5,06	0,022	6,30	0,024	5,91	0,024	5,64	0,024	5,83	0,021	6,84
hm	6	0,044	6,99	0,044	6,97	0,044	6,87	0,044	6,96	0,044	7,11	0,044	7,00	0,045	6,88	0,045	6,98	0,041	7,40
ea	7	0,027	7,51	0,027	7,54	0,028	7,40	0,027	7,51	0,027	8,16	0,029	7,84	0,029	7,67	0,029	7,83	0,027	9,84
em	8	0,030	3,91	0,030	3,91	0,030	3,86	0,030	3,90	0,030	4,04	0,030	3,95	0,030	3,93	0,030	3,94	0,031	4,41

aa, am, ca, cm, ha, hm, ea, em: direct and maternal breed additive genetic effects, direct and maternal complementarity, heterosis and epistatic loss non-additive genetic effects, respectively; **k_i**: ridge parameter (**k** = θ * $(VIF_i/VIF_{max})^{½}$), i=1 to 8; **WG**: weaning gain; **PG**: post-weaning gain; **WC**: weaning conformation; **PC**: post-weaning conformation; **WP**: weaning precocity; **PP** post-weaning precocity; **WM**: weaning muscling; **PM**: post-weaning muscling; **SC**: scrotal circumference.

Table 8

Significance of the models tested against each possible reduced model

modelo	AC	AH	AE	ACH	ACE	AHE	ACHE	ACH	ACE	AHE	ACHE	ACH	ACE	AHE	ACHE	ACH	ACE	AHE	ACHE	ACHE	ACHE	ACHE
reduction	**A**	**A**	**A**	**A**	**A**	**A**	**A**	**AC**	**AC**	**AC**	**AC**	**AH**	**AH**	**AH**	**AH**	**AE**	**AE**	**AE**	**AE**	**ACH**	**ACE**	**AHE**
trait																						
WG	***	***	***	***	***	***	***	***	***	***	***	ns	ns	ns	***	***	***	***	***	***	***	***
WC	***	***	***	***	***	***	***	***	***	***	***	ns	ns	***	***	***	***	***	***	***	***	***
WP	***	***	***	***	***	***	***	***	***	***	***	ns	ns	***	***	***	***	***	***	***	***	***
WM	***	***	***	***	***	***	***	***	***	***	***	ns	ns	ns	***	***	***	***	***	***	***	***
PG	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
PC	***	***	***	***	***	***	***	***	***	***	***	***	ns	***	***	***	***	***	***	***	***	***
PP	***	***	***	***	***	***	***	***	***	***	***	ns	ns	***	***	***	***	***	***	***	***	***
PM	***	***	***	***	***	***	***	***	***	***	***	ns	ns	***	***	***	***	***	***	***	***	***
SC	***	ns	ns	***	***	***	***	***	***	**	***	***	***	***	***	***	***	***	***	***	***	***

*** P<0.001; ** P<0.01; **ns**: non significant (P>0.1); **A:** model including only the breed additive (direct and maternal) effect; **AC:** model including the breed additive (direct and maternal) and complementarity (joint additive) (direct and maternal) effects; **AH:** model including the breed additive (direct and maternal) and heterosis (dominance)(direct and maternal) effects; **AE:** model including the breed additive (direct and maternal) and epistatic loss (individual and maternal) effects; **ACH:** model including the breed additive (direct and maternal), complementarity (individual and maternal) and heterosis (individual and maternal) effects; **ACE:** model including the breed additive (direct and maternal), complementarity (direct and maternal) and epistatic loss (direct and maternal) effects; **AHE:** model including the breed additive (direct and maternal), heterosis (direct and maternal) and epistatic loss effects (direct and maternal) and the complete model **ACHE:** the breed additive (direct and maternal), complementarity (direct and maternal), heterosis (direct and maternal) and epistatic loss (direct and maternal) effects; **WG**: weaning gain; **PG**: post-weaning gain; **WC**: weaning conformation; **PC**: post-weaning conformation; **WP**: weaning precocity; **PP** post-weaning precocity; **WM**: weaning muscling; **PM**: post-weaning muscling; **SC**: scrotal circumference.

Table 9

Estimates (as a deviation from Angus breed) of breed additive and non-additive genetic effects for pre and post-weaning traits , obatined by ridge regression.

	WG	WC	WP	WM	PG	PC	PP	PM	SC
Model **A**									
aa	-0,249 ^{ns} (0,234)	0,013 ^{ns} (0,010)	-0,041 ** (0,011)	-0,045 ** (0,010)	-0,538 ^{ns} (0,275)	-0,128 ** (0,013)	-0,152 ** (0,015)	-0,185 ** (0,015)	-1,126 ** (0,067)
am	1,388 ** (0,138)	0,047 ** (0,006)	0,012 ^{ns} (0,006)	0,016 ** (0,006)	4,443 ** (0,162)	0,225 ** (0,008)	0,215 ** (0,009)	0,146 ** (0,009)	-0,541 ** (0,038)
Model **AC**									
aa	0,234 ^{ns} (0,265)	0,027 * (0,011)	-0,038 ** (0,012)	-0,034 ** (0,012)	-1,793 ** (0,321)	-0,154 ** (0,015)	-0,191 ** (0,018)	-0,210 ** (0,017)	-1,133 ** (0,089)
am	1,893 ** (0,154)	0,062 ** (0,007)	0,022 ** (0,007)	0,033 ** (0,007)	3,517 ** (0,181)	0,204 ** (0,009)	0,177 ** (0,011)	0,122 ** (0,010)	-0,641 ** (0,042)
ca	16,098 ** (0,681)	0,391 ** (0,029)	0,182 ** (0,032)	0,175 ** (0,031)	12,698 ** (0,803)	0,412 ** (0,040)	0,399 ** (0,048)	0,350 ** (0,044)	-0,010 ^{ns} (0,196)
cm	15,905 ** (0,361)	0,413 ** (0,015)	0,359 ** (0,017)	0,509 ** (0,016)	-15,405 ** (0,425)	-0,189 ** (0,022)	-0,302 ** (0,026)	-0,195 ** (0,023)	-0,049 ^{ns} (0,099)
Model **AH**									
aa	0,939 ** (0,248)	0,046 ** (0,010)	-0,021 ^{ns} (0,011)	-0,022 * (0,011)	-1,128 ** (0,296)	-0,131 ** (0,014)	-0,168 ** (0,017)	-0,197 ** (0,016)	-1,147 ** (0,078)
am	1,741 ** (0,161)	0,045 ** (0,007)	0,011 ^{ns} (0,008)	0,024 ** (0,007)	2,008 ** (0,190)	0,134 ** (0,010)	0,094 ** (0,012)	0,060 ** (0,010)	-0,536 ** (0,045)
ha	7,424 ** (0,163)	0,229 ** (0,007)	0,215 ** (0,008)	0,176 ** (0,007)	7,845 ** (0,200)	0,357 ** (0,010)	0,423 ** (0,012)	0,326 ** (0,011)	-0,026 ^{ns} (0,049)
hm	10,337 ** (0,113)	0,289 ** (0,005)	0,311 ** (0,005)	0,337 ** (0,005)	-5,413 ** (0,131)	0,016 * (0,006)	0,006 ^{ns} (0,008)	0,005 ^{ns} (0,007)	0,022 ^{ns} (0,033)
Model **AE**									
aa	-0,967 ** (0,260)	-0,010 ^{ns} (0,011)	-0,060 ** (0,012)	-0,071 ** (0,012)	0,963 ** (0,311)	-0,086 ** (0,015)	-0,094 ** (0,018)	-0,136 ** (0,017)	-1,096 ** (0,081)
am	1,763 ** (0,151)	0,044 ** (0,006)	0,004 ^{ns} (0,007)	0,020 ** (0,007)	2,680 ** (0,179)	0,150 ** (0,009)	0,113 ** (0,011)	0,078 ** (0,010)	-0,576 ** (0,044)
ea	4,286 ** (0,181)	0,083 ** (0,008)	0,069 ** (0,008)	0,126 ** (0,008)	-9,783 ** (0,211)	-0,217 ** (0,010)	-0,272 ** (0,012)	-0,202 ** (0,011)	-0,071 ^{ns} (0,053)
em	-3,785 ** (0,157)	-0,140 ** (0,007)	-0,204 ** (0,007)	-0,150 ** (0,007)	-0,796 ** (0,183)	-0,090 ** (0,009)	-0,135 ** (0,010)	-0,079 ** (0,010)	-0,038 ^{ns} (0,045)
Model **ACH**									
aa	0,912 ** (0,274)	0,056 ** (0,011)	-0,015 ^{ns} (0,012)	-0,016 ^{ns} (0,012)	-1,955 ** (0,331)	-0,149 ** (0,016)	-0,177 ** (0,018)	-0,212 ** (0,017)	-1,293 ** (0,092)
am	2,090 ** (0,167)	0,058 ** (0,007)	0,016 * (0,008)	0,035 ** (0,008)	2,397 ** (0,198)	0,158 ** (0,010)	0,104 ** (0,012)	0,073 ** (0,011)	-0,675 ** (0,048)
ca	9,448 ** (0,873)	0,140 ** (0,036)	-0,078 * (0,040)	-0,054 ^{ns} (0,039)	7,865 ** (1,039)	-0,010 ^{ns} (0,051)	-0,107 ^{ns} (0,059)	-0,038 ^{ns} (0,056)	0,050 ^{ns} (0,242)
cm	7,449 ** (0,576)	0,182 ** (0,024)	0,073 ** (0,026)	0,199 ** (0,026)	-5,696 ** (0,678)	-0,048 ^{ns} (0,033)	-0,160 ** (0,038)	-0,053 ^{ns} (0,036)	-0,097 ^{ns} (0,163)
ha	7,163 ** (0,209)	0,232 ** (0,009)	0,229 ** (0,009)	0,189 ** (0,009)	7,336 ** (0,261)	0,356 ** (0,013)	0,432 ** (0,015)	0,328 ** (0,014)	0,009 ^{ns} (0,062)
hm	7,885 ** (0,205)	0,232 ** (0,009)	0,275 ** (0,009)	0,278 ** (0,009)	-4,265 ** (0,240)	0,031 ** (0,012)	0,046 ** (0,013)	0,020 ^{ns} (0,012)	0,022 ^{ns} (0,061)
Model **ACE**									
aa	-0,552 ^{ns} (0,288)	0,015 ^{ns} (0,012)	-0,057 ** (0,013)	-0,063 ** (0,013)	-0,446 ^{ns} (0,351)	-0,126 ** (0,017)	-0,142 ** (0,019)	-0,190 ** (0,018)	-1,304 ** (0,099)
am	2,201 ** (0,174)	0,053 ** (0,007)	0,002 ^{ns} (0,008)	0,027 ** (0,008)	2,720 ** (0,205)	0,160 ** (0,010)	0,104 ** (0,013)	0,074 ** (0,011)	-0,696 ** (0,050)
ca	24,296 ** (0,739)	0,633 ** (0,031)	0,357 ** (0,035)	0,327 ** (0,033)	21,622 ** (0,870)	0,735 ** (0,044)	0,749 ** (0,052)	0,654 ** (0,048)	0,195 ^{ns} (0,215)
cm	19,279 ** (0,658)	0,634 ** (0,027)	0,652 ** (0,030)	0,707 ** (0,029)	-7,951 ** (0,770)	0,254 ** (0,037)	0,238 ** (0,043)	0,192 ** (0,041)	0,058 ^{ns} (0,192)
ea	0,344 ^{ns} (0,273)	-0,059 ** (0,011)	-0,073 ** (0,012)	-0,015 ^{ns} (0,012)	-8,932 ** (0,320)	-0,307 ** (0,015)	-0,364 ** (0,018)	-0,280 ** (0,017)	-0,105 ^{ns} (0,080)
em	-7,083 ** (0,231)	-0,254 ** (0,010)	-0,318 ** (0,010)	-0,267 ** (0,010	-0,009 ^{ns} (0,270)	-0,157 ** (0,013)	-0,202 ** (0,015)	-0,136 ** (0,014)	-0,068 ^{ns} (0,066)
Model **AHE**									
aa	0,409 ^{ns} (0,281)	0,031 ** (0,012)	-0,034 ** (0,013)	-0,041 ** (0,012)	-0,263 ^{ns} (0,343)	-0,105 ** (0,017)	-0,129 ** (0,019)	-0,174 ** (0,018)	-1,200 ** (0,095)
am	1,695 ** (0,170)	0,030 ** (0,007)	-0,017 * (0,008)	0,007 ^{ns} (0,008)	1,841 ** (0,202)	0,113 ** (0,010)	0,053 ** (0,012)	0,036 ** (0,011)	-0,657 ** (0,050)
ha	8,077 ** (0,170)	0,224 ** (0,007)	0,193 ** (0,008)	0,162 ** (0,008)	8,072 ** (0,210)	0,331 ** (0,010)	0,383 ** (0,012)	0,304 ** (0,011)	-0,017 ^{ns} (0,052)
hm	8,657 ** (0,200)	0,262 ** (0,008)	0,291 ** (0,009)	0,303 ** (0,009)	-3,159 ** (0,234)	0,098 ** (0,011)	0,104 ** (0,013)	0,075 ** (0,012)	0,057 ^{ns} (0,060)
ea	0,763 ** (0,287)	-0,045 ** (0,012)	-0,093 ** (0,013)	-0,051 ** (0,013)	-4,558 ** (0,337)	-0,194 ** (0,016)	-0,244 ** (0,019)	-0,170 ** (0,018)	-0,120 ^{ns} (0,085)
em	-3,325 ** (0,160)	-0,130 ** (0,007)	-0,198 ** (0,007)	-0,142 ** (0,007)	-0,652 ** (0,187)	-0,084 ** (0,009)	-0,131 ** (0,010)	-0,077 ** (0,010)	-0,054 ^{ns} (0,046)
Model **ACHE**									
aa	0,728 * (0,306)	0,076 ** (0,013)	-0,002 ^{ns} (0,014)	-0,018 ^{ns} (0,014)	-1,103 ** (0,378)	-0,135 ** (0,018)	-0,145 ** (0,020)	-0,215 ** (0,020)	-1,581 ** (0,109)
am	2,505 ** (0,185)	0,042 ** (0,008)	-0,024 ** (0,009)	0,020 * (0,008)	2,191 ** (0,220)	0,152 ** (0,011)	0,063 ** (0,014)	0,051 ** (0,012)	-0,863 ** (0,056)
ca	15,026 ** (1,199)	0,326 ** (0,050)	0,073 ^{ns} (0,054)	0,052 ^{ns} (0,053)	14,750 ** (1,460)	0,186 ** (0,071)	0,117 ^{ns} (0,081)	0,129 ^{ns} (0,078)	0,541 ^{ns} (0,334)
cm	12,960 ** (0,905)	0,431 ** (0,038)	0,406 ** (0,042)	0,453 ** (0,040)	-3,956 ** (1,059)	0,187 ** (0,051)	0,143 * (0,060)	0,142 * (0,056)	-0,015 ^{ns} (0,254)
ha	8,314 ** (0,278)	0,237 ** (0,012)	0,221 ** (0,012)	0,190 ** (0,012)	7,496 ** (0,355)	0,333 ** (0,017)	0,410 ** (0,019)	0,317 ** (0,019)	0,016 ^{ns} (0,081)
hm	7,923 ** (0,290)	0,244 ** (0,012)	0,280 ** (0,013)	0,284 ** (0,013)	-2,125 ** (0,338)	0,105 ** (0,016)	0,122 ** (0,019)	0,080 ** (0,018)	0,044 ^{ns} (0,084)
ea	-1,384 ** (0,398)	-0,133 ** (0,017)	-0,179 ** (0,018)	-0,122 ** (0,018)	-6,457 ** (0,473)	-0,267 ** (0,023)	-0,321 ** (0,026)	-0,228 ** (0,025)	-0,178 ^{ns} (0,118)
em	-5,561 ** (0,267)	-0,200 ** (0,011)	-0,259 ** (0,012)	-0,207 ** (0,012)	-0,329 ^{ns} (0,314)	-0,118 ** (0,015)	-0,155 ** (0,017)	-0,104 ** (0,017)	-0,084 ^{ns} (0,076)

** P<0,01; * P<0.05; ns: non significant (P>0.1); **aa, am, ca, cm, ha, hm, ea, em**: direct and maternal breed additive genetic effects, direct and maternal complementarity, heterosis and epistatic loss non-additive genetic effects, respectively. **WG, WC, WP, WM**: weaning gain, conformation, precocity, muscling respectively; **PG, PC, PP, PM**: post-weaning gain, conformation, precocity, muscling respectively; **SC**: Scrotal circumference. Standard errors are between parenthesis.

[5]CAPÍTULO IV

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Comparing methodologies to estimate fixed genetic effects and to predict genetic values for an Angus x Nellore population.

C. D. Bertoli[*,§,2], J. Braccini[§], V. M. Roso[#]

[*] Departamento de Agropecuária, Instituto Federal Catarinense Campus Camboriú (IFC-Camboriu), Camboriú, SC, Brasil; [§]Departamento de Zootecnia, Universisdade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brazil and [#]GenSys Consultores Associados, Porto Alegre, RS, Brazil.

[2] Correspondig author: cdbertoli@gmail.com

ABSTRACT : The objectives of this study were to compare the methodologies least squares with the ridge regression in the estimation of fixed genetic effects and in the prediction of genetic values for a multiracial population and also to compare two different ways of determining the best ridge parameter. A large crossbred Angus x Nellore population with 294.045 records for weaning gain (WG) and 148,443 records for post-weaning gain (PG) was used. Phenotypic visual scores varying from 1 to five for weaning (WC) and post-weaning (PC) conformation, weaning (WP) and post-weaning (PP) precocity, weaning (WM) and post-weaning (PM) muscling and scrotal circumference (SC) were also used. Three models were used to compare the least squares (LS) and the ridge regression (RR) methodologies: model **AHEC** including direct and maternal breed additive and direct and maternal heterosis, epistatic loss and complementarity non-additive effects; model **AHE**, including the direct and maternal breed additive and the direct and maternal heterosis and epistatic loss non-additive effects and; model **AH**, including only the direct and maternal breed additive and the direct and maternal heterosis non-additive effects. All models included the fixed contemporary group effect and random animal, maternal and permanent environment effects. Two methods to choose the ridge parameter were also tested (R1 and R2). For the estimation of fixed genetic effects, LS proved to be the best methodology for the models **AH** and **AHE**, and R1 proved to be the best methodology for the **AHEC** model. For the prediction of across-breed estimated breeding values (AB-EBV) in the **AH** model, LS proved to be the most appropriate methodology and in the **AHEC** model, R1 proved to be the most appropriate methodology. More studies are needed on the **AHE** model because the results were unclear. It was also identified that, in sub-sets of consistent data with large number of animals and proper distribution structure of the fixed genetic effects classes, R1 and LS may be equivalent in the estimation of fixed genetic effects, although this equivalence may not be the same to the AB-EBV.

key words: complementarity, crossbred beef cattle evaluation, epistatic loss, heterosis, non-additive genetic effects, ridge regression.

INTRODUCTION

The benefit of crossbreeding beef cattle includes improvement in growth and carcass traits (Williams et al., 2010) and has been studied by many researchers over the past decade (Cardoso et al 2008 Roso et al, 2005a, b; Carvalheiro et al 2006; Dias et al, 2011). In animal breeding of crossbred populations, for the purpose of selection for production, the greatest challenge is the non-biased comparison of breeding bulls and dams of different breed compositions. In crossbred populations, effects that are assumed to be null in pure populations become important and must be taken into account. For a fair comparison, a multiracial genetic evaluation including crossbred and purebred individuals in the same dataset is required, as proposed by Arnold et al. (1992).

Multibreed analysis involving pure and crossbred animals requires the inclusion of many effects, which are direct and maternal breed, heterosis (Williams et al., 2010; Carvalheiro et al., 2006; Cardoso et al.; 2008), epistatic loss (Dias et al, 2011) and complementarity between different breeds (Carvalheiro et al., 2006; Cardoso et al., 2008). The inclusion of these effects can often be problematic, depending on the over-parameterization of the models (Roso et al., 2005a). The additive genetic effect for each breed involved and their combination ability, general or specific, should be considered. When the number of breeds is very large, an alternative is to form groups of genetically similar breeds (Dias et al. 2011). The non-additive genetic effects are usually included as covariates, where the predictor variables are derived from the breeds of the animals included in the analysis. (Roso et al, 2005a, b; Cardoso, 2008; Carvalheiro et al., 2006; Dias et al, 2011.)

The inclusion of these non-additive genetic effects as covariates brings up a problem: collinearity or multicollinearity. When there is a strong linear relationship between the covariates of a regression model, the estimates obtained by the method of least squares tend to be unstable, often generating large standard errors (Schabenberger & Pierce, 2002). When the estimates are unstable with large standard errors, the regression coefficients might be highly confounded, and are easily affected by changes in the dataset (Roso et al., 2005b); estimates of this nature can lead to erroneous inferences (Dias et al., 2011) and, consequently, affects the direction of selection and, thus, the development of breeding programs.

Many studies propose the ridge regression as an alternative to overcome the collinearity (Roso et al., 2005b; Carvalheiro et al., 2006; Cardoso et al.,2008; Dias et al., 2011; Petrini et al., 2012;);.The ridge regression estimator consists of adding a small positive amount on the diagonal of the X'X matrix, causing a reduction in the variance of the estimates at the expense of introducing some bias. Thus, the RR estimator of b takes the general form $\hat{b}_k = (\mathbf{X'X} + k\mathbf{I})^{-1}\ \mathbf{X'y}$, where $\mathbf{K} = \mathrm{diag}\ (k_1, k_2, ..., k_p)$. and $k_i>0$. When all ki elements are equal to zero, $\hat{b}_k$ reduces to least squares estimator. This method, however, usually proposes an empirical choice of the values of **K**. The **K** value should be large enough to break the existing linear relationship between the covariates and small enough to produce the smallest possible bias (Schabenberger & Pierce, 2002). Roso et al. (2005b) proposed two methods to determine the best ridge parameter to use.

The objective of this study is to compare the least squares and the ridge regression methodologies in the estimation of fixed genetic effects and in the prediction of genetic values for a multiracial population of Angus and Nellore beef cattle. It is also our objective to compare two different ways of determining the best ridge parameter to use.

MATERIALS AND METHODS

Data from different breed compositions, resulting from crosses between Angus and Nellore cattle, were used. This data came from more than 200 herds distributed in the Brazilian states of Rio Grande do Sul, Paraná, São Paulo, Mato Grosso, Mato Grosso do Sul and Goiás and also from Paraguay. All herds were participants of "Programa Natura de Melhoramento Genético de Bovinos" (Natura Cattle Breeding Program). (Table 1)

A connectedness analysis between contemporary groups was carried out according to Roso *et al.* (2004). The total number of direct genetic links between contemporary groups, due to the existence of any common ancestors, was used. Contemporary groups with more than two calves and with at least five direct links were considered connected and retained for analysis. Roso *et al.* (2004) related that as the degree of connectedness among test groups decreases, the accuracy of comparisons of predicted breeding values (EBV) of bulls in different test groups also decreases. As one of the final objectives of a genetic evaluation is to obtain accurate EBVs, we tested the connectedness, using only animals of connected contemporary groups in this analysis.

The considered fixed genetic effects were direct and maternal breed additive and heterosis, epistatic loss and complementarity non-additive effects. The contribution of Nellore genes in the genetic composition of the animal(**aa**) and their dams (**am**) were used to estimate the direct and maternal breed genetic effect. To avoid dependence in incidence matrix columns, only the Nellore coefficient was used, giving an estimation of the deviation from the Angus breed performance. To estimate the direct and maternal heterosis effects, the heterozigosity coefficients **ha** and **hm** were used as described by Bertoli (1991) and Schenkel (1993), also used by Cardoso *et al.* (2008), Pimentel *et al.* (2007) and Roso *et al.* (2005b). These coefficients are given by **ha** = $(1-\sum_{i=1}^{2}\ (Sire\ breed_i\ *\ Dam\ breed_i))$ and **hm** = $(1-\sum_{i=1}^{2}\ (Maternal\ Grand\ Sire\ breed_i\ *\ Maternal\ Grand\ Dam\ breed_i))$ where i=1 refers to Angus breed proportion and i=2 refers to Nellore breed proportion.To estimate the direct and maternal epistatic loss effects, the epistazygosity coefficients **ea** and **em** were used, as proposed by Fries *et al.* (2000, 2002) and also used by Roso *et al.* (2005a,b), Pimentel *et al.* (2006), Carvalheiro *et al.* (2006) and Cardoso *et al.* (2008). These coefficients are given by **ea**= ½ [Hs + Hd] and **em**= ½ [Hmgs + Hmgd], where Hs is the sire heterozygosities, Hd is the dam heterozygosities, Hmgs is the maternal grand sire heterozygosities and Hmgd is the maternal grand dam heterozygosities. When the breed composition of a cow was not known (all products had known breed composition), the cow was considered to be *inter se* mating. Finally, the coefficients, proposed by Kinghorn (1993) and also used by Fries *et al.* (2000), Piccoli *et al.* (2002), Cardoso *et al.* (2008), were used to estimate the breed complementarity effects. The direct complementarity (**ca**) coefficient is described as **ca** = **aa***(1.0 - **aa**) and the maternal complementarity (**cm**) coefficient is described as **cm** = **am***(1.0 - **am**), where **aa** is the Nellore fraction of the animal breed and **am** is the Nellore fraction of the dam breed composition.

Nine traits were used in this analysis: weaning gain (WG), post-weaning gain (PG), phenotypic scores of conformation (WC), precocity (WP) and muscling (WM) taken at weaning, phenotypic scores of conformation (PC), precocity (PP) and muscling (PM) as well as scrotal circumference (SC) taken at post-weaning. The phenotypic score for each trait is given on a five-point scale, where one is the worst, and five is the best score for each management group.

The general model is described by equation (1). The pair-traits WG-PG, WC-PC, WP-PP, WM-PM and WG-SC were analysed in a two-trait analysis using the general model,

$$\mathbf{y = X}\boldsymbol{\beta}\mathbf{ + W}\boldsymbol{\gamma}\mathbf{ + Z}\boldsymbol{\alpha}\mathbf{ + }\boldsymbol{\varepsilon} \qquad \mathbf{(1)},$$

where **y** is the vector of observations of trait 1 and trait 2; **β** is the vector of fixed effects of environment, which includes contemporary group; **γ** is the vector of fixed genetic effects; **α** is the vector of random direct, maternal and permanent environmental of the dam effects and; **ε** is the vector of random residual effects. Incidence matrices **X**, **W** and **Z** relate records to fixed environmental effect of CG, to fixed genetic effects and to random direct and maternal additive genetic and permanent environmental effects, respectively.

The vectors of random effect **α** and **ε** were assumed to have (co)variance = **V**(**α**)= $\begin{bmatrix} \mathbf{A}\otimes\boldsymbol{G_a} & \mathbf{A}\otimes\boldsymbol{G_{am}} & 0 \\ \mathbf{A}\otimes\boldsymbol{G_{am}} & \mathbf{A}\otimes\boldsymbol{G_m} & 0 \\ 0 & 0 & \mathbf{I}\otimes\mathbf{Pe} \end{bmatrix}$ and **V**(**ε**) = **I**⊗**R**. **A** is the additive numerator relationship matrix among animals and **I** is the identity matrix; **G_a**= $\begin{bmatrix} \sigma_{a1}^2 & \sigma_{a1a2} \\ \sigma_{a1a2} & \sigma_{a2}^2 \end{bmatrix}$, **G_m**= $\begin{bmatrix} \sigma_{m1}^2 & \sigma_{m1m2} \\ \sigma_{m1m2} & \sigma_{m2}^2 \end{bmatrix}$, **G_{am}**= $\begin{bmatrix} \sigma_{a1m1} & \sigma_{a1m2} \\ \sigma_{a2m1} & \sigma_{a2m2} \end{bmatrix}$, **Pe**= $\begin{bmatrix} \sigma_{p1}^2 & \sigma_{p1p2} \\ \sigma_{p1p2} & \sigma_{p2}^2 \end{bmatrix}$ and **R**= $\begin{bmatrix} \sigma_{e1}^2 & \sigma_{e1e2} \\ \sigma_{e1e2} & \sigma_{e2}^2 \end{bmatrix}$, where σ^2 refers to variance and σ refers to covariance; ***a*** refers to direct additive genetic; ***m*** to maternal additive genetic; ***p*** to permanent environmental effects; **e** to residual; ***1*** refers to the first and; ***2*** to the second trait on a two-trait analysis.

Two reductions of this general model were also analyzed. One of these reductions (**AHE** model) does not include the effect of complementarity, neither direct nor maternal, on **γ** vector. The other reduction (**AH** model) includes only the direct and maternal breed additive and heterosis effects on **γ** vector. All other effects included in the general model (1) are also included in the reductions. The considered fixed genetic effects for each analyzed model are presented in Table 2.

The models described above were analyzed using the least squares (LS) and ridge regression methodologies (R1 and R2) in a two-trait analysis. Data was pre-adjusted for fixed effects of animal age, dam age and birth date (julian). GenSys Consultores Associados developed the analysis programs in Fortran 95.

The ridge regression methodology (RR) is "...an **ad-hoc** regression method to combat collinearity. The ridge regression estimator allows for some bias in order to break the collinearity and thus reduce the mean square error compared to Ordinary Least Squares. The user must choose the ridge parameter, a small number by which to shrink the least squares estimates." (Schabenberger & Pierce, 2002). The ridge regression estimator consists of adding a small positive number - the ridge parameter (k) - on the diagonal of the **W'W** matrix in order to break the relationship between the columns of the **W'W**. No clear rule exists to choose a value for k so it must be empirically determined (Dias et al., 2011). Two methods of determining the ridge parameter, that is the values of the non-negative diagonal elements of **K** ($k_1, k_2, \ldots, k_i$), were used in this study.

The first method (R1) was adapted from Roso et al. (2005b) and estimated as $k_i = \theta^*\left(\sqrt{\frac{VIF_i}{VIF_{max}}}\right)$, where *i* is the i^{th} element of the diagonal matrix **K**; VIF_i is the variance inflation factor of the i^{th} predictor variable and; VIF_{max} is the maximum value of all VIF_i. VIF was given by VIF $=\frac{1}{1-R_i^2}$, where R_i^2 is the coefficient of determination (Schabenberger & Pierce, 2002). The magnitude of the elements k_i will be proportional to the variance inflation factor of each predictor variable. To choose the value of θ, the bootstrap procedure, originally proposed by Efron (1979) and described by Roso (2005b) was performed. This is an iterative process, with the value of **θ** ranging from 0.000 to1.000 with increments of 0.002. For each value of **θ**, ten bootstrap samples were used to estimate all effects of the model (1) as well as VIF. For each value of **θ**, an average of VIF, obtained with the ten bootstrap samples, was calculated. The lower value of θ, whose average bootstrap samples generated VIF below ten for all fixed genetic effects, was used in each analysis. With this value of θ, a new analysis was performed, containing the complete data set, for the estimation of all effects according to model (1) and its reductions. Carvalheiro et al. (2006) used a similar method, choosing different values where all VIF also became lower than ten.

For the second method (**R2**), the θ was chosen based on the graphical analysis that related fixed genetic estimates with different values of θ**,** used in the **K** matrix calculation. Cardoso et al. (2008) and Piccoli et al. (2002) used the value of 0.06 and Lopes et al. (2010) used 0.05 for the diagonal of **K**. For this analysis, the chosen value of θ was 0.06.

In the present study, the RR analysis were carried out in the standardized form of the model, using the correlation matrix. After estimation the estimates were transformed to the original scale and were presented in this way.

For the collinearity analysis among the predictor covariables of fixed genetic effects, the eigenvalues and eigenvectors of the correlation matrix of prediction variables (**W**), the structure of the variance decomposition and, the Variance Inflation Factor (VIF) were analyzed. To compare the methodologies and models, we used the Relative Efficiency (RE), the stability of the estimates over several generations and the comparison between the across-breed estimated breeding values (AB-EBV). The RE of f(y) compared to g(y) as estimators of λ was measured by the ratio of their mean square errors (MSE). The RE, described in Schabenberger and Pierce (2002), comprises: RE [f(y), g(y)|λ] $=\frac{\text{MSE }[g(y),\lambda]}{\text{MSE }[f(y),\lambda]}$. These authors suggest that if RE [f(y), g(y)|λ]> 1 then f (y) should be preferred.

The across breed estimated breeding values (AB-EBV) are the EBV added to the direct breed additive effect, proportional to its breed composition.

RESULTS AND DISCUSSION

Multicollinearity

Eigenvalues and Condition Index

Figure 1 shows the eigenvalues of the correlation matrix among perdition variables of the fixed genetic effects and corresponding Condition Index (CI) for all traits to the **AHEC** model. This model simultaneously considers all covariates tested in this study, and is the most likely model to eliminate problems of collinearity between covariates. It can be noted that, for any of the traits the CI, is lower than 30. The CI associated with the last eigenvalue were between 20 and 30 for all traits. The CI associated with the second smallest eigenvalue were greater than 10. When we consider the **AHE** and **AH** models (not shown), all CI were lower than10 (the highest CI was 7.71 for SC in the **AHE** model).

According to Schabenberger & Pierce (2002), a good way to measure the multicollinearity between covariates in a regression can be obtained from the eigenvalues of the correlation matrix and their corresponding Condition Index. If the values of the eigenvalues are close to zero, high CI will be generate, showing that the collinearity problem is present in the analysis (Schabenberger & Pierce, 2002). Although the Principal Components, which are derived from the eigenvalues and eigenvectors of the correlation matrix, are orthogonal rotations of the original variables, they may not reflect the true sources of variability, hidden under the columns of incidence matrix (Schoeman et al., 2002). Dias et al. (2011) considered that collinearity is strong when CI is greater than 30 and weak when it is between 10 and 30. For CI below 10, the linear dependence that eventually exists should not be considered problematic (Schabenberger & Pierce, 2002; Dias et al., 2011; Roso et al., 2005b). The results presented here show intermediate values within this range (up 10 to 30), so other variables need to be considered in the analysis of multicollinearity beyond the eigenvalues and CI.

The variance-decomposition proportions associated with the largest CI, presented in table 3, suggest that the strongest collinearity problem is between the covariates used to estimate the effects of the maternal components of heterosis, epistatic loss and complementarity. When the largest CI was analyzed, these covariates showed variance fractions greater than 80% for all traits. Observing the second largest CI, the strongest association is between covariates that are estimating the direct components of the same effects (heterosis, epistatic loss and complementarity) involving fractions around 60-70%. This is the best method to detect collinearity between covariates.

When we are trying to estimate different effects from the same information, we will just find collinearity. Roso et al. (2005b) state that "Multicollinearity involving breed composition can be partially explained by the mathematical constraint among breeds because breed proportions of the breed composition of an animal add to one and the breed composition of a calf is equal to average breed compositions of the sire and the dam". The use of breed composition, however, is presented as a relatively simple measure to obtain and can be interpreted as if we were looking at the same object from several different perspectives (Fries et al., 2000). Dias et al. (2011) mentioned the value of 0.5 as a threshold to empirically determine a strong linear relationship between the different components of variance. Independent of this empirical value, the used data has shown really high values (above 0.80) for the fixed effects components. In this case make a further check through Variance Inflation Factors (VIF) is still possible. (Roso et al., 2005b; Dias et al., 2011; Schabenberger & Pierce, 2002; Petrini et al., 2012)

Variance Inflation Factor

The Variance inflation factor (VIF) of the regression coefficients is another simple, but effective measure for diagnosing collinearity (Schabenberger & Pierce, 2002). Fig. 2 shows the VIF for all tested models and traits. It can easily be seen that the **AHE** and **AH** models, regardless of the methodology used to estimate the fixed genetic effects, show no evidence of collinearity, whether strong or moderate. Only the **AHE** model, when estimated by LS presented a VIF greater than 10 and it is only for the SC trait (10.66) for direct epistatic loss.

The **AHEC** model, when estimated by LS, shows VIF above 10 and sometimes above the upper threshold of 30 (110 for **ca** for SC trait). Even in this model, the breed additive components do not present VIF indicating moderate or severe collinearity problems in the estimation of the fixed genetic effects.

The prediction variable of direct heterosis presented values above 10 only for post-weaning traits and SC, under the **AHEC** model and LS methodology. For this same model and methodology, the prediction variable of component of complementarity remains at the same level for all traits (between 10 and 23); maternal covariates, both as complementarity and heterozygosity, presented a VIF above 30 for all traits and the epistatic loss components showed values above 10 and below 30 for all tested traits.

If a covariate is orthogonal to all the others, their VIF is one (Schabenberger and Pierce, 2002). As the linear dependence increases, the VIF also increases. Dias et al. (2011) suggest that the VIF may overestimate the presence of multicollinearity, not differentiating between high and low values, making it impossible to distinguish "*quasi*-dependence". It is possible to use the value of VIF is equal to10 as a parameter to indicate that collinearity may be causing problems in the estimation. Also it is possible to use values above 30 to indicate severe problems with collinearity between covariates (Schabenberger & Pierce, 2002; Dias et al., 2011; Schoeman et al., 2002 Roso et al., 2005b). Dias et al. (2011) proposed only to verify the directions (positive or negative signals) of the values of fixed genetic effects. In this study, the directions have not changed with the use of different methodologies; only their magnitudes have changed. But this will be reflected in the breeding values, which will be discussed later.

When different methodologies are being considered to overcome the problem of collinearity, Schabenberger & Pierce (2002) suggest the concept of relative efficiency (RE) as an aid in decision making. Sometimes we will have to choose between different optimal properties of estimation and it is necessary to establish clear rules. It is not always possible to gather all the desirable properties in the same estimation process.

Methodologies and Models

Relative Efficiency

Unbiasedness of an estimator may not necessarily be the most desirable property. An estimator with a small bias, but with high accuracy, may be preferred when the unbiased estimator has a high variance. Schabenberger and Pierce (2002) proposed relative efficiency (RE), based on the mean square error (MSE) of the functions that generated such estimators.

The RE between the tested methodologies is presented in table 4. The values of the chosen θ are also presented in table 4 and vary from 0.062 to 0.082. For the model **AHEC**, methodologies R1 and R2 showed a slight (1%) superiority over LS for the traits PP and SC. The R2 showed better RE compared to LS and also in relation to R1 method for PG. For all other traits, there is no difference in relative efficiency between tested methodologies.

For the **AHE** model, estimates with LS and R1 are the same for all traits, except for SC. For this trait, R1 and R2 showed a slightly higher efficiency (1%) in the estimation of the parameter when compared with LS. For this model (**AHE**), when comparing LS with R2, the biased estimator (R2) shows better relative efficiency just for post weaning traits (PG, PC, PP, PM).

With respect to the **AH** model, the comparison shows slight superiority for R2 over LS for PG, PP, PM and SC. For the other traits, RE was equal to all different methodologies.

According to the results obtained for RE, all tested models have many similarities to each other, with methodology R2 showing a slight advantage over the other two for some of the post-weaning traits. No references were found with the use of RE in the choice of methodologies for estimation of these parameters.

The evolution over time

The change in the estimated values for the fixed genetic effects for the traits of WG and PG over 16 years of genetic evaluations taken every two years (1994-2010) is shown in Fig. 3. The number of observations available in each analyzed period is shown in table 5. In the early years, the variation of the estimated values for each of the fixed genetic effect was large compared to the variation in recent years, regardless of the method and model employed in this estimate. Overall, from 2002, estimates became more stable for all tested methodologies and models for the nine analyzed traits and a clear tendency to stabilization can be seen since 2002.

Over the years, estimates for **aa, am, ha** and **hm** were identical to WG, using the LS and R1 under the **AH** model. For **AHE** model, estimates of **am**, **ha**, **ea** and **em** for WG were equal to the LS and R1 from the year 2000. This suggests that there is no benefit in using R1 as an alternative to LS in the AHE model.

For the direct (**aa**) and maternal (**am**) breed additive effects, the greatest variation in estimates over the years, occurred when using the **AHEC** model with R1. Estimates for direct heterosis (**ha**) effect varied very little over time, showing a little larger fluctuation in **AH** models estimated by LS (WG) or R2

(PG). For evaluations subsequent to 2002, the estimated values of **ha** remain almost constant, although they show differences between used models and methodologies. These differences also remained relatively stable since 2002. When we report to the maternal heterosis, the largest oscillation is, undoubtedly, with the **AHEC** model and the LS, showing an inverted peak in 1998.

Estimates of direct epistatic loss effect showed similar values for R1 and R2 under the full model (**AHEC**), both for WG (Fig. 3A) and for PG (Fig. 3B) and even for the other analyzed traits, not shown because they had similar behavior. Regarding maternal epistatic loss effect, it is possible to observe a very similar behavior to that observed in maternal heterosis estimates, but found greater proximity of the estimated values from the different methodologies. For PG, different models did not produce very different estimates.

For the direct and maternal complementarity effects, the wide variation appears in the use of LS methodology in the early years. From 2000 began a period of stabilization and from 2002 the variation becomes very small, even for the LS method. Although it can perceived a parallel deviation, except for **ca,** for the trait WG (Fig. 3a), this bias tends to remain constant, which can be seen from almost parallel lines on the chart. Estimates of fixed genetic effects for the other traits showed equivalent behavior when estimated over the 16 years.

One of the major problems of multicollinearity is the instability of the estimates and also is the high standard errors of these estimates. Most authors cite or justifies that collinearity makes the estimates unstable and with high standard deviations (Schabenberger & Pierce, 2002; Roso et al., 2005a,b; Schoeman et al., 2002; Dias et al., 2011; Bueno et al., 2012, Carvalheiro et al., 2006; Cardoso et al., 2008). Petrini et al. (2012) claim that the multicollinearity can also be the result of a deficient sample data besides the interrelationship among the variables. When not all combinations of predictor variables are represented in the sample, as in the case of combinations of different breeds in sire and dam, variables involved can have a collinear relationship (Petrini et al., 2012). The data used in this study show that the greatest variation in the estimated values for the fixed genetic effects occurred in the first years of the breeding program, when many of breed compositions were not represented in the sample, producing an inadequate structure of data or the number of evaluated animals was much lower in these years.

From 2002 it can be clearly seen a general stabilization probably because of the increase in the number of animals and/or the improvement in the data structure, with the advancement in the breeding program, were responsible for this behavior. The argument that the structure of the data affects the results obtained was also defended by Petrini et al. (2012), although they agree that this reason does not always apply to every situation. As more generations were included in our database, different breed compositions were represented in the analyzed sample and the number of analyzed animals grew. This was beneficial to the stabilization of values of fixed genetic effects. Nevertheless it can be seen that as the methodology used, the difference between the estimated values remain relatively stable. (Fig. 3)

Several identical estimates were found. This result was expected in some cases. When the ridge parameter used in R1, which is set according to the VIF

<= 10, is zero, in fact there is no ridge regression, remaining in use the LS. When the ridge parameter used in R1 is very close to that used by R2 (**θ** (R2) = 0.06 and **θ**(R1) = 0.062 or **θ**(R1) = 0.064), very close estimates are generated.

The large variation identified in **AHEC** model can be explained, at least in part, because this method uses different values for the ridge parameter depending on each analyzed period. As the ridge parameter is depending on the VIF values, it is calculated for each analysis and the oscillation of the values presented higher amplitude. Petrini et al. (2012) suggest as an alternative, in addition to improving and increasing the amount of data, reducing the number of covariates in the model. This is also clear in this study, comparing the curves of the three analyzed models, presented in Fig. 2 and Fig. 3. However, according to Lopes et al. (2010) and Carvalheiro et al. (2006), it is important to include the effects of epistatic loss in the evaluation model for prediction of breeding values of crossbred. animals The inclusion of complementarity also appears to be important, although it should be further investigated (Carvalheiro et al., 2006).

We could not identify a reason that would justify the reversal of the estimated values for the fixed effects in 1998. Such behavior of the estimates may come from the collected raw data or data structure in that generation. What we can see is, since 2000, relative stability in the estimates of fixed genetic effects begins.

Schoeman et al. (2002) state that, in cases of linear dependence between the variables of the incidence matrix (**W** in this study), the regression coefficient become extremely unstable and "very sensitive to small random errors in Y" and may have large fluctuations with the addition or removal of variables in the model. Our data showed this behavior only in the early years, showing stability after a certain point. Petrini et al. (2012) mention of this instability over time but neither, Schoeman et al. (2002) or Petrini et al.(2012), presents results relating to this variation, so it was not possible to make comparisons with other populations in this regard.

When there are unstable estimates from one year to another, we can still make use of features such as using literature data for pre adjust our data (Williams et al., 2009).

Across-breed Estimated Breeding Values Comparisons

Comparisons between the AB-EBV obtained by different methodologies and different models of estimation were made by correlations of Pearson and Spearman (Fig. 4) and the percentage of coincident animals in different percentages selection (top 1, 5, 10, 20 and 40%). (Fig. 5) Estimated breeding value of the animals was increased by the additive direct genetic effect of breed, proportional to its breed composition, aimed at across breed comparison. The crop presented relates only to calves born in 2009, aiming to simulate the latest genetic evaluation of the tested herd, using data from individuals with complete information on weaning and yearling. Comparisons of AB-EBV bulls and cows are not displayed because they had a similar pattern to calves.

Correlations between AB-EBV obtained by LS, R1 and R2

All correlations can were high, ranging from 0.83 to 1.0.(Table 4) **AHEC** model in R1 and R2 have values equal to one. The ridge parameters used in these evaluations were very close, which would explain this quasi-identity between the breeding values. The same situation is repeated in **AHE** and **AH** models for LS and R1. In this case, the ridge parameter chosen by the methodology R1 is equal to zero (equal to LS) for traits WP, WM and WC, which showed correlations very close to one. Among all comparisons, the lowest correlation was found for WG, followed by PG, between LS X R1 and R2 x LS.

Coincidences for different proportions of selected animals

For the model **AHEC,** R1 and R2 were almost perfectly correlated for all the tested traits (99 to 100%), and also were LS and R1 for **AHE** and **AH** models (90 to 100%), except for SC. This is true even when only 1% of the top animals were selected. (Fig. 5) This is possibly due to the ridge parameter obtained in the R1 be sometimes coincident with R2, sometimes coincident with zero (LS). This is a result proper of the R1, which sets the ridge parameter depending on the VIF. These results are in complete agreement with the correlations presented in Fig. 4.

When comparisons are made on the basis of 1% top animals, the percentages of coincidences varied between 59.14% and 99.46%, Lower percentage of coincidences were observed for WG in the **AHEC** models (LS x R1 and R2 x LS, both 59.14%) and **AHE** (LS x R2 - 65.59% and R1 x R2 - 66.67%). These results show that the changes in methodology, for these models, caused an important re-ranking of the AB_EBV.

Roso et al. (2005b) found 78-80% of coincidences among the top 40% AB-EBV estimated by least squares and ridge regression using an equivalent model to **AH** and around 80-85% for an equivalent model to **AHE**. Inversely, when the comparison was made for the top 1% selected animals, the coincidence has dropped to 60-65% in both cases. Our data showed greater coincidence in general, with few below 60% (WG (**AHEC**) for LSxR1 and LSxR2, SC (**AHE**) for LSxR2) and the great majority over 70% of the Top 1% selected animal coincidences. These differences confirm the fact that the choice of methodology has significant consequences on the genetic selection on the animals, resulting in different rankings of animals on the basis of AB-EBV.

Petrini et al. (2012) argue that the presence of collinearity can affect the accuracy of estimates, regardless of the intensity and consequently, the accuracy of inferences based on these results. This can turn into wrong choices, of the animals, in applied breeding programs. Roso et al. (2005a) conclude that inadequate separation of non-additive genetic effects in the evaluation model and multicollinearity in the analysis may affect the ranking of animals when compared between different breeds. Carvalheiro et al. (2006) suggest that the ridge regression can and should be used to correct the multicollinearity problems as in the estimation of the effects of regression as in the predicted genetic values. They affirm that the prediction surfaces present themselves more acceptable from a biological point of view under this methodology. Dias et al. (2011) found no differences in the signal (positive/negative) of the estimates for LS and RR, but found differences in magnitudes and standard errors. They suggest that LS overestimates the values, being RR more reliable by decreasing the standard error of estimates and increasing the accuracy, despite of the inclusion of the bias.

CONCLUSIONS

In the genetic evaluation of crossbred populations, when only the effects of heterosis (dominance) are considered (model **AH**), the Least Squares methodology was shown to be fully adequate for estimating fixed genetic effects with this model. The covariates do not presented evidence of high collinearity and were not identified major differences between the AB-EBV of selected animals from different tested methodologies. When epistatic loss effects are considered in the model (model **AHE**), collinearity not appear to be a problem, whereas all condition index were below eight and all VIF were below eleven. It should be considered however, that the comparisons between the AB-EBV correlations for weaning traits were not too high and deserve further study on the prediction of breeding values for selection purposes. In the estimation with the effects of heterosis (dominance), epistatic loss and complementarity (model **AHEC**), the ridge regression methodology was the most suitable to overcome the collinearity between covariates, and R1 as indicated by introducing the lowest possible bias to break this collinearity without prejudice to the estimates. When the data reached certain number and structure, as observed from the year 2004 in the evolution over time, the stability of the estimates of fixed genetic effects is similar between LS and RR, suggesting that the LS methodology could be used in certain data set. This, however, needs to be studied thoroughly in the light of the discrepancies found in the AB-EBV of selected animals.

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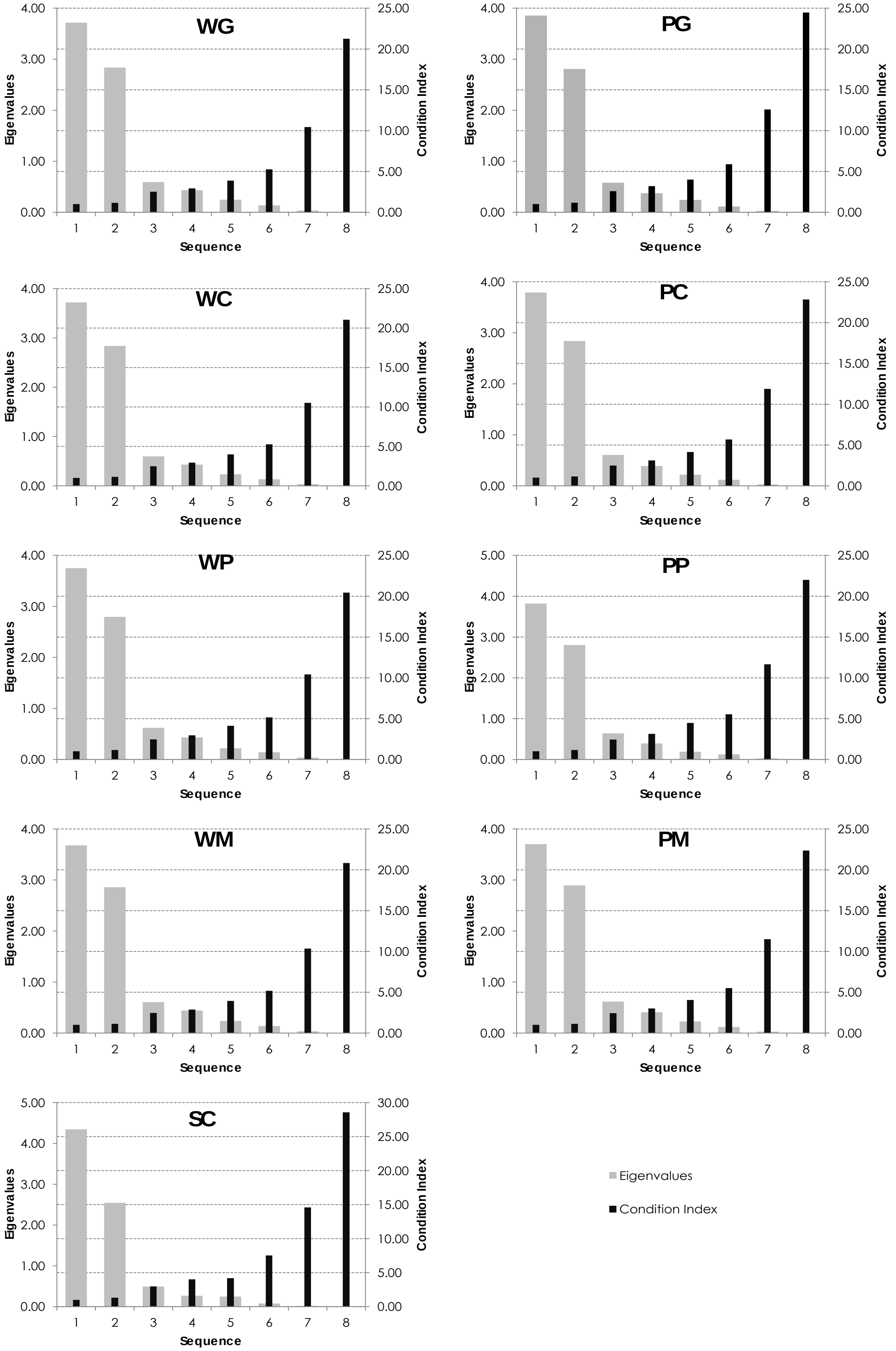

Figure 1 - Eigenvalues and Condition Index of the correlation matrix among the prediction variables of fixed genetic effects under model **AHEC**.

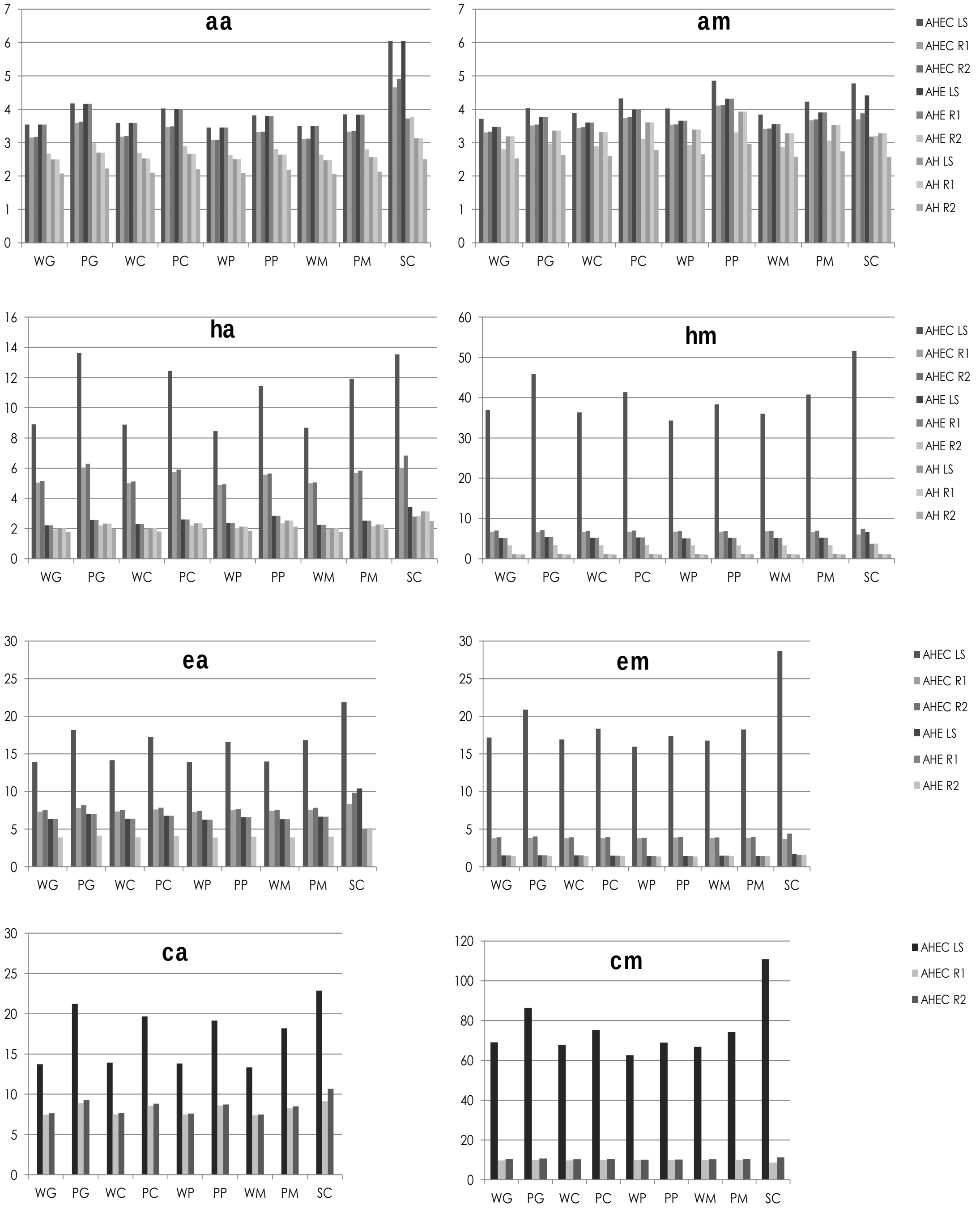

Figure 2 - Variance Inflation Factors for the fixed genetic effects, under three models (**AHEC**, **AHE** and **AH**) and three methodologies (LS, R1 and R2)

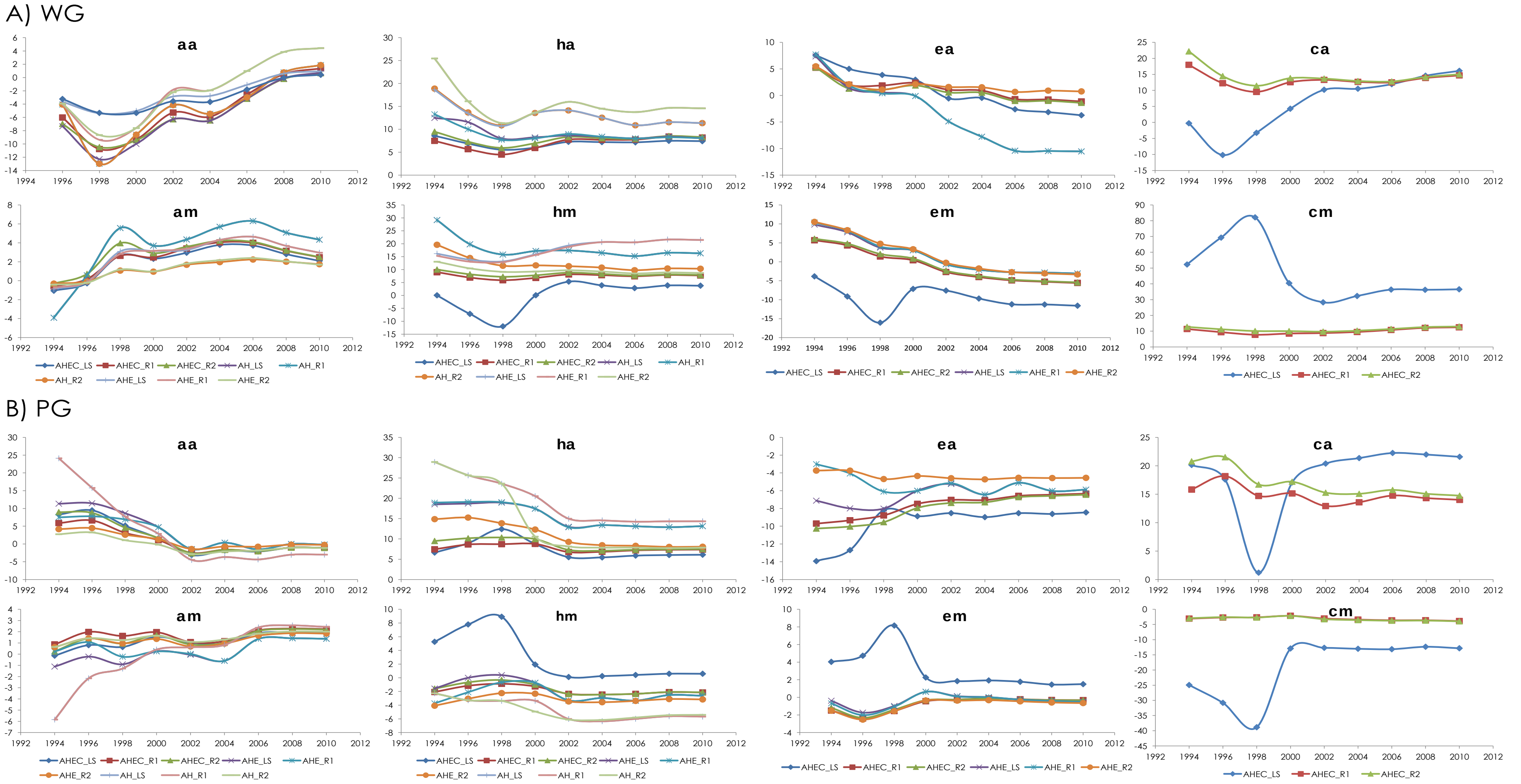

Figure 3 - Fixed genetic effects estimated for A) weaning gain(WG) and B) post-weaning Gain (PG) traits, estimated by three distintic methodologies (LS, R1 and R2) and models (**AHEC**, **AHE** and **AH**).

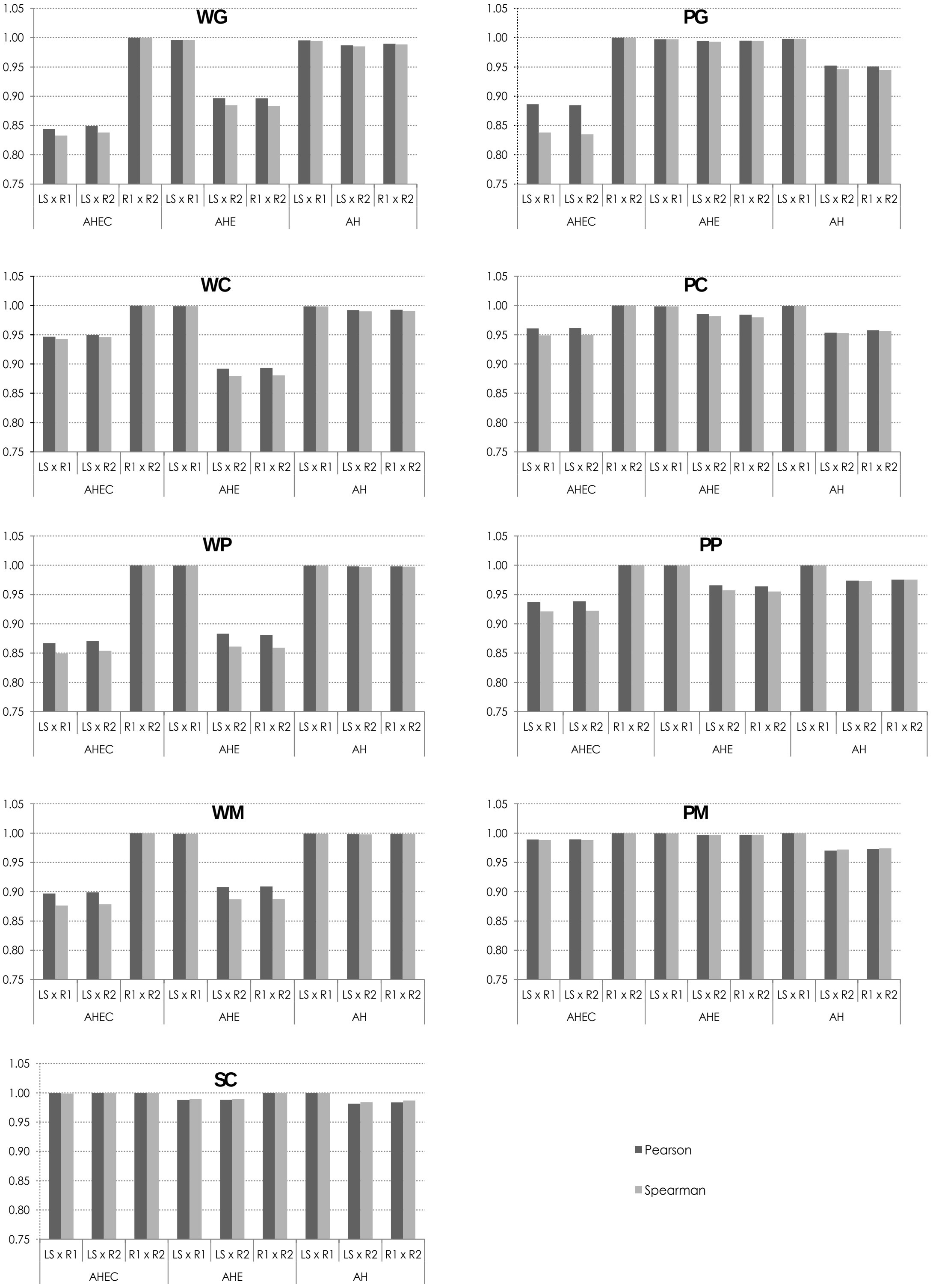

Figure 4 - Pearson and Spearman Correlations for direct across-breed estimated breeding values (AB-EBV) for weaning gain (WG), post-weaning gain (PG), weaning conformation (WC), post-weaning conformation (PC), weaning precocity (WP), post-weaning precocity (PP), weaning muscling (WM), post-weaning muscling (PM) and scrotal circumference (SC), given by different methodologies (LS, R1 and R2) and models (**AHEC**, **AHE** and **AH**).

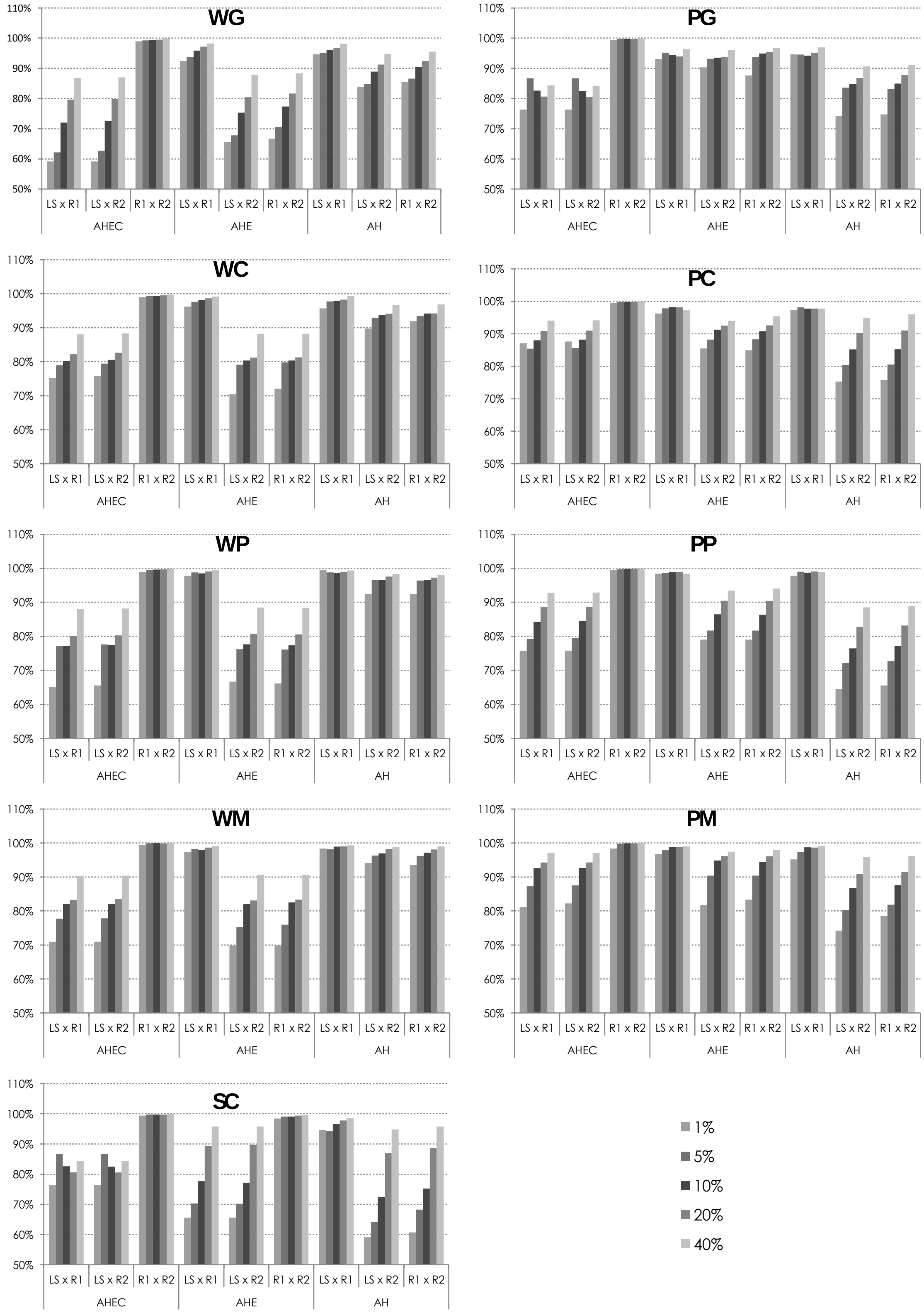

Figure 5 - Percentage of coincidence for different proportion (top 1, 5, 10, 20 and 40%) of selected calves on the basis of direct across breed estimated breeding value (AB-EBV) for weaning gain (WG) and post-weaning gain(PG) given by different methodologies (LS, R1 and R2) and models (**AHEC**, **AHE** and **AH**).

Table 1
Distributions of animals according to sire and dam breed composition, presented as percentage of Nellore (N).

		Dams									
		Angus	**1/8N**	**2/8N**	**3/8N**	**4/8N**	**5/8N**	**6/8N**	**7/8N**	**Nellore**	**Total**
Sires	**Angus**	27,795	96	698	3,164	6,219	4,048	20,243	194	28,330	90,787
	1/8N	52	5	24	10	71	0	2	0	17	181
	2/8N	85	206	760	1434	6,780	163	3,520	1	502	13,451
	3/8N	1,305	371	2,238	78,159	43,194	2,690	6,061	148	18,713	152,879
	4/8N	47	125	96	687	4,066	218	1,587	28	5,947	12,801
	5/8N	1,170	0	14	443	1,046	1,186	1,084	21	1,053	6,017
	6/8N	8,668	4	5	697	466	181	285	3	185	10,494
	7/8N	0	0	0	0	5	0	0	0	13	18
	Nellore	241	31	52	1,341	4,726	236	738	51	1	7,417
	Total	39,363	838	3,887	85,935	66,573	8,722	33,520	446	54,761	294,045

Values are approximated to the closest class composition. Every class included fractions equal or smaller than the mentioned breed proportions

Table 2

Fixed genetic effects included in the three genotypic models (**AH**, **AHE** and **AHEC**) considered in this study

	Effects included on **γ**							
Model	**aa**	**am**	**ha**	**hm**	**ea**	**em**	**ca**	**cm**
AH	★	★	★	★				
AHE	★	★	★	★	★	★		
AHEC	★	★	★	★	★	★	★	★

aa, am, ha, hm, ea, em, ca, cm: direct and maternal breed additive effect, direct and maternal heterosis, epistatic loss and complementarity non-additive effects, respectively.

Table 3 - Decomposition of the variance structure of the parameters estimates, associated with the two largest condition indices (model **AHEC**)

	WG		**WC**		**WP**		**WM**		**SC**	
Condition index	21,25	10,44	21,06	10,53	20,44	10,41	20,82	10,34	28,57	14,59
aa	0,00	0,06	0,00	0,07	0,00	0,07	0,00	0,07	0,00	0,11
am	0,01	0,09	0,01	0,10	0,01	0,11	0,01	0,10	0,01	0,18
ha	0,18	0,62	0,18	0,62	0,18	0,60	0,17	0,62	0,12	0,68
hm	0,94	0,01	0,94	0,01	0,94	0,01	0,94	0,01	0,94	0,02
ea	0,15	0,73	0,15	0,73	0,16	0,72	0,15	0,74	0,10	0,78
em	0,84	0,09	0,83	0,09	0,83	0,10	0,84	0,09	0,89	0,06
ca	0,18	0,65	0,18	0,65	0,19	0,64	0,18	0,65	0,12	0,70
cm	0,96	0,03	0,96	0,03	0,96	0,04	0,96	0,03	0,97	0,02

	PG		**PC**		**PP**		**PM**	
Condition index	24,46	12,58	22,83	11,88	22,00	11,66	22,35	11,50
aa	0,01	0,07	0,01	0,07	0,01	0,08	0,01	0,08
am	0,01	0,09	0,01	0,09	0,02	0,11	0,01	0,10
ha	0,23	0,63	0,26	0,59	0,25	0,57	0,25	0,59
hm	0,95	0,00	0,95	0,00	0,95	0,00	0,95	0,00
ea	0,20	0,67	0,23	0,65	0,23	0,65	0,22	0,66
em	0,83	0,11	0,81	0,13	0,80	0,14	0,81	0,12
ca	0,24	0,65	0,26	0,62	0,26	0,62	0,25	0,62
cm	0,95	0,04	0,95	0,05	0,94	0,05	0,95	0,04

aa, am, ha, hm, ea, em, ca, cm: direct and maternal breed additive effect, direct and maternal heterosis, epistatic loss and complementarity non-additive effects, respectively.

Table 4 - Relative efficiency between LS (least squares), R1 (ridge regression 1) and R2 (ridge regression 2) methodologies for the three tested models.

	AHEC				**AHE**				**AH**
	θ	**RE(LS/R1)**	**RE(LS/R2)**	**RE(R1/R2)**	**θ**	**RE(LS/R1)**	**RE(LS/R2)**	**RE(R1/R2)**	**RE(LS/R2)**
WG	0,064	1,00	1,00	1,00			1,00		1,00
WC	0,064	1,00	1,00	1,00			1,00		1,00
WP	0,062	1,00	1,00	1,00			1,00		1,00
WM	0,062	1,00	1,00	1,00			1,00		1,00
PG	0,066	1,00	1,01	1,01			1,01		1,01
PC	0,064	1,00	1,00	1,00			1,01		1,00
PP	0,062	1,01	1,01	1,00			1,01		1,01
PM	0,064	1,00	1,00	1,00			1,01		1,01
SC	0,082	1,01	1,01	1,00	0.062	1,01	1,01	1,00	1,01

Values of **θ** relates to R1 method. Values not shown of **θ** are equal to zero.

For R2 method θ is equal to 0.06 and for LS θ is equal to zero.

WG: weaning gain; WC;weaning conformation; WP; weaning precocity; WM;weaning muscling; PG: post-weaning gain; PC: post-weaning conformation; PP: post-weaning precocity; PM: post-weaning muscling and SC: Scrotal circumference

Table 5 - Number of observations in the analysis over the years for weight Gain at Weaning (WG) and Post-weaning (PG).

Year	1994	1996	1998	2000	2002	2004	2006	2008	2010
WG	48,826	54,442	75,468	105,165	149,820	193,439	227,156	275,138	294,045
PG	20,526	28,423	38,439	54,644	76,253	96,515	115,748	136,332	138,075

CAPÍTULO V

CONSIDERAÇÕES FINAIS

A produção de carne bovina vai muito além do aspecto econômico em si. A produção de carne bovina é a produção de proteína animal de alta qualidade a partir de plantas forrageiras, as quais não são adequadas para o consumo humano. Nesta transformação fantástica reside a riqueza desta produção, que tem como meta final a saciedade da fome no mundo. Com matéria prima de baixo custo econômico e ecológico é possível produzir alimento proteico de alta qualidade.

Buscando este objetivo, o uso de bovinos de corte cruzados se tornou uma realidade. Tanto os diferentes sistemas de acasalamento quanto o uso de populações sintéticas para produção de carne bovina de qualidade vêm sendo utilizados há várias décadas. Explorando os efeitos genéticos não aditivos, a produção pode aumentar expressivamente. No entanto, sem seleção criteriosa, mesmo este ganho extra obtido pelos cruzamentos tenderia a estagnar.

A seleção intra-racial produziu efeitos importantes nas últimas décadas e segue produzindo em todas as espécies zootécnicas de importância econômica. A seleção inter-racial, embora reconhecidamente importante nos dias de hoje, ainda caminha a passos lentos. Os pesquisadores ainda não são unânimes quanto aos efeitos não aditivos que devem ou não ser considerados nem quanto à metodologia que deve ser utilizada. Os efeitos genéticos fixos (aditivo de raça e não aditivos) foram desprezados por tanto tempo que ficaram quase esquecidos.

Na época da seleção genômica e dos grandes avanços na área da tecnologia, os estudos com avaliações genéticas inter-raciais começa a despertar. Embora não tão charmoso quanto os milhares de bases recém sequenciadas no genoma bovino, os QTLs e os marcadores, os efeitos genéticos fixos vêm surgindo como a necessidade atual na seleção de bovinos cruzados. Assim como os SNPs, os efeitos fixos trazem com eles a necessidade de voltarmos no tempo e redescobrirmos a genética quantitativa e a estatística como ferramentas indissociáveis do melhoramento dos animais domésticos.

Com este trabalho, comfirmamos a importância da inclusão dos efeitos não aditivos nos modelos de avaliação para seleção de reprodutores. Os modelos estatísticos para avaliação inter-racial devem, necessariamente, incluir os efeitos de domonância e perdas epistáticas. Os efeitos de complementariedade precisam ainda de maiores estudos, mas também fica claro que há um efeito não linear decorrente da combinação entre as raças, embora a maneira de tratá-lo ainda não seja tão clara.

Neste estudo também pudemos vislumbrar a importância da quantidade e estrutura dos dados usados nas avaliações genéticas. Este assunto pode e deve ser mais assiduamente estudado, em simulações ou com dados reais. Estes estudos devem ter como objetivo esclarecer o quanto a ampla distribuição dos genótipos sobre as distintas composições raciais interfere com a qualidade e acurácia das estimativas obtidas.

O conhecimento sobre as composiçoes raciais dos ancestrais também pode ser fruto de maiores investigações, simuladas ou não, buscando conhecer o quanto é perdido quando há pressuposição de acasalamentos inter se que de fato não ocorreram. Essas pressuposições podem ser mais importantos do que pensamos, há que se investigar mais.

Além disso, estudos sobre o desempenho dos animais oriundos de cruzamentos em diferentes ambientes devem estar na mente dos pesquisadores. Como cada raça foi originada em ambiente específico, a medida que as raças são combinadas podem perder ou não sua capacidade de adaptação a determinados climas e/ou latitudes, bem como se comportar de maneira intermediária ou ainda, de forma totalmente diversa à das raças parentais envolvidas.

O estudo dos efeitos genéticos fixos (aditivo de raça e os não aditivos) tem seu espaço e ainda há muito que aprender sobre eles. Este trabalho tenta lançar alguma luz, no rastro de outros pioneiros, buscando atingir um conhecimento necessário para o futuro da produção de carne bovina. Este trabalho não traz a solução nem pretende ser o dono da verdade, mas representa mais um passo em direção às avaliações genéticas multirraciais de bovinos. Espero que seja útil e abra novos horizontes aos novos pesquisadores da área, assim como de áreas afins.

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VITA

Claudia Damo Bertoli, filha de Nilsa Teolides Damo Bertoli e Gentil Bertoli, nasceu em Caçador - Santa Catarina em 22 de setembro de 1964.

Concluiu o ensino fundamental em 1978, no Colégio Dom Bosco, no município de Rio do Sul - SC e o ensino médio, juntamente com o Curso Técnico em Análises Químicas em 1981, no Colégio Catarinense, no Município de Florianópolis - SC. Cursou Engenharia Agronômica na Universidade Federal de Santa Catarina- UFSC de 1982 a 1986, em Florianópolis - SC. Durante a graduação foi bolsista na área de avicultura de corte junto ao professor Dr. José Carlos Fiad Padilha.

Após a graduação participou do I Curso Latino Americano de Etologia Aplicada aos Animais Domésticos, na Universidade Federal de Santa Catarina - UFSC, durante o primeiro semestre de 1987. A partir de agosto de 1987 trabalhou na EMATER-Pr, no município de Laranjeiras do Sul - PR , como extensionista municipal, até fevereiro de 1988.

Em 1988 iniciou o curso de mestrado em Zootecnia, na Universidade Federal do Rio Grande do Sul (UFRGS) sob orientação do Professor Dr. Luiz Alberto Fries, desenvolvendo pesquisa relacionada ao melhoramento genético de bovinos de corte, trabalhando mais assiduamente com cruzamentos e seus efeitos (principalmente heterose). Obteve o grau de mestre em abril de 1991, com a dissertação: SISTEMA CRUZA - Controle de produção e avaliação dos valores genéticos dentro de uma população bovina sintética". Ainda Durante o mestrado foi sócia fundadora da Empresa GenSys Consultores Associados, à qual permaneceu vinculada até 1995, prestando serviços de consultoria e assessoria em melhoramento genético de bovinos e ovinos de corte.

Em 1995 ingressou como professora substituta no então Colégio Agrícola de Camboriu - Universidade Federal Santa Catarina (UFSC) e atualmente Instituto Federal Catarinense (IFC-Camboriu)), passando a professora efetiva em janeiro de 1997. Desde 1997 até 2010 trabalhou em várias atividades ligadas ao ensino da zootecnia e da preservação ambiental, desenvolvendo vários projetos junto aos seus alunos..

Em 2011 iniciou o curso de doutorado em Zootecnia na Universidade Federal do Rio Grande do Sul (UFRGS) sob a orientação do Professor Dr José Braccini Neto e co-orientação da Professora Dra. Concepta McMannus, desenvolvendo pesquisas na área de cruzamentos de bovinos de corte e seus efeitos (principalmente epistasia e complementariedade)

Entre 2012 e 2013 foi contemplada com bolsa CAPES de doutorado sanduíche no exterior por 12 meses. Neste período trabalhou em pesquisas na área de genômica de bovinos cruzados junto ao Professor Dr Flávio Schenkel na University of Guelph, em Guelph - Canadá.

Retornou ao Brasil em setembro de 2013 para finalizar seus estudos e submeter-se a avaliação de defesa da Tese de doutorado no Programa de Pos Graduação em Zootecnia, área de concentração Produção Animal - Sub área de Melhoramento Genético Animal (UFRGS)