

UNIVERSIDADE FEDERAL DE MINAS GERAIS

**Implicações da interação genótipo x
ambiente na seleção de bovinos da raça
Nelore**

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Belo Horizonte

2016

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ambiente na seleção de bovinos da raça
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Tese apresentada ao Programa de Pós-Graduação em Zootecnia da Escola de Veterinária da Universidade Federal de Minas Gerais como requisito parcial para a obtenção do grau de Doutor em Zootecnia.

Área de concentração: Genética e Melhoramento Animal

Prof. Orientador: Dr. Fabio Luiz Buranelo Toral

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RESUMO

A seleção de reprodutores pode ocorrer em ambientes favoráveis, desafiadores ou similares aqueles de criação da progênie dado que o ambiente de criação do bezerro nem sempre é definido antes de sua produção. A identificação do ambiente que forneça maior resposta à seleção, direta e indireta, facilitaria o processo de seleção e avaliação do desempenho dos candidatos à seleção. Dessa forma, objetivou-se comparar a eficiência dos sistemas de produção a pasto ou em confinamento para avaliação do desempenho e seleção de tourinhos de corte. Foram obtidos parâmetros genéticos para peso final (PF), ganho médio diário em peso (GMD) e perímetro escrotal (PE) de tourinhos Nelore criados em testes de desempenho individual a pasto ou em confinamento. As estimativas de variância genética aditiva e residual variaram em função do ambiente e os maiores valores foram obtidos para animais criados em confinamento. A correlação genética entre a mesma característica mensurada a pasto ou em confinamento diferiu da unidade. As características de menor herdabilidade são mais sensíveis à interação genótipo x ambiente. Variações na intensidade de seleção praticada a pasto ou em confinamento contribuem para reduzir diferenças nas respostas à seleção, direta e indireta, obtidas nesses dois ambientes. Adicionalmente, foram obtidas respostas correlacionadas para características de crescimento e reprodução em animais criados em rebanhos comerciais a pasto ou em confinamento quando a seleção foi aplicada em tourinhos em teste de desempenho individual nos dois ambientes. As herdabilidades para características de crescimento e PE foram maiores em animais criados em testes de desempenho individual do que nos animais em rebanhos comerciais. As correlações genéticas entre características mensuradas em tourinhos criados em testes de desempenho individual e animais de rebanhos comerciais foram positivas, exceto para os pares que incluíram idade ao primeiro parto (IPP). A IPP apresentou correlação genética favorável com GMD e PE de tourinhos em testes de desempenho a pasto, entretanto essas associações não foram significativas quando se considerou o desempenho de tourinhos criados em testes de desempenho em confinamento. Dessa forma, os testes de desempenho individual a pasto podem ser utilizados como ferramenta de avaliação do desempenho e seleção de reprodutores independente do ambiente de criação das progênies.

Palavras-chave: sistema de produção, crescimento, reprodução, intensidade de seleção, herdabilidade.

ABSTRACT

The selection of bulls may be done in favorable, challenging or similar environments to raised their progeny, because the environment to raised the progenie's of bulls is not defined in advance their production. The identification of the environment that results in the greater, direct and indirect, response to selection, would facilitate the process of selection and evaluation of the performance for selection candidates. Thus, this study aimed to compare the efficiency of pasture or feedlot production systems for performance evaluation and selection of sires in beef cattle. Genetic parameters for final weight (FW), average daily weight gain (ADG) and scrotal circumference (SC) of Nellore young bulls raised in individual performance tests on pasture or in feedlot were obtained. The additive genetic and residual variances and heritability vary according to environment and the greater values were observed for animals raised in feedlot systems. The genetic correlations between the same trait measured on pasture or in feedlot were lower than one. Traits of lower heritability are more sensitive to genotype x environment interaction. Variations in the selection intensity practiced on pasture or in feedlot contribute for reducing differences in, direct and indirect, responses to selection obtained in these two environments. Additionally, we presented correlated responses for growth and reproductive traits in commercial animals when selection was applied in performance-tested young bulls, both on pasture and feedlots. Heritabilities for growth and SC are greater in performance-tested young bulls than in commercial animals. The genetic correlations between traits in performance-tested and commercial herds were positive, except for pairs that included age at first calving (AFC). The AFC was genetically related to ADG and SC in performance-tested young bulls on pasture, however it was not related to these traits in performance-tested young bulls in feedlots. Thus, the individual performance test on pasture can be used for performance evaluation and selection of sires regardless of raised environment of the progenies.

Keywords: growth, heritability, production systems, selection intensity, reproduction.

1.0 INTRODUÇÃO

A pecuária brasileira tem importante papel na economia e desenvolvimento do País. Atualmente o Brasil é o segundo maior produtor, exportador e consumidor de carne bovina do mundo. A bovinocultura de corte contribui para o agronegócio brasileiro com faturamento de mais de R\$ 50 bilhões/ano e oferece cerca de 7,5 milhões de empregos (ABIEC, 2016). Entretanto, para manter os mercados ou conquistar novos, inclusive de melhor remuneração, é necessário disponibilizar produtos de qualidade a preços acessíveis (FAO, 2015). No Brasil existe ampla variabilidade de sistemas de produção, manejo e alimentação, e clima, mas há predominância de produção em pastagens tropicais.

A intensificação dos sistemas de produção pode ser realizada por meio de suplementação alimentar, que permita o atendimento das exigências nutricionais de cada categoria animal, fertilização do solo, rotação de culturas, irrigação, uso de consorciação com leguminosas e de gramíneas adaptadas a região. Essas estratégias de manejo, associadas ao uso de animais de alto potencial genético, podem contribuir para aumentar a produtividade nos sistemas de produção de bovinos de corte. Variações no uso dessas tecnologias resultam em grandes diferenças nos sistemas de produção. Isso pode alterar as variâncias e correlações genéticas, residuais e fenotípicas, herdabilidades e valores genéticos preditos dos candidatos à seleção para as características de interesse. As diferenças na expressão entre os genótipos dos animais em função do ambiente caracteriza a interação genótipo x ambiente (IGA, Falconer e Mackay, 1996).

A existência de IGA para características de interesse econômico em sistemas de produção de bovinos de corte foi reportada na literatura por meio de diferentes metodologias (Bressan et al., 2011; Espasandin et al., 2011; Carvalho et al., 2013; Saavedra-Jiménez et al. 2013; Santana Júnior et al., 2015; Terakado et al., 2015). Apesar do grande número de pesquisas relacionadas a esse tema, ainda há incerteza sobre o melhor ambiente para avaliação do desempenho e seleção de reprodutores. Essa dúvida persiste porque o ambiente de criação do bezerro nem sempre está definido antes de sua produção.

Uma alternativa para incluir a IGA nas avaliações genéticas seria prever a diferença esperada nas progênes de candidatos à reprodução em ambientes onde o seu desempenho ou de sua progênie não foram mensurados. Esses resultados podem ser obtidos por meio de análises multicaracterísticas com os dados de parentes mensurados nos ambientes de interesse. Adicionalmente, seria necessário identificar o ambiente para avaliação e seleção de

reprodutores que proporcionem maior progresso genético para as características de interesse econômico, independente do sistema de produção adotado para criação das progênes. Dessa forma, a seleção de reprodutores poderia ser realizada em apenas um ambiente.

O ambiente para mensuração e seleção de reprodutores deve proporcionar respostas correlacionadas iguais ou superiores àquelas obtidas por meio da seleção direta nos demais sistemas de produção de bovinos de corte. Isso possibilitaria redução de custos, maior eficiência na coleta de dados e, conseqüentemente, maior acurácia na predição dos valores genéticos aditivos e na seleção de reprodutores. Dessa forma, objetivou-se comparar a eficiência dos sistemas de produção a pasto ou em confinamento para avaliação do desempenho e seleção de touros jovens para utilização em rebanhos comerciais.

À vista disso, foi realizada uma revisão de literatura e dois artigos científicos foram produzidos. A revisão de literatura contemplou procedimentos para análise da interação genótipo x ambiente e considerações sobre o impacto do manejo nutricional na seleção de reprodutores. No primeiro artigo, “Genotype x environment interaction in individual performance and progeny tests in beef cattle”, objetivou-se estimar parâmetros genéticos para características de crescimento e perímetro escrotal de tourinhos Nelore em provas de ganho em peso a pasto ou em confinamento e estudar o efeito da interação genótipo x ambiente na classificação dos animais para desempenho individual ou teste de progênie. Esse manuscrito foi publicado no Journal of Animal Science em abril de 2015 (doi:10.2527/jas2014-7983). O segundo artigo, “Selection of young bulls in performance tests and indirect responses in commercial beef cattle herds on pasture and feedlot” foi realizado para estimar parâmetros genéticos para características de crescimento e reprodução em testes de desempenho individual e em rebanhos comerciais e analisar a eficiência do teste de desempenho individual a pasto ou em confinamento como ferramenta de seleção para programas de melhoramento genético de bovinos de corte em rebanhos comerciais.

Esperamos que os resultados desse trabalho possam contribuir para identificação do melhor ambiente para avaliação e seleção de reprodutores por meio da análise das diferenças nos parâmetros genéticos para as mesmas características mensuradas em testes de desempenho individual ou rebanho comercial, ambos no pasto ou em confinamento, e das estimativas de correlações genéticas e repostas a seleção, diretas e indiretas, obtidas em cada ambiente.

2.0 REVISÃO DE LITERATURA

2.1 AVALIAÇÃO DA INTERAÇÃO GENÓTIPO X AMBIENTE

A escolha de animais geneticamente superiores para reprodução pode ser realizada por meio da predição dos valores genéticos dos animais a partir dos registros fenotípicos. O fenótipo é determinado pelo genótipo, pelo ambiente e pela interação desses dois fatores. Diferenças na expressão dos genótipos em função do ambiente caracterizam a IGA (Falconer e Mackay, 1996). A IGA pode causar alteração no desempenho dos animais, nos valores absolutos ou relativos das variâncias genéticas, de ambiente e fenotípicas (Santana Júnior et al., 2015), nos critérios de seleção (Henderson, 1984) e nas respostas direta e indireta à seleção.

A IGA pode ser avaliada por meio da análise da correlação genética entre a mesma característica mensurada em diferentes ambientes (Falconer, 1952). A análise de variância em experimentos fatoriais, comparação de modelos contendo um fator aleatório atribuído a IGA e utilização de normas de reação via modelos de regressão aleatória também são alternativas utilizadas para sua avaliação. A escolha da metodologia a ser utilizada no estudo da IGA deve levar em consideração os dados disponíveis para análise ou o delineamento do experimento a ser executado. Dessa forma, serão apresentadas informações sobre como analisar a interação genótipo x ambiente e sobre o impacto do manejo nutricional na seleção de reprodutores.

2.1.1 ANÁLISE DE VARIÂNCIA EM EXPERIMENTOS FATORIAIS

A análise de variância em experimentos fatoriais inclui todas as combinações de vários conjuntos de níveis e fatores. Portanto, permite o estudo da interação entre as causas de variação de interesse. No caso de estudos de IGA, os genótipos podem ser representados por raças, linhagens, grupos genéticos ou mesmo populações distintas de um mesmo grupo genético e o ambiente como um fator avaliado (temperatura, dietas, densidade populacional, ou quaisquer outros fatores que possam ser controlados). Dessa forma, a obtenção de repetições de determinados genótipos e a criação em classes específicas de ambientes permite por meio da análise de variância estimar os efeitos atribuídos ao ambiente, ao genótipo e à interação entre eles por meio da análise de variância (Squilassi, 2003).

Na interpretação dos resultados, a presença de significância do termo de interação indica que as diferenças nos fenótipos dependem do ambiente. Por isso, qualquer consideração feita a respeito do genótipo deve ser feita especificando-se o ambiente avaliado. Por outro lado, a ausência de interação indica que as diferenças entre os genótipos não dependem do ambiente.

Com o resultado desse tipo de experimento é possível definir o melhor genótipo para cada ambiente. A principal desvantagem desta metodologia está na pressuposição da análise de variância que diz respeito à homocedasticidade, o que na realidade não ocorre em função da tendência de maior variação nos melhores ambientes (Burdon, 1977). No caso de heterogeneidade de variâncias é possível agrupar, ou dividir, os ambientes de forma que exista homogeneidade de variância dentro do grupo. Ainda, seria possível decompor o quadrado médio dos resíduos em componentes apropriados as comparações de interesse. Entretanto, análises com modelos mistos permitem a inclusão de efeitos aleatórios e da matriz de parentesco. Isso resulta em classificação e seleção de reprodutores mais adequada, uma vez que as previsões para os valores genéticos obtidos por meio da metodologia de modelos mistos são mais acuradas que os valores fenotípicos ajustados pela metodologia dos quadrados mínimos (Torral e Alencar, 2010).

2.1.2 INTERPRETAÇÃO DE CORRELAÇÕES GENÉTICAS

A correlação genética entre uma mesma característica mensurada em diferentes ambientes pode ser utilizada para identificar a IGA (Falconer, 1952). Esse autor relatou que uma determinada característica medida em ambientes diferentes pode ser interpretada como sendo características diferentes uma vez que os mecanismos bioquímicos, fisiológicos ou comportamentais são, de algum modo, diferentes. Ainda, se essa correlação é significativamente pequena sugere-se que a classificação dos animais com base nos valores genéticos preditos para cada ambiente pode não ser a mesma. Robertson (1959) sugeriu que correlação genética abaixo de 0,80 seria indício da existência de IGA. Já para Falconer (1952), qualquer valor de correlação abaixo da unidade seria suficiente para estabelecer sua existência. Adicionalmente, James (1961) e Mulder et al. (2006) estudaram os ganhos genéticos em dois ambientes para comparar estratégias de seleção e recomendaram que a seleção fosse específica para cada ambiente quando as correlações genéticas fossem menores que 0,70 e 0,61, respectivamente.

A utilização da correlação genética para estudo da IGA é ferramenta útil para o conhecimento das respostas indiretas à seleção obtidas por meio da seleção em diferentes ambientes. Ainda, a eficiência da resposta indireta demonstra o quanto se espera ganhar, ou perder, fazendo a seleção em um ambiente distinto do qual a população melhorada será criada (Falconer e Mackay, 1996). A abordagem que utiliza a correlação genética entre a mesma característica em diferentes ambientes para estudo da IGA é análoga do modelo multicaracterística, por exemplo, do peso em duas idades diferentes (De Jong, 1990).

Esta abordagem pode ser encontrada nos estudos sobre interação touro x região (Toral et al., 2004; Espasandin et al., 2011; Araujo et al., 2011; Diaz et al., 2011; Sousa Junior et al., 2012; Carvalho et al., 2013 e Saavedra-Jiménez et al., 2013); interação touro x sistema de produção (Bhuiyan et al., 2004; Durunna et al., 2011) e interação touro x estação de reprodução (Alencar et al., 2005 e Mascioli et al., 2006). Caso a inclusão da interação genótipo x ambiente nas avaliações genéticas seja necessária, uma alternativa para sua modelagem seria realizar a padronização do ambiente, que pode ser feita considerando o sistema de produção adotado, extensivo ou intensivo, por exemplo, obter as correlações genéticas garantindo a inclusão da informação de parentes criados nos diferentes ambientes avaliados e publicar nos sumários de touros as diferenças esperadas na progênie preditas para cada ambiente. Isso pode auxiliar no processo de seleção dos animais de reprodução quando a interação genótipo x ambiente estiver presente. Entretanto, um elevado número de ambientes pode resultar em matrizes muito esparsas e alto custo computacional para solução das equações de modelos mistos. Adicionalmente, esses resultados podem ser de difícil interpretação para parte de usuários dos catálogos de touros. Para isso, seria possível utilizar índices com ponderações adequadas para cada sistema de produção.

2.1.3 INCLUSÃO DA INTERAÇÃO GENÓTIPO X AMBIENTE COMO EFEITO ALEATÓRIO NÃO CORRELACIONADO

A comparação de modelos é largamente utilizada para avaliar a importância do efeito não correlacionado genótipo x ambiente no modelo de análise, por meio do teste de Razão de Verossimilhança. Segundo a descrição de Freund e Wapole (1980) a estatística do teste (λ), define a razão entre o máximo da função de verossimilhança sob o modelo reduzido (L_R), ou seja, sem o efeito aleatório não correlacionado, e o máximo da função de verossimilhança sob o modelo completo (L_C), este com o efeito aleatório não correlacionado. A partir da distribuição do valor de $-2 \log$ da razão de verossimilhança pode-se avaliar a significância

deste efeito no modelo. Esta estatística pode ser obtida por: $\lambda = (-2 \log L_R) - (-2 \log L_C)$. Dessa forma, quando $\lambda \geq \chi^2_{\alpha,1}$, em que α é o nível de significância com 1 grau de liberdade, pode-se afirmar que o efeito testado foi significativo a este nível, e o componente de variação de interação genótipo x ambiente deve ser incluído no modelo. O valor $\chi^2_{\alpha,1}$ é obtido em uma tabela da distribuição qui-quadrado, com 1 grau de liberdade, com a área à direita de $\chi^2_{\alpha,1}$.

A inclusão desse efeito no modelo permite estimar diferenças no manejo de animais contemporâneos, mas nascidos em épocas (Alencar et al., 2005) ou regiões diferentes (Espasandin et al., 2011 e Toral et al., 2011). Esse modelo identifica a presença de interação entre dois fatores por meio da estimação de soluções para cada nível de combinação desses dois fatores. Entretanto, ele não permite a obtenção de parâmetros genéticos específicos para cada ambiente.

2.1.4 NORMAS DE REAÇÃO VIA MODELOS DE REGRESSÃO ALEATÓRIA

A norma de reação descreve a variação dos fenótipos produzidos por um genótipo como uma função contínua da variação ambiental, normalmente representada por uma função num gráfico de mensuração de uma característica fenotípica sobre um fator ambiental. Dessa forma, os modelos de norma da reação expressam o fenótipo como função polinomial do valor ambiental, onde os coeficientes dos polinômios sofrem influência genética, representando mudanças graduais e contínuas dos fenótipos em diferentes ambientes (De Jong, 1995). As normas de reação dos genótipos podem ser classificadas em plásticas (com maior sensibilidade) ou robustas (com menor sensibilidade). Genótipos com maior plasticidade apresentam maior variação fenotípica quando expostos a diferentes ambientes, mas essa variação fenotípica é reduzida nos genótipos robustos.

A sensibilidade do mesmo genótipo em diferentes ambientes pode ser quantificada pela regressão do fenótipo em cada ambiente, em relação ao gradiente ambiental (Pégolo et al., 2009 e 2011; Cardoso e Tempelman, 2012; Santana Júnior et al., 2013 e 2015; Terakado et al., 2015; Chiaia et al., 2015). O desempenho do genótipo é, então, regredido em relação à média do desempenho populacional em cada ambiente. Dessa forma, o desempenho médio de todos os genótipos em cada ambiente é determinado pela diferença entre as médias produtivas em cada ambiente por exemplo, o nível médio da produção do rebanho, temperatura, umidade, alimentação (Perkins e Jinks, 1973; Kolmodin et al., 2002 e 2003; Calus e

Veerkamp, 2003; Cardoso et al., 2005; Su et al, 2006). Dessa forma estima-se uma regressão fixa dos valores médios fenotípicos da população em cada ambiente sobre o gradiente ambiental, a partir da qual a norma de reação individual pode ser predita pela regressão aleatória dos valores fenotípicos de animais aparentados no gradiente ambiental, uma vez que o mesmo indivíduo não pode ser medido em muitos ambientes. As estimativas que resultam da análise de regressão aleatória são os valores genéticos dos animais para os coeficientes da função que descreve a norma de reação e, além disso, as covariâncias daqueles coeficientes são estimadas (Kolmodin et al., 2003). Assim, os coeficientes podem ser usados para construir os valores genéticos dos animais para o desempenho ao longo do gradiente ambiental.

Em um modelo de norma de reação com regressão aleatória linear atribuem-se, a cada animal avaliado, dois coeficientes de regressão aleatórios (intercepto e linear). O intercepto representa a média para o valor genético aditivo ao longo do gradiente ambiental e maiores valores de coeficientes de regressão linear significam maior sensibilidade à mudança ambiental. Mudança na sensibilidade ambiental pode ser o resultado da ação da seleção diretamente nos coeficientes da norma de reação ou uma resposta correlacionada à seleção para valores fenotípicos dentro de diferentes ambientes (Via et al., 1995).

Como a IGA pressupõe diferença de sensibilidade nos indivíduos avaliados, a magnitude do componente de variância atribuído ao coeficiente de regressão linear é a chave para avaliar a existência da interação. Altos valores, ou seja, normas de reação com diferentes inclinações pressupõem heterogeneidade de sensibilidades (Figura 2.1, A). Situações como esta apresentam modificações de variância genética ou até modificações na ordem de classificação nos diferentes pontos do intervalo de ambientes considerados. Baixos valores para o coeficiente de regressão linear pressupõem normas de reação paralelas em relação ao eixo dos ambientes, sem modificações de variância genética aditiva e de ordem de classificação em diferentes pontos do intervalo (Figura 2.1, B). Nesta situação, não há necessidade de se procurar os melhores genótipos em ambientes diferentes, basta classificar os animais com base nos interceptos.

Além da variância dos coeficientes de regressão linear, a correlação entre os coeficientes (intercepto e linear) também influencia a forma da correlação genética entre ambientes. Dada uma mesma variação no coeficiente linear, a alta correlação entre o intercepto e o coeficiente linear leva a maior reclassificação. Comparado com o ambiente médio, uma correlação positiva ou negativa promove mais reclassificação em piores ou melhores ambientes, enquanto a reclassificação é simétrica em torno da média quando o intercepto e coeficiente linear são não correlacionados (Strandberg, 2006).

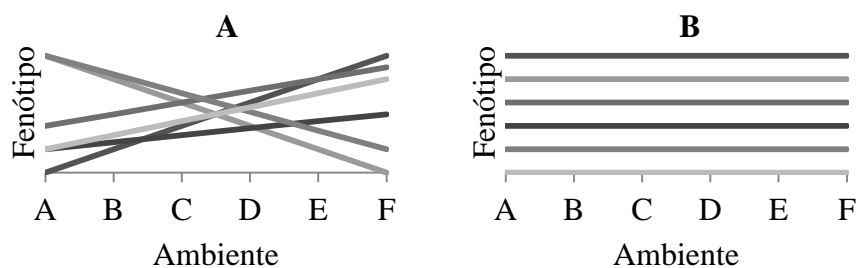


Figura 2.1. Representação gráfica para normas de reação de diferentes genótipos, para animais sensíveis (A) ou robustos (B), identificados nos gráficos pelas linhas.

A vantagem do modelo de normas de reação em descrever as características para todos os pontos diferentes em tempo ou espaço, ou seja, de forma contínua no gradiente ambiental, confere superioridade computacional, pois com muitas observações e um modelo linear, poucos parâmetros precisam ser estimados. Com este benefício, a predição da resposta à seleção é mais acurada, em função dos componentes de variâncias e respostas diretas e correlacionadas serem estimados também com mais confiança e para todos os pontos ao longo da trajetória ambiental (Kolmodin et al., 2003).

É importante destacar que a estrutura dos dados, composições genéticas fora da média, isto é grupos ambientais compostos por animais de valores genéticos cuja média foi tendenciosa, e baixa conectividade genética, podem resultar em viés na estimação da função de covariância para descrever IGA com modelos de norma de reação (Calus et al., 2004). A melhor solução encontrada por esses autores foi o uso da função de covariância combinada a um grande número de animais por rebanho. Assim, é possível concluir que a utilização da norma de reação nas avaliações genéticas possibilita a identificação da IGA, desde que haja distribuição dos dados de parentes ao longo de diferentes ambientes.

2.2 IMPACTO DO MANEJO NUTRICIONAL NA SELEÇÃO DE REPRODUTORES

Ambientes favoráveis permitem máxima expressão das características de crescimento em diferentes espécies (Hammond, 1947). Entretanto, não há consenso na literatura que esse deve ser o ambiente utilizado para avaliação e seleção de reprodutores (Falconer, 1960). A seleção em ambiente similar ao ambiente de criação da progênie é indicada como alternativa para reduzir os impactos da interação genótipo x ambiente (Dalton, 1967). Ainda, a seleção

em ambientes restritos pode resultar em progresso genético para características de interesse em ambientes favoráveis, mas a seleção em ambientes favoráveis pode não resultar em incremento na média da característica de interesse em ambientes desfavoráveis (Falconer, 1960).

Em bovinos Cachim, Mascioli (2000) classificou, de acordo com peso final, os touros criados em testes de desempenho individual em confinamento (aproximadamente 400 dias de idade) ou a pasto (aproximadamente 570 dias de idade) como superiores ($n = 7$ ou 9), intermediários ($n = 6$ ou 9), e inferiores ($n = 6$ ou 8), respectivamente. Posteriormente, Mascioli (2000) realizou testes de progênie a pasto ou em confinamento. Para os touros criados em testes de desempenho individual em confinamento esse autor não observou efeito significativo para o peso aos 12 e 18 meses de idade e ganho médio diário em peso dos 12 aos 18 meses da progênie. Por outro lado, os resultados com touros Cachim criados em testes de desempenho individual a pasto demonstrou que as progênies de touros classificados como superiores apresentaram maiores pesos ao nascimento, desmama e 12 meses de idade quanto comparada aos grupos dos intermediários e inferiores (Mascioli, 2000). Esse autor concluiu que a seleção de touros Cachim em testes de desempenho individual a pasto foi mais eficiente que a seleção realizada em confinamento.

Um delineamento experimental em esquema fatorial foi aplicado por Bhuiyan et al. (2004) para estimar a correlação genética entre peso pós-demama de animais puros e cruzados Simental e Charolês criados a pasto e em confinamento. As correlações genéticas entre o peso pós-demama de animais em rebanhos comerciais e centrais de teste foi de 0,004, entre rebanho seleção e centrais de teste foi de 0,004 e entre rebanho comercial e rebanho de seleção foi de 0,013. Dessa forma, os autores concluíram que a avaliação genética e seleção de reprodutores para peso corporal pós-desmama deve ser realizada de acordo com o ambiente (Bhuiyan et al., 2004).

Ainda, Bressan et al. (2011) avaliaram a composição e deposição de gordura subcutânea em touros *Bos taurus* e *Bos indicus* criados a pasto ou em confinamento. Touros *Bos indicus* criados a pasto apresentaram teores de ácidos graxos saturados e monoinsaturados no músculo *Longissimus dorsi* similares e teores de ácidos graxos polinsaturados superiores aqueles apresentados por touros *Bos taurus*. Por outro lado, o músculo *Longissimus dorsi* de animais *Bos taurus* terminados com dietas de alto grão apresentou menor teor de ácidos graxos saturados, maior de teor de ácidos graxos monoinsaturado e teores de ácidos graxos polinsaturados similares aos animais *Bos indicus*. Dessa forma, o manejo nutricional para acabamento de carcaça utilizado para um determinado

grupo genético não pode ser extrapolado para outros grupos genéticos ou ambientes (Bressan et al., 2011).

A correlação genética entre ganho médio diário e consumo alimentar residual de tourinhos de corte cruzados, Angus x Simental, mensurados em períodos com dieta de crescimento e de terminação (sucessivas) foram diferentes da unidade, indicando existência de interação genótipo x manejo nutricional (Durunna et al., 2011). Apesar do confundimento entre idade e manejo nutricional, os autores sugeriram que a seleção deve ser realizada no período com fornecimento de dieta de terminação. Essa dieta apresenta maior custo e isso poderia ser revertido em maior lucro para os sistemas de produção de bovinos de corte, caso fossem identificados animais mais eficientes (Durunna et al., 2011). Outra alternativa seria considerar a diferença entre os custos de produção e intensidade de seleção praticadas a pasto e no confinamento. No Brasil, por exemplo, o sistema de produção a pasto possui menor custo quando comparado ao confinamento. Isso permite avaliação de maior número de candidatos e possibilidade de praticar maior intensidade de seleção. Dessa forma, os sistemas de produção a pasto podem proporcionar maior progresso genético para características de interesse econômico.

A variância genética aditiva e herdabilidade para características de crescimento em bovinos Brahman criados em centrais de teste foi superior àquela obtida para as mesmas características em rebanhos comerciais (Rashid et al., 2016). Esses autores estudaram o peso de bovinos Brahman aos 3, 6, 9, 12 e 18 meses de idades e a correlação genética entre a mesma característica mensurada em centrais de teste e rebanhos comerciais foram de 0,74; 0,74; 0,72; 0,64; 0,53 e 0,57, respectivamente. Dessa forma, a interação genótipo x ambiente foi mais intensa com o aumento da idade. Isso pode ser explicado pela maior influência do ambiente no desempenho dos animais no período pós-desmama (Rashid et al., 2016).

As estimativas de correlações genéticas diferentes da unidade entre a mesma característica mensurada em manejos nutricionais distintos evidencia a existência de interação genótipo x ambiente (Falconer, 1952). Ainda, ambientes sem restrição qualitativa ou quantitativa de nutrientes permitem maior expressão das diferenças genéticas para características de crescimento entre os animais. Entretanto, a literatura não indica o melhor ambiente para seleção e avaliação de reprodutores. Apenas experimentos com camundongos (Falconer, 1960) e outro com número reduzido de bovinos de corte da raça Canchim (Mascioli, 2000) avaliaram a eficiência dos diferentes ambientes por meio da obtenção do fenótipo da progênie dos reprodutores selecionados em ambiente diferentes. Nos dois experimentos citados, os animais identificados e selecionados como superiores em ambientes

restritos (Falconer, 1960) e em testes de desempenho a pasto (Mascioli, 2000) foram mais eficientes para aumentar a média da característica de interesse quando comparados aos animais selecionados em ambientes favoráveis. Dessa forma, é possível sugerir que ambientes desafiadores são indicados para avaliação e seleção de reprodutores.

3.0 GENOTYPE X ENVIRONMENT INTERACTION IN INDIVIDUAL PERFORMANCE AND PROGENY TEST IN BEEF CATTLE

ABSTRACT: The study reported here evaluate genotype-environment interaction in individual performance and progeny tests in beef cattle. Genetic parameters for final weight (FW), ADG and scrotal circumference (SC) of 33,013 Nellore young bulls tested on pasture or in feedlot were analyzed. The posterior means (highest posterior density interval with 90% of samples, HPD90) of heritability for traits measured on pasture-raised and feedlot-raised animals were 0.44 (0.40; 0.48) and 0.50 (0.43; 0.56) for FW, 0.26 (0.23; 0.29) and 0.26 (0.20; 0.32) for ADG and 0.53 (0.48; 0.59) and 0.65 (0.55; 0.74) for SC, respectively. The posterior means (HPD90) of genetic correlations for FW, ADG and SC on pasture and in feedlot were 0.75 (0.66; 0.87), 0.49 (0.31; 0.66) and 0.89 (0.83; 0.97), respectively. When the selection intensity was kept the same for both the environments, the greatest direct responses for FW and ADG were exhibited by the animals reared and selected in feedlot. The correlated responses relative to production on pasture and based on selection in feedlot were similar to the direct responses, whereas the correlated responses for production in feedlot and based on selection on pasture were lower than the direct responses. When the selection intensity on pasture was higher than the selection intensity in feedlot, the responses to direct selection were similar for both the environments, and correlated responses obtained in feedlot by selection on pasture were similar to the direct responses in feedlot. Analyses of few or poor indicators of genotype-environment interaction result in incorrect interpretations of its existence and implications. The present work demonstrated that traits with lower heritability are more susceptible to genotype-environment interaction and that selection intensity plays an important role in the study of genotype-environment interaction in beef cattle.

Key words: EPD, feedlot, genetic correlation, heritability, pasture, selection intensity

3.1 INTRODUCTION

The individual performance test is a tool for genetic evaluation of candidates for selection. The test contributes to assessments between herds and allows for the early evaluation of sires and reductions of generation intervals (Razook et al., 1997). In a progeny test, candidates for selection are evaluated based on data from their progeny; compared to the individual performance test, the cost of progeny testing is higher, and the generation interval is longer. Preselection of candidates for progeny testing by means of individual performance testing might increase the efficiency and reduce costs in beef cattle breeding programs (Morris et al., 1980).

Individual performance and progeny tests can be conducted in different environments, such as pasture and feedlots. Analysis of the results of such tests by animal model allows for the data from relatives raised in different environments to improve the accuracy and predict the breeding value of candidates for selection in different environments (Henderson and Quaas, 1976).

Changes in the classification of beef cattle by breeding values of growth traits have been observed through sire x region interaction (Toral et al., 2004; Diaz et al., 2011; Espasandin et al., 2011; Guidolin et al., 2012) or by reaction norm approach (Pégolo et al., 2009 e 2011; Cardoso and Tempelman, 2012; Santana Júnior et al., 2013). Kearney et al. (2004) investigate the existence of genotype-environment interaction for production traits of US Holsteins in pasture versus feedlot herds, but genotype-environment interaction between pasture and feedlots has not yet been evaluated in beef cattle. We estimated genetic parameters for growth and reproductive traits of young bulls raised on pasture or in feedlots and studied the effect of the genotype-environment interaction on the animals' ranking in individual performance and progeny tests.

3.2 MATERIALS AND METHODS

The present study was based on data corresponding to 33,013 Nellore young bulls that were subjected to 751 official Brazilian Zebu Breeders Association performance tests from 2003 to 2012 in the northern states (Acre – AC, Roraima – RO, Pará – PA and Tocantins – TO), northeastern states (Bahia – BA and Maranhão – MA), midwestern states (Goiás – GO,

Mato Grosso – MT and Mato Grosso do Sul – MS), southeastern states (Espírito Santo – ES, Minas Gerais – MG and São Paulo – SP) and southern states (Paraná – PR and Rio Grande do Sul – RS) of Brazil. A total of 24,910 animals participated in 538 tests conducted on pasture in the abovementioned states, except for RS; and 8,103 animals participated in 213 tests conducted in feedlots in the abovementioned states, except for AC, RO, TO, MA and BA. Table A7.1 and A7.2 presents the number of Nellore young bulls evaluated on pasture or in feedlot and number of sires with progeny in both the environments across states.

The tests conducted on pasture lasted 294 days (70 days for adaptation and 224 days for testing). The tests conducted with the animals in feedlots lasted 168 days (56 days for adaptation and 112 days for testing). The animals were weighed at the beginning and end of the adaptation period and at the end of the testing period. The assessed traits included the final weight (FW), ADG and scrotal circumference (SC). The FW was adjusted for 550 days of age in the performance tests on pasture and for 426 days of age in feedlot tests according the duration of each type of test. Individual records for each trait that exceeded the intervals given by the performance test means plus or minus 3.5 standard deviations were excluded, and all animals from performance tests on pasture or in feedlots with fewer than 20 and 8 animals, respectively, were also excluded. The descriptive statistics for growth and reproductive traits are shown in Table 3.1.

Table 3.1. Descriptive statistics for final weigh (FW), ADG and scrotal circumference (SC) of Nellore young bulls in performance tests

	Environment	N	Mean	SD	CV
Initial age, days	Pasture	24,910	329.05	24.39	7.41
	Feedlot	8,103	311.59	26.41	8.48
Initial age ¹ , days	Pasture	14,888	328.72	25.24	7.68
	Feedlot	4,676	308.73	28.01	9.07
FW ² , kg	Pasture	24,910	350.35	53.09	15.15
	Feedlot	8,103	371.65	57.13	15.37
ADG, kg/d	Pasture	24,910	0.54	0.16	29.78
	Feedlot	8,103	0.83	0.26	31.68
SC, cm	Pasture	14,888	26.61	3.38	12.69
	Feedlot	4,676	25.41	3.31	13.03

¹Animals with SC.

²Final weight adjusted to 550 and 426 days of age for animals on pasture and in feedlot, respectively.

The numerator relationship matrix was constructed from pedigree data that consisted of an animal's data and data for some of its ancestors. The ancestors retained in the pedigree

were those that were parents of the animals with data or that were connected to other animals in the pedigree (Toral and Alencar, 2010). The relationship matrix included records of 140,498 animals. Two other relationship matrices that only considered the animals tested on pasture or in feedlots were constructed to study the genetic basis for the relationships and connectability among animals raised on pasture or in feedlots. The number of animals for each relationship matrix is shown in Table 3.2. A total of 3,842 animals were identified in the genetic bases of both the databases, indicating the presence of a genetic association between the investigated environments. This kind of association contributes to the accuracy of the predicted correlations (Weigel et al., 2001).

Table 3.2. Number of observations of the pedigree of Nellore young bulls tested in performance tests

Records	Pasture	Feedlot	Total
Animals with records	24,910	8,103	33,013
Bulls with progeny	2,047	688	2,356
Bulls with own records and progeny in the same environments	143	7	150
Bulls with own records and progeny in different environments	9	4	13
Bulls with own records and progeny in both environments	13	4	17
Cows with offspring	19,101	5,476	24,118
Animals in the pedigree	115,743	43,609	140,498
Animals in the base population	13,688	5,742	15,588

A total of 379 bulls sired progenies tested for FW and ADG on pasture and in feedlots (mean offspring number = 54, minimum = 2, and maximum = 1,020), and 249 bulls had progeny tested for SC (mean offspring number = 45, minimum = 2, and maximum = 494). The 379 bulls sired 20,577 animals (13,624 tested on pasture and 6,933 tested in feedlots). The 249 bulls with progeny tested for SC sired 11,214 animals (7,393 on pasture and 3,821 in feedlots).

Among the 165 bulls that had their own performance measured in pasture, 156 sired young bulls raised on pasture, and nine sired young bulls raised in feedlots. Of the 15 bulls that had their own performance measured in feedlots, 11 sired young bulls that were raised in feedlots, and four sired young bulls raised on pasture. Of the 180 bulls with data regarding their individual performance and tested progenies, 17 had sired young bulls that were tested in both the considered environments.

Samples of the posterior distributions of genetic parameters were obtained by means of Bayesian methods using a Gibbs sampler on single-trait and two-trait analyses. The following general statistical model was used:

$$y_{hijk} = u_h + T_{hj} + b_{h(j)}(A_k - \overline{A_j}) + a_{hi} + e_{hijk},$$

where y_{hijk} represents the observed value of trait h of animal i in test j with final age k ; u_h is the general constant present in all of the observations relative to trait h ; T_{hj} is the effect of test j (j had 538 and 213 levels for pasture and feedlot, respectively) on trait h ; $b_{h(j)}$ is the linear regression coefficient of final age k on trait h , nested in test j ; A_k is the age k ; $\overline{A_j}$ is the mean final age of animals in test j ; a_{hi} is the breeding value of animal i relative to trait h ; and e_{hijk} is the residual associated with each observation.

In matrix notation, the general model used in single-trait analysis is as follows:

$$y = X\beta + Za + e,$$

where y represents the vector of observations; X is the incidence matrix of fixed effects (performance test and final age as a covariate nested within each test); β is the vector of solutions of fixed effects; Z is the incidence matrix of random effects; a is the vector of solutions for each animal's breeding value; and e is the vector of the residual associated with each observation. Two databases were used for the single-trait analysis: one corresponded to the animals tested on pasture, and the other corresponded to the animals tested in feedlots.

For inferences on the distributions of the parameters of interest, flat distributions were assumed for fixed effects (β), normal distributions were assumed for random effects ($a | A\sigma_a^2$ and $e | I\sigma_e^2$), and scaled inverted chi-squared distributions (χ^{-2}) were assumed for variances ($\sigma_a^2 | \nu_a, S_a^2$ and $\sigma_e^2 | \nu_e, S_e^2$), where A represents the matrix of relationships between animals; σ_a^2 represents the additive genetic variance; I represents the identity matrix; σ_e^2 represents the residual variance; ν_a and S_a^2 represent the hyper-parameters of the χ^{-2} distribution of the additive genetic variance; and ν_e and S_e^2 represent the hyper-parameters of the χ^{-2} distribution of residual variance. Information on the complete conditional posterior distributions is available from Sorensen (1996).

In matrix notation, the following general model was used in two-trait analyses:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & \Phi \\ \Phi & X_2 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} + \begin{bmatrix} Z_1 & \Phi \\ \Phi & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix},$$

where the terms are the same as those described above except the analyzed traits are distinguished by indices 1 and 2 as follows: the FW in the tests conducted on pasture were defined as trait 1, and the FW in the tests conducted in feedlots were defined as trait 2. The same distinction applies to the ADG and SC. Samples of the posterior distributions of the genetic correlations were used to determine the genotype-environment interaction according to Falconer (1952).

Flat prior distributions were assumed for the fixed effects $\left(\begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} \right)$, and normal distributions were assumed for the random effects $\left(\begin{bmatrix} a_1 \\ a_2 \end{bmatrix} \middle| G \text{ and } \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \middle| R \right)$, whereas an inverted Wishart distribution was assumed for (co)variance matrices $(G_0 | \nu_a, S_a \text{ and } R | \nu_e, S_e)$, where $G = G_0 \otimes A$ represents the genetic (co)variance matrix; $G_0 = \begin{bmatrix} \sigma_{a_1}^2 & \sigma_{a_1 a_2} \\ \sigma_{a_2 a_1} & \sigma_{a_2}^2 \end{bmatrix}$ represents the matrix of genetic (co)variance between traits 1 and 2; $\sigma_{a_h}^2$ represents the additive genetic variance of trait h ; $\sigma_{a_1 a_2}$ represents the additive genetic covariance between traits 1 and 2; $R = R_0 \otimes I$ represents the residual variance matrix; $R_0 = \begin{bmatrix} \sigma_{e_1}^2 & 0 \\ 0 & \sigma_{e_2}^2 \end{bmatrix}$ represents the matrix of residual variance of traits 1 and 2; $\sigma_{e_h}^2$ represents the residual variance of trait h ; ν_a and ν_e (degrees of freedom of the inverted Wishart distributions) and S_a and S_e (2×2 matrices with the prior “guess” for the variance components) represent the hyper-parameters of the inverted Wishart distributions of genetic and residual (co)variances; and the other terms are the same as those described above. The complete conditional posterior distributions are available from Sorensen and Gianola (2002).

Gibbs chains of 410,000 iterations were generated for each parameter, with a burn-in period of 10,000 iterations and a sampling interval of 200 iterations in GIBBS1F90 program (Misztal et al., 2002). Convergence diagnostics were performed following Geweke’s (1992) and Heidelberger and Welch’s (1983) techniques, and visual analysis of trace plots was performed using the Bayesian Output Analysis (BOA, Smith, 2005) program in R software 2.9.0 (R Development Core Team, 2009). The Geweke test (Geweke, 1992) compares the

means from the early and late parts of the Markov chain to detect failure of convergence in such a way that the null hypothesis tested confirms convergence because probabilities of less than 0.05 provide evidence against convergence of the chain. In the Heidelberger and Welch (1983) diagnostic test, the null hypothesis is that sample values come from a stationary process. If there is evidence of nonstationarity, the test is repeated after discarding the first 10% of the iterations. This process continues until 50% of the iterations have been discarded or until the chain analyzed passes the test. The Heidelberger and Welch (1983) test uses the Cremer-von-Mises statistic. Visual inspection consists of the observation of the plots generated, and convergence of the chains is evaluated by the tendency and areas of density of distribution of the chains.

Samples of the posterior distributions of the direct and indirect responses to selection were obtained with the samples of the (co)variance components, and selection of 5% of the males with phenotypic data (selection intensity = 2.06) was initially considered. Because only the selection of males was considered, the average selection intensity used in the calculations of responses was 1.03. Based on the number of animals that were tested on pasture, there was a need to select 1,246 young bulls. If these animals were selected from the group tested in feedlots, the percentage of selected animals would be 15%, and the mean selection intensity would be 0.78. Those values were used to simulate conditions with different selection intensities as a function of the environment. The responses to direct selection per generation were calculated using the following equation:

$$\Delta G_h = i_h h_h^2 \sigma_{P_h},$$

Where ΔG_h represents the expected genetic gain per generation; i_h represents the selection intensity; h_h^2 represents the heritability; and σ_{P_h} represents the phenotypic standard deviation corresponding to trait h .

The correlated responses per generation were calculated using the following equation:

$$\Delta G_{YX} = r_{a_Y a_X} h_Y h_X i_X \sigma_{P_Y},$$

where ΔG_{YX} represents the expected correlated response per generation relative to a given trait in environment Y by selecting for the same trait in environment X ; $r_{a_Y a_X}$ represents the genetic correlation of a trait measured in environment X and environment Y obtained in two trait analysis; h_Y represents the square root of the heritability for trait in environment Y ; h_X represents the square root of the heritability for trait in environment X ; i_X represents the

selection intensity in environment X ; and σ_{P_Y} represents the phenotypic standard deviation in environment Y .

Mean EPD of bulls with genetic evaluation on pasture and feedlot ($n = 2,356$ for FW and ADG; and $n = 1,567$ for SC) ranked as TOP15%, TOP10% and TOP5% for each trait on pasture or in feedlot were calculated. Pearson's and Spearman's correlations were estimated among EPD for each trait of bulls with progeny on pasture and in feedlot ($n = 379$ for FW and ADG; and $n = 249$ for SC) and bulls with larger number of progenies in both environment. In this case, the FW and ADG EPD were evaluated for 38 bulls (average offspring number = 306, minimum = 123, and maximum = 1,020), and SC EPD were evaluated for 25 bulls (average offspring number = 226, minimum = 109, and maximum = 494).

3.3 RESULTS AND DISCUSSION

Table 3.3 describes the posterior means and highest posterior density intervals with 90% of samples (HPD90) of the genetic parameters corresponding to the assessed traits in single-trait analysis. The additive genetic and residual variances for FW and ADG were higher in the animals raised in feedlots when compared to the animals raised on pasture in single-trait (Table 3.3) and two-trait (Figures 3.1 and 3.2) analyses. However, heritability for FW and ADG were similar on pasture and in feedlots.

Table 3.3. Posterior means (highest posterior density interval with 90% of samples) of the parameters for final weight (FW), ADG and scrotal circumference (SC) of Nellore young bulls tested in performance tests on pasture or in feedlot according to single-trait analyses

Parameters ¹	FW	ADG	SC
Pasture			
σ_a^2	408.51 (368.70; 549.40)	0.019 (0.016; 0.021)	3.42 (3.00; 3.82)
σ_e^2	519.79 (490.50; 550.80)	0.053 (0.051; 0.055)	2.98 (2.69; 3.30)
h^2	0.44 (0.40; 0.48)	0.26 (0.23; 0.29)	0.53 (0.48; 0.59)
Feedlot			
σ_a^2	716.10 (597.30; 827.50)	0.063 (0.047; 0.078)	4.43 (3.60; 5.25)
σ_e^2	707.92 (620.50; 784.00)	0.181 (0.169; 0.193)	2.36 (1.83; 2.97)
h^2	0.50 (0.43; 0.56)	0.26 (0.20; 0.32)	0.65 (0.55; 0.74)

¹ σ_a^2 = additive genetic variance, σ_e^2 = residual variance, and h^2 = heritability.

The posterior means for FW (ADG) heritability were lower than the values of 0.73 (0.31) and 0.60 (0.55) estimated by Fragomeni et al. (2013) and Marques et al. (2013) for Nellore young bulls raised on pasture or in feedlots, respectively. Nevertheless, the magnitude of those values is considered to be high and indicates that those traits may be used as selection criteria and that phenotypic selection in individual performance tests might permit genetic progress.

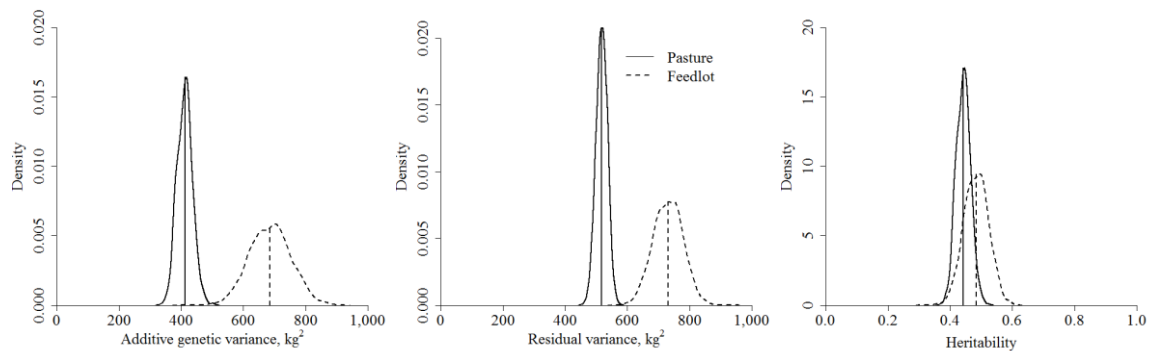


Figure 3.1. Posterior densities and means (vertical line) of the genetic parameters for the final weight of Nellore young bulls tested in performance tests on pasture or in feedlots in a two-trait analysis.

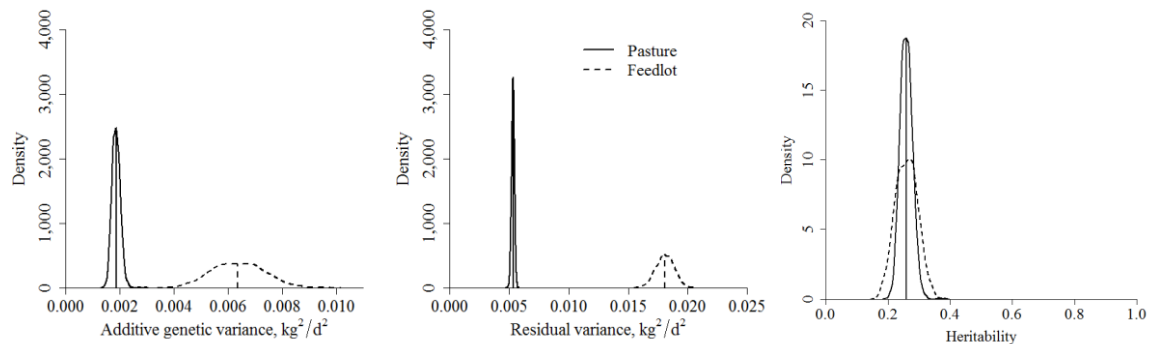


Figure 3.2. Posterior densities and means (vertical line) of the genetic parameters for the ADG of Nellore young bulls tested in performance tests on pasture or in feedlots in a two-trait analysis.

The mean and standard deviation of FW were similar in both the studied environments, but the means of ADG differed between the environments (Table 3.1). The pasture in which the animals were raised limited the expression of genetic differences for growth of the candidates for selection because the genetic variances for FW and ADG were greater among the animals raised in feedlots (Table 3.3). The results of this experiment

corroborate those obtained by Hammond (1947) and Kearney et al. (2004), indicating that selection would be more efficient in the environment that allows the maximum expression of genetic differences. The relationship between the additive genetic and phenotypic variances (heritability) was similar in both the environments, albeit for different reasons. The greater genetic variance for FW and ADG of animals raised in feedlots indicates that expression of the genetic differences for these traits were more intense in feedlots; however, the differences in the number of animals and means of the traits did not contribute to a reduction of the residual variance.

The posterior means of variances and heritability for SC were similar in animals raised on pasture or in feedlots, and the HPD90 overlapped in single-trait (Table 3.3) and two-trait (Figure 3.3) analyses.

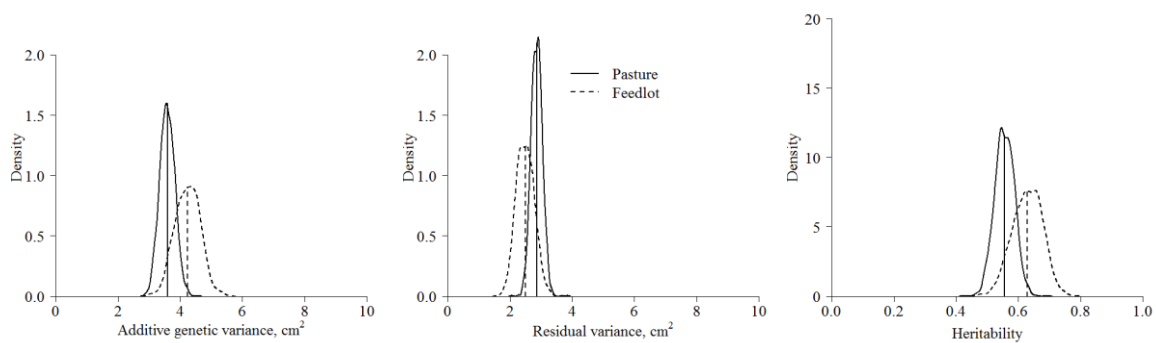


Figure 3.3. Posterior densities and means (vertical line) of the genetic parameters for the scrotal circumference of Nellore young bulls tested in performance tests on pasture or in feedlots in a two-trait analysis.

The means of heritability for SC were similar to the value of 0.60 reported by Marques et al. (2013) and higher than the values of 0.42 estimated by Boligon et al. (2010) and 0.43 estimated by Yokoo et al. (2010) for Nellore cattle at 18 months of age. The results of the present study show that differences in age (550 vs. 426 d) combined with differences in the feeding system (pasture vs. feedlot) did not induce significant changes in the SC variances and heritability. Loaiza-Echeverri et al. (2013) also did not find effect of age (550 vs. 450 d) on the posterior means of the SC variances and heritability in Guzarat yearling bulls raised on pasture. The heritability \pm SE reported by Yokoo et al. (2010) for SC in Nellore young bulls at 450 and 550 d of age were 0.51 ± 0.05 and 0.43 ± 0.09 . Although Yokoo et al. (2010) assumed

significant differences in the heritability estimates, the SE presented might suggest that this age interval (450 to 550 d) exerted little or no effect on heritability. In the present study, although the animals were assessed at different ages and under different feeding systems, the mean, standard deviation and coefficient of variation relative to SC were similar in both groups of animals (Table 3.1), which accounted for the similarity in the variance and heritability estimates.

The means of posterior distributions for genetic correlation (HPD90) corresponding to each trait assessed on pasture and in feedlot were 0.75 (0.66; 0.87) for FW; 0.49 (0.31; 0.66) for ADG; and 0.89 (0.83; 0.97) for SC. The presence of genotype-environment interactions in these traits (particularly ADG) was established based on the genetic and residual variance differences for both the environments and on the genetic correlation estimates of each trait assessed in different environments with values less than 1.0, as proposed by Falconer (1952), or less than 0.8, as recommended by Robertson (1959). James (1961) and Mulder et al. (2006) studied genetic gain in two environments comparing different breeding strategies, including one or two environments in the breeding goal, splitting up the population of test bulls by testing part of the bulls in environment 1 and another part in environment 2 and progeny testing bulls in one or two environments. James (1961) considered the same selection intensity in both environment and Mulder et al. (2006) considered the same truncation point for selection in both environments. Thereby, when the genetic correlation was lower than 0.70 and 0.61 for James (1961) and Mulder et al. (2006), respectively, it was optimal to have two environment-specific breeding programs of progeny testing an equal number of bulls in their own environment only. If we just look at the variances and genetic correlations among ADG in different environments, we would recommend a breeding program for pasture and another breeding program for feedlot animals. James (1961), Mulder et al. (2006) and Diaz et al. (2011) made similar recommendations. However, the possibility of having differences in the selection intensity for each environment highlight another point of view for this recommendation and it will be discussing latter in this paper.

In the present study, the trait with lower heritability (ADG) was more susceptible to the effects of genotype-environment interaction than the trait with greater heritability (SC). Genotype-environment interaction was significant for body weight change ($h^2 = 0.07$) and body condition score ($h^2 = 0.08$) but it was not important for milk production ($h^2 = 0.32$) in upgraded Holstein-Friesian dairy cows (Berry et al., 2003). Sire x contemporary group interaction was significant for body weight ($h^2 = 0.39$), fat depth ($h^2 = 0.26$), loin muscle depth ($h^2 = 0.23$) and other traits with $h^2 < 0.5$ in Merino sheep but this interaction was not

significant for staple length ($h^2 = 0.61$) and fiber curvature ($h^2 = 0.51$) (Pollott and Greeff, 2004). The genetic correlation among weaning weight ($h^2 = 0.41$ to 0.44) of Canchim cattle (approximately $5/8$ Charolais + $3/8$ Zebu) born in two seasons (rainy or dry season) was 0.80 and among ADG from weaning to yearling ($h^2 = 0.14$) of calves born in two seasons was 0.65 (Mascioli et al., 2006). Genotype-environment interaction was significant for shape traits (h^2 from 0.08 to 0.14) but it was minor for harvest weight ($h^2 = 0.55$) and for growth ($h^2 = 0.47$) of Nile tilapia (*Oreochromis niloticus*, Trong et al., 2013). Annual average productivity of the cow ($h^2 = 0.14$) and post-weaning weight gain ($h^2 = 0.27$) were more affected by genotype-environment interaction than SC ($h^2 = 0.54$) in Nellore cattle (Santana Júnior et al., 2014). Genotype-environment interaction is a function of differences in genotypes and environments, but a joint and detailed analysis of the results presented in this paper and others from the literature confirm our hypothesis that traits with lower heritability are more susceptible to the effects of genotype-environment interaction.

The genotype-environment interaction was found by Diaz et al. (2011) to be relative to the yearling weight of Nellore cattle raised in different Brazilian states (GO, MT, MS, MG and SP). Those authors found genetic correlation for the same trait in different states lower than 0.80 and changes in the posterior distributions of the genetic and residual variances and heritability estimates among the various states and in the breeding values when the proportion of selected animals was 1%, 5% and 10%. Therefore, the authors recommended two groups of states for genetic evaluation: the first included the states of Minas Gerais (MG) and Mato Grosso (MT), and the second included the states of Goiás (GO), São Paulo (SP) and Mato Grosso do Sul (MS). Changes in animal management (nutritional and sanitary practices) may be disregarded when the classification of environments relative to the assessment of the genotype-environment interaction is exclusively based on the geographical or climatic characteristics of a given area (Weigel et al., 2001). The use of nutritional management to categorize environments might provide an efficient alternative to study the genotype-environment interaction. No studies were found in the literature that assessed genotype-environment interaction in beef cattle reared on pasture or in feedlots. A joint data analysis for animals raised in different environments and their relatives raised in both the environments determined the impact of the genotype-environment interaction on the variances of growth traits of young bulls based on the individual performance test; the analysis also produced EPD estimates for different environments. This joint analysis can enable the selection of genetically superior animals in each environment or animals that exhibit satisfactory genetic values for the different environments.

Figure 3.4 shows the expected responses to selection for FW, ADG and SC on pasture or in feedlots. Assuming the same selection intensity for both the environments, the greatest expected direct responses corresponded to FW and ADG in the animals raised in feedlots. The expected genetic gains for SC were similar in both the environments. Upon assessing the weight at 550 days of age (W550), ADG and SC of Nellore cattle from farms participating in the Brazilian Nellore Breeding Program, Araujo Neto et al. (2011) found genetic gains of 11.90 kg/generation, 0.043 kg/d/generation and 0.56 cm/generation, respectively. The genetic gains for W550 and SC reported by those authors were lower than the estimates found in the present study, whereas the genetic gain for ADG was higher. Those discrepancies might have been caused by differences in the heritability, selection intensity as evidenced by Mulder and Bijma (2005) and changes in the number of founders and selection objectives among the samples of Araujo Neto et al. (2011) and the present datasets. However, the responses to selection found by Araujo Neto et al. (2011) and the expected values according to the results of the present study indicate the possibility of increase the means of these traits through selection.

The results (Figure 3.4) indicate that similar genetic gains for SC might be achieved on pasture by selecting for improvement this trait in feedlots when selection intensity is both the environment is the same. When selection intensity applied to animals tested in feedlots was lower than the intensity applied to animals tested on pasture (0.78 vs. 1.03), direct selection based on the performance on pasture was more efficient for the three traits evaluated (Figure 3.4).

The most efficient approach for increasing FW and ADG in animals in feedlots is direct selection in that same environment, provided that the selection intensity is the same in both the environments. However, when the selection intensity for animals tested on pasture was greater than selection intensity for animals in feedlots (1.03 vs. 0.78, respectively), the responses to indirect selection (selection based on the performance on pasture) were similar to the responses to direct selection (selection based on the performance in feedlots).

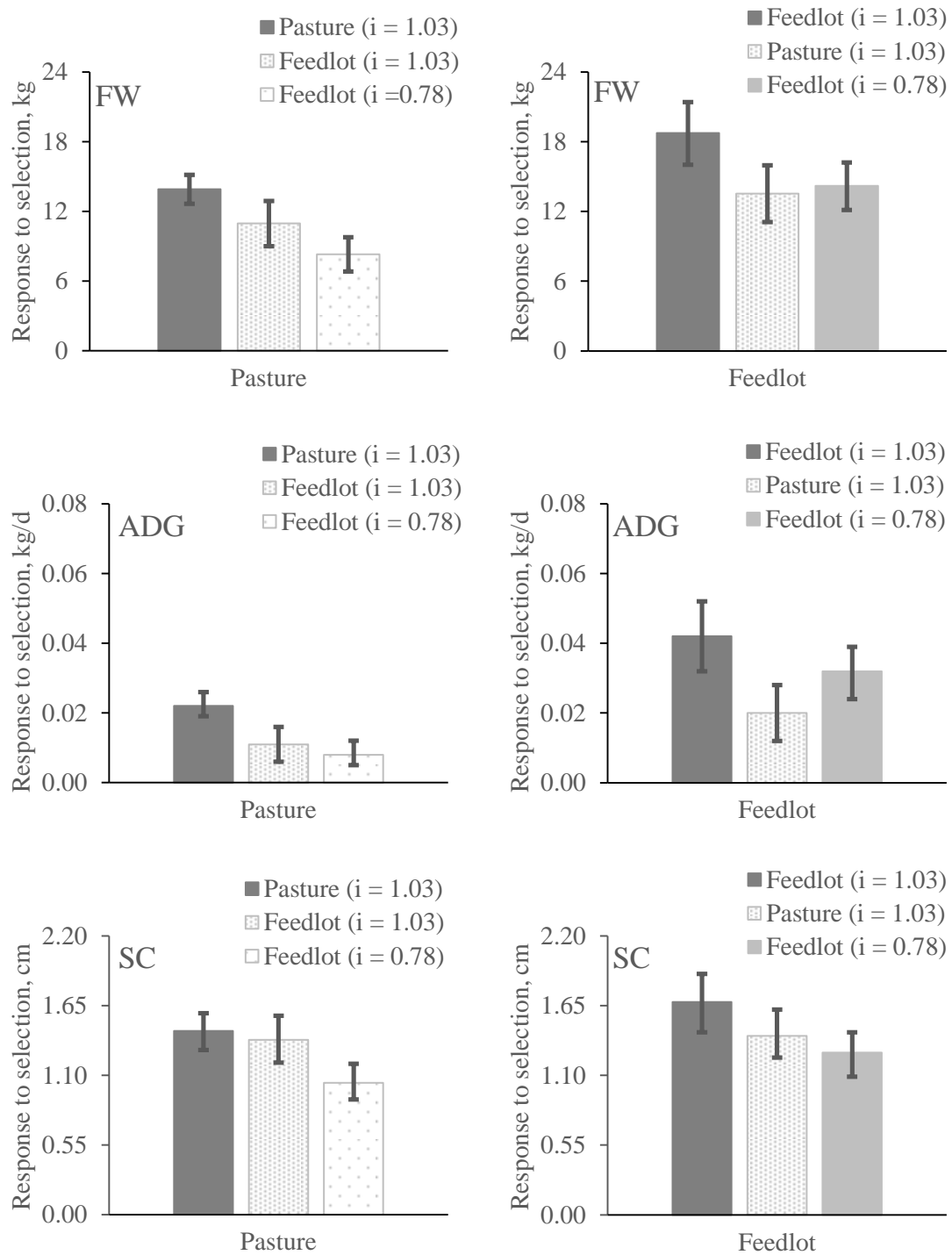


Figure 3.4. Posterior means (and highest posterior interval with 90% of samples) of the responses to direct (solid bars) or indirect (dashed bars) selection per generation for final weight (FW), ADG and scrotal circumference (SC) of Nellore young bulls on pasture (left) and in feedlot (right), according to environment and selection intensity (i).

The results show that differences in selection intensity should also be considered when studying genotype-environment interactions. The cost of assessing candidates for selection in feedlots is higher compared to the tests conducted on pasture. Therefore, the number of animals assessed in feedlots is lower than the number of animals tested on pasture; whenever a predetermined number of sires must be selected, there will be differences in the selection intensity. If the difference in selection intensity is close to the intensity applied in the present study, the selection of animals based on the performance in pasture is as efficient as direct selection under feedlot conditions of progenies raised in feedlots and more efficient than selection based on performance in feedlots of progenies raised on pasture.

The Pearson's (Spearman's) correlation among EPD of Nellore bulls (with progenies on pasture and in feedlot) from single-trait analysis were 0.34 (0.34) for FW; 0.18 (0.19) for ADG; and 0.65 (0.53) for SC. Relative to the EPD from two-trait analysis, the same correlations were 0.81 (0.79) for FW, 0.45 (0.43) for ADG and 0.96 (0.96) for SC. The Pearson's and Spearman's correlations were expected to be higher with EPD from two-trait analysis than the same correlations with EPD from single-trait analysis because the two-trait analysis includes the genetic correlations between traits and data collected in both the environments that contribute to the prediction of genetic values for both the environments. Even the results of the two-trait analysis could determine changes in the sire ranking as a function of the environment in which their progenies were raised, particularly for FW and ADG (Figure 3.5). These findings indicate that sires with highest EPD for a given trait assessed in progenies raised on pasture are no longer superior when that same trait is assessed in their progenies raised in feedlots.

The results of the present study corroborate the findings of Mattar et al. (2011), who investigated the effect of genotype-environment interaction for the W550 of Canchim cattle, and of Santana Júnior et al. (2013), who assessed weaning weight, post-weaning weight and yearling scrotal circumference in the Montana Tropical Composite Breeding Program. Those authors recommended including genotype-environment interactions in models for genetic evaluations to identify the most appropriate sires for each production system.

The genotype-environment interaction also led to changes in the ranking of the bulls with the largest number of progenies (Figure 3.5). The bulls that bred more often and with greater accuracy in EPD also exhibited different EPD as a function of the environment. Figure 3.5 further reveals a preference for using bulls with higher EPD for FW at the expense of ADG and SC. When FW is the most significant selection criterion for ranking animals, differences in their initial weight might be decisive for final ranking of animals because the

length of the period of adaptation might not be sufficient to reset significant differences in animals' weight at the beginning of the performance test.

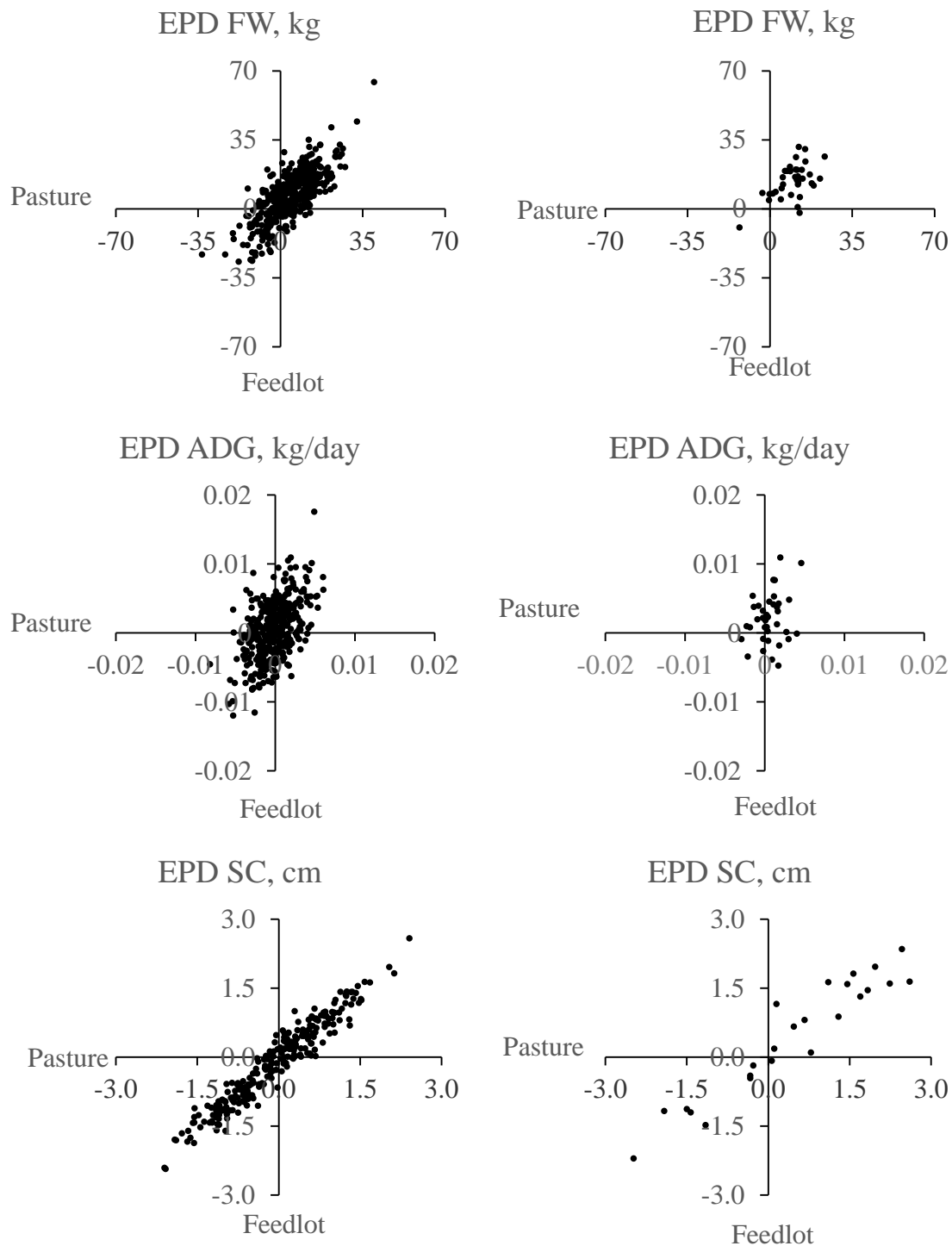


Figure 3.5. Distribution of EPD for final weight (FW), ADG and scrotal circumference (SC) on pasture and in feedlot of Nellore sires with progenies in both the environments (left, FW and ADG, $N = 379$; SC, $N = 249$) and with greater number of progenies in both the environments (right, FW and ADG, $N = 38$; SC, $N = 25$) in two-trait analysis.

Based on two-trait genetic analysis and the sample of bulls with progeny on pasture ($n = 2,047$ for FW and ADG, and $n = 1,347$ for SC), 307, 205 and 102 animals with the highest EPD for FW and ADG were ranked as TOP15%, TOP10% and TOP5%, respectively; and 203, 135 and 67 animals with the highest EPD for SC were ranked as TOP15%, TOP10% and TOP5%, respectively. For bulls with progeny that were tested in feedlots ($n = 688$ for FW and ADG, and $n = 469$ for SC), 103, 69 and 34 bulls with the highest EPD for FW and ADG were ranked as TOP15%, TOP10% and TOP5%, respectively; and 70, 47, and 23 animals with highest EPD for SC were ranked as TOP15%, TOP10% and TOP5%, respectively.

Among the bulls considered to be superior for FW (ADG) [SC] in the performance test on pasture, 34 (25) [29] were also included in groups TOP15%, 19 (16) [20] in groups TOP10%, and 11 (7) [8] in TOP5%, respectively, which corresponded to their performance in feedlots. Therefore, 33% (25%) [41%] in group TOP15%, 28% (23%) [43%] for TOP10%, and 33% (21%) [35%] for TOP5%, of the best animals for FW (ADG) [SC] tested in feedlots were identified based on the results of their progenies tested on pasture.

Approximately 11% (8%) [14%], 9% (8%) [15%] and 11% (7%) [12%] of animals considered to be superior for FW (ADG) [SC], respectively, in the performance tests in feedlot were also included in the groups TOP15%, TOP10% and TOP5%, respectively, which corresponded to their performance on pasture.

The absolute number or percentage of bulls selected for both the environments is an indicator of practical implications of genotype-environment interactions (Mulder and Bijma, 2006; Mattar et al., 2011; Santana Júnior et al., 2013). In addition, differences in selected animals will only induce changes in responses to selection when their EPD are also different (Toral and Alencar, 2010). The mean EPD for FW, ADG and SC of bulls ranked as TOP15%, TOP10% and TOP5% on pasture and in feedlot are show in Figure 3.6.

Despite the differences in ranking of top bulls for FW, ADG and SC on pasture and in feedlots, a comparison of the mean EPD corresponding to both of the environments did not indicate significant differences as a function of the overlapping of the HPD90 when the percentage of selected sires was the same. This finding suggests that under such conditions, the selection of the top bulls based on EPD for those traits in one environment induces similar results in the other environment. In beef cattle breeding programs, the development of breeding goals with different weights for pasture and feedlot EPD, according to the frequency of each production system (Harris et al., 1984; Mulder et al., 2006), may be a suitable

alternative because the feeding regimen of weaned calves may not be defined when the producers choose the bulls for breeding their cows.

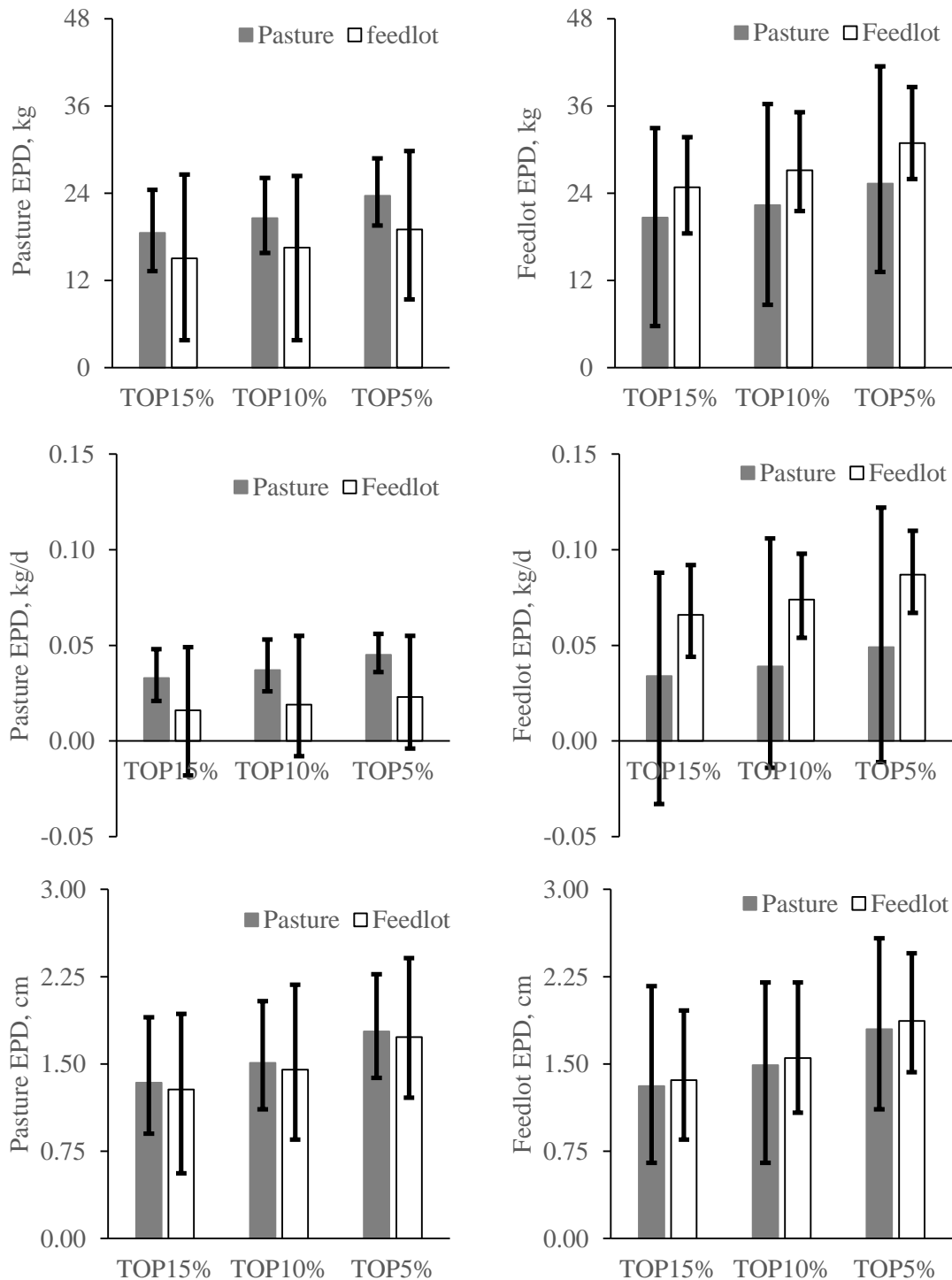


Figure 3.6. Posterior means (and highest posterior density interval with 90% of EPD) of the EPD for final weight (FW), ADG and scrotal circumference (SC) on pasture (left) or in feedlot (right) of the TOP15%, TOP10% and TOP5% Nellore bulls selected based on EPD on pasture or in feedlot in two-trait analysis.

The genetic evaluation on pasture could determine approximately 30% of the top bulls for production in feedlots, but the mean EPD corresponding to production in feedlots of animals ranked superior for production on pasture were the same (when the selection intensities were the same in both the environments) or superior (when the selection intensity of the animals tested on pasture was greater) compared to mean EPD corresponding to production in feedlots of the animals ranked superior for production in feedlots.

The pasture EPD for FW and ADG of bulls ranked superior for production in feedlots are not greater than the EPD of those same traits corresponding to the best sires identified based on the data of progenies raised on pasture. According to Mascioli (2000), the selection of animals in favorable environments (feedlots) does not produce the same responses to selection in restricted environments (pasture). Mascioli (2000) conducted progeny tests on pasture and in feedlots with Canchim young bulls ranked superior ($n = 7$), intermediate ($n = 6$) and inferior ($n = 6$) for FW on a performance test in feedlot (~ 400 days old) and did not find significant effects of the young bulls' rank on the weight of the progenies at weaning, 12 and 18 months of age or on their ADG from age 12 to 18 months.

The results of the present study show that selection of bulls on pasture is efficient in identifying superior bulls for production in more favorable environments. The results further show that selection in favorable environments under lower selection intensity is not more efficient than direct selection in a more restricted environment (Figure 4, ΔG_{PF} and $i = 0.78$ vs. ΔG_p and $i = 1.03$).

An isolated analysis of some of the indicators of genotype-environment interaction can lead to misguided interpretations of the existence and implications of such interaction. By considering only the variance estimates and genetic correlations, the behavior of the investigated traits changed according to the type of environment. This result was corroborated by the analysis of the animals ranked as superior for production on pasture or in feedlots. However, an analysis of the direct and indirect responses to selection and EPD corresponding to the animals ranked superior for production of progeny in both of the environments indicated possible small, practical effects of genotype-environment interaction, especially when selection intensity differed between the investigated environments.

The genotype-environment interaction induced changes in variances for growth traits but did not change genetic parameters corresponding to SC. Traits with lower heritability are more susceptible to the effects of genotype-environment interaction.

Selection intensity is an important parameter to consider when studying genotype-environment interaction, and it influences the efficiency of direct (in the same environment in which a progeny was raised) and indirect (candidates and progenies are raised in different environments) selection. When there are no differences in selection intensity applied to candidates for selection, feedlot production is the most efficient environment for achieving responses under the feedlot condition, and the magnitude of the indirect responses is the same as that for direct responses to selection performed on pasture considering progenies also raised on pasture.

Indirect responses similar to direct responses achieved by production in a feedlot may be achieved when the selection intensity applied to the candidates for selection assessed on pasture is greater than the intensity applied to the candidates assessed in the feedlot.

4.0 SELECTION OF YOUNG BULLS IN PERFORMANCE TESTS AND INDIRECT RESPONSES IN COMMERCIAL BEEF CATTLE HERDS ON PASTURE AND FEEDLOT

ABSTRACT: Central testing is a tool for the selection of young bulls which are likely to contribute to increased commercial herd net income. We present genetic parameters for growth and reproductive traits in performance-tested young bulls and commercial animals on pasture and feedlots. Records of young bulls and heifers in performance tests or commercial herds were used. Genetic parameters for growth and reproductive traits were estimated by multiple-trait animal models. Correlated responses in commercial animals when selection was applied in performance-tested young bulls were computed. Heritabilities for final weight, average daily gain and scrotal circumference were 0.45, 0.26 and 0.52 for performance-tested young bulls on pasture, 0.52, 0.26 and 0.63 for performance-tested young bulls in feedlots, 0.31, 0.16 and 0.40 for commercial animals on pasture, and 0.33, 0.19 and 0.46 for commercial animals in feedlots, respectively. Heritability for age at first calving in commercial herds on pasture was 0.18. The genetic correlations between traits in performance-tested and commercial herds were positive, except for pairs that included age at first calving. Age at first calving was genetically related to average daily gain (-0.26) and scrotal circumference (-0.23) in performance-tested young bulls on pasture, however it was not related to these traits in performance-tested young bulls in feedlots (-0.06 and -0.11). Heritabilities for growth and scrotal circumference are greater in performance-tested young bulls than in commercial animals. The evaluation and selection for increased growth and scrotal circumference of young bulls in performance tests is efficient to improve growth, scrotal circumference and age at first calving in commercial animals. The evaluation and selection of young bulls in performance tests on pasture is more efficient than evaluation and selection of young bulls in performance tests in feedlots.

Key words: genetic evaluation, genotype x environment interaction, Nellore, selection

4.1 INTRODUCTION

Central testing of beef cattle has been used quite widely worldwide since the 1950s, especially in the United States and Canada (Cain and Wilson, 1983), Europe (Simm, 2000) and Brazil (Tundisi et al., 1965). The aim of testing is to identify young bulls as parents of the next generation which are likely to contribute to increased commercial herd net income. The young bulls should be exposed to uniform housing, feeding, management and data recording for further establishing the genetic merit of each animal. Measurements of growth, carcass, feed efficiency and scrotal circumference are taken during the test or at the end-of-test (Crowley et al., 2011a; Crowley et al., 2011b; Neves et al., 2014, Grion et al., 2014 e Raidan et al., 2015). Performance tests can be conducted on pasture or in feedlots. The feeding costs for testing young bulls on pasture is smaller than the feeding costs for testing young bulls in feedlots. However, pasture performance tests take longer than feedlots tests (Schenkel et al., 2002; Riley et al., 2007; Baldi et al., 2012; Fragomeni et al., 2013 and Neves et al., 2014).

After individual testing, the outstanding young bulls can be progeny-tested or sold to cow-calf producers. Therefore, the impact of selection for improved economic traits in performance-tested young bulls on growth and reproductive traits in young bulls and heifers in commercial herds is of particular importance. The genetic correlations (\pm standard error) between growth traits in performance-tested young bulls in feedlots with postweaning weight (12 to 36 months of age) and age at first calving in commercial animals are 0.33 ± 0.15 and 0.21 ± 0.15 for average daily gain, and 0.56 ± 0.14 and -0.18 ± 0.13 for midtest body weight (Crowley et al., 2011a and 2011b). The genetic correlations between growth in performance tests with growth in commercial herds are moderate but the genetic correlations between growth in performance tests with age at first calving in commercial herds are inconclusive because they are associated with large standard errors. Moreover, genetic correlations between growth and scrotal circumference in performance tests and between growth and age at first calving in commercial conditions in different feeding regimens (pasture and feedlot) are unknown. The knowledge of these correlations will permit to estimate the efficiency of selection in performance tests for the improvement of economic traits in commercial herds, as well as to define the best environment for performance testing of young bulls. Thereby, the aim of this study was to estimate genetic parameters for growth and reproductive traits in performance-tested young bulls and commercial young bulls and heifers on pasture and feedlot. In addition, we analyzed the impact of selection for growth and scrotal circumference

in performance-tested young bulls on growth and reproductive traits in young bulls and heifers in commercial herds, both on pasture and feedlots.

4.2 MATERIALS AND METHODS

4.2.1 Data

Ethics committee approval was not obtained for this study because the data were obtained from an existing database. We used growth traits and scrotal circumferences (SC) of Nellore young bulls in official performance tests on pasture and feedlot and growth and reproductive traits (SC and age at first calving, AFC) in young bulls and heifers in a joint official performance recording scheme. The performance records and pedigree information were provided by Associação Brasileira de Criadores de Zebu (ABCZ).

The performance of 33,013 animals was evaluated in 751 performance tests carried out from 2003 to 2012 in the North (Acre, Rondônia, Pará, and Tocantins), Northeast (Bahia and Maranhão), Central West (Goiás, Mato Grosso and Mato Grosso do Sul), Southeast (Espírito Santo, Minas Gerais and São Paulo) and South (Paraná and Rio Grande do Sul) regions of Brazil. A total of 24,910 animals from 538 tests conducted on pasture and 8,103 animals from 213 tests conducted in feedlots were used. The pasture tests were 294 days long (70 days for adaptation and 224 days for testing). The feedlot tests were 168 days long (56 days for adaptation and 112 days for testing). The animals were weighed at beginning and end of the adaptation period and at end of the testing period. The assessed traits included final weight (FW), average daily gain (ADG) and SC. The ADG was calculated as the difference between body weight at end of the testing period (W_{EndT}) and body weight at the end of adaptation period (W_{EndA}), divided by difference between age at the end of testing period and age at the end of adaptation period (A_{EndA}). The FW was calculated by the equations $FW = W_{EndA} + [ADG \times (550 - A_{EndA})]$ and $FW = W_{EndA} + [ADG \times (426 - A_{EndA})]$ for performance-tested young bulls on pasture and in feedlots, respectively. The 550 and 426 are the official standard final age (in days) according to ABCZ. Individual records for each trait that exceeded the intervals given by the performance test means plus or less 3.5 standard deviations were excluded, and all animals from performance tests on pasture and in feedlots with less than 20 and 8 animals, respectively, were also excluded.

The performance records of young bulls and heifers were from the official performance recording scheme of ABCZ for commercial purebred herds in Central West (Goiás, Mato Grosso and Mato Grosso do Sul) and Southeast (Minas Gerais and São Paulo) regions of Brazil. The records were collected from 2005 to 2010. The animals were weighed at weaning (from 145 to 265 days of age, mean age of 205 days) and at yearling (from 490 to 610 days of age, mean age of 550 days). The assessed traits included FW and ADG of young bulls and heifers, SC of young bulls, both on pasture and feedlot, and AFC of heifers on pasture. The ADG was calculated as the difference between body weight at yearling (YW) and body weight at weaning (WW), divided by difference between age at yearling and age at weaning (AW). The FW was calculated by the equation: $FW = WW + [ADG \times (550 - AW)]$. Individual records for each trait that exceeded the intervals given by contemporary group means plus or less 4 standard deviations were excluded, and all animals from contemporary groups with less than 10 animals were also excluded. The contemporary groups considered animals from the same herd, year and month of birth, sex, and feeding regimen at weaning and yearling (pasture with or without mineral supplementation, or feedlot). The levels of energy and/or protein supplementation were not available in the data set, and the feeding regimen at yearling of animals fed with any type of energy and/or protein supplementation was considered as a feedlot. A total of 84,565 animals (from 4,148 contemporary groups on pasture) and 4,468 animals (from 266 contemporary groups in feedlots) were used in this work. The AFC records were from heifers with growth records (FW and ADG) in the dataset. Those heifers were from 540 contemporary groups on pasture. The heifers with AFC records represented 17.7% of heifers with growth records. The summary statistics of the data are shown in Table 4.1. The distributions of animals and sires across regions are presented in Table 4.2.

The numerator relationship matrix considered pedigree data of 122,046 animals with records and connected animals, resulting in 377,217 animals. The environmental connectedness through the utilization of common sires is shown in Figure 4.1.

Table 4.1. Summary statistics^a for growth and reproductive traits in performance-tested and commercial young bulls and heifers on pasture and feedlot

Trait ^b	N	Mean	SD	CV (%)
Performance test on pasture				
Final age (days) ^c	24,910	553.05	24.39	4.41
Final age (days) ^d	14,888	552.72	25.24	4.57
FW (kg)	24,910	350.35	53.09	15.15
ADG (kg/day)	24,910	0.54	0.16	29.63
SC (cm)	14,888	26.61	3.38	12.70
Commercial on pasture				
Final age (days) ^c	84,565	549.46	24.30	4.42
Final age (days) ^d	14,663	548.35	24.39	4.45
FW (kg)	84,565	312.54	58.05	18.57
ADG (kg/day)	84,565	0.36	0.14	10.12
SC (cm)	14,663	25.91	3.67	14.14
AFC (days)	8,060	1,164.83	180.52	15.50
Performance test on feedlot				
Final age (days) ^c	8,103	423.59	26.41	6.23
Final age (days) ^d	4,676	420.73	28.01	6.66
FW (kg)	8,103	371.65	57.13	15.37
ADG (kg/day)	8,103	0.83	0.27	32.53
SC (cm)	4,676	25.41	3.31	13.03
Commercial on feedlot				
Final age (days) ^c	4,468	549.62	24.17	4.40
Final age (days) ^d	1,365	548.59	24.16	4.40
FW (kg)	4,468	389.41	71.41	18.34
ADG (kg/day)	4,468	0.54	0.18	11.82
SC (cm)	1,365	28.46	3.95	13.89

^aN = number of records, SD = standard deviation, and CV = coefficient of variation (in %).

^bFW = final weight, ADG = average daily gain, SC = scrotal circumference, and AFC = age at first calving.

^cOnly for animals with FW and ADG data.

^dOnly for animals with SC data.

Table 4.2. Distribution of animals and sires across regions^a

Trait ^b	Animals					Sires					Total
	NO	NE	CW	SE	SO	NO	NE	CW	SE	SO	
Performance tests on pasture											
Growth	4,874	1,317	7,816	9,769	1,134	672	288	903	901	120	2,047
SC	3,243	1,094	4,581	5,413	557	480	236	571	579	72	1,347
Commercial on pasture											
Growth	-	-	46,878	37,687	-	-	-	2,136	1,423	-	3,021
SC	-	-	8,090	6,573	-	-	-	958	578	-	1,313
AFC	-	-	4,456	753	-	-	-	3,604	510	-	1,053
Performance tests in feedlots											
Growth	69	-	4,307	3,051	676	20	-	463	303	80	688
SC	69	-	3,281	1,288	38	20	-	369	170	10	469
Commercial in feedlots											
Growth	-	-	2,458	2,010	-	-	-	325	308	-	527
SC	-	-	760	605	-	-	-	146	133	-	227

^aNO = North, NE = Northeast, CW = Central West, SE = Southeast, and SO = South.

^bGrowth = includes final weight and average daily gain, SC = scrotal circumference, and AFC = age at first calving.

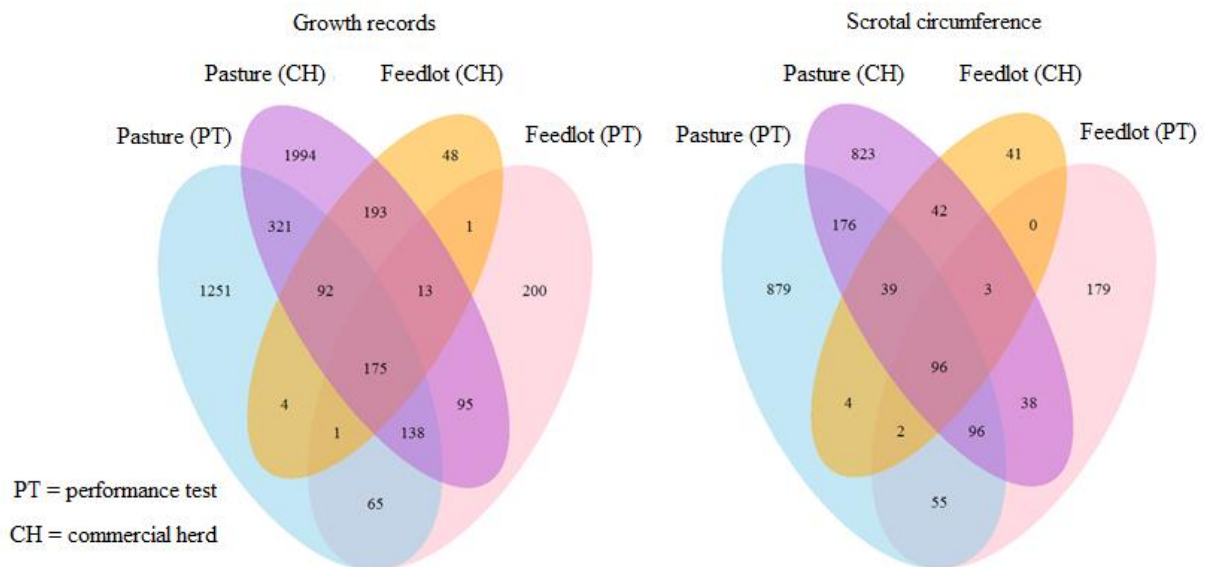


Figure 4.1. Number of sires with progeny records for growth and scrotal circumference across performance tests and commercial herds on pasture and feedlot.

4.2.1 Statistical Analyses

Samples of the posterior distributions of the genetic parameters were obtained using a Bayesian approach and Gibbs sampler on multiple-trait analyses. The following general statistical model was used:

$$y_{hijk} = u_h + CG_{hj} + b_{h(j)}(A_k - \bar{A}_j) + a_{hi} + e_{hijk},$$

where y_{hijk} is the observation for trait h on animal i in performance test (or contemporary group) j with final age k ; u_h is the general constant present in each observation for trait h ; CG_{hj} is the effect of performance test (or contemporary group) j for trait h ; $b_{h(j)}$ is the linear regression coefficient of final age for trait h , nested in the performance test (or contemporary group) j ; A_k is the age k ; \bar{A}_j is the mean for final age in animals from the contemporary group j ; a_{hi} is the breeding value of animal i for trait h ; and e_{hijk} is the residual effect for each observation. The effect of age was not included for AFC.

In matrix notation, the following general model was used in multiple-trait analyses:

$$\begin{bmatrix} y_1 \\ \vdots \\ y_8 \end{bmatrix} = \begin{bmatrix} X_1 & \Phi & \dots & \Phi \\ \Phi & X_2 & \dots & \Phi \\ \vdots & \vdots & \ddots & \vdots \\ \Phi & \Phi & \dots & X_8 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \\ \vdots \\ \beta_8 \end{bmatrix} + \begin{bmatrix} Z_1 & \Phi & \dots & \Phi \\ \Phi & Z_2 & \dots & \Phi \\ \vdots & \vdots & \ddots & \vdots \\ \Phi & \Phi & \dots & Z_8 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \\ \vdots \\ a_8 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ \vdots \\ e_8 \end{bmatrix},$$

where y_h is the vector of records for trait h , X_h is the incidence matrix of fixed effects; β_h is the vector of fixed effects, Z_h is the incidence matrix of random effects; a_h is the vector of breeding values for trait h , and e_h is the vector of residual for trait h . The Φ is the symbol for empty matrix. The indexes h are as follows: FW, ADG and SC in performance-tested animals on pasture or in feedlots were defined as trait 1, FW, ADG, SC, AFC in commercial animals on pasture were defined as traits 2, 3, 4 and 5, respectively, and FW, ADG and SC in commercial animals in feedlots were defined as traits 6, 7 and 8, respectively. Thereby, six multiple-trait analyses were done.

Flat prior distributions were assumed for fixed effects $\left(\begin{bmatrix} \beta_1 & \beta_2 & \dots & \beta_8 \end{bmatrix}^t \right)$, and normal distributions were assumed for random effects $\left(\begin{bmatrix} a_1 & a_2 & \dots & a_8 \end{bmatrix}^t \mid G \right)$ and

$\left[\begin{matrix} e_1 & e_2 & \cdots & e_8 \\ \sim & \sim & & \sim \end{matrix} \middle| R \right]$, whereas inverted Wishart distributions were assumed for (co)variance

matrices $(G_0 | \nu_a, S_a$ and $R | \nu_e, S_e)$, where $G = G_0 \otimes A$ represents genetic (co)variance matrix;

$$G_0 = \begin{bmatrix} \sigma_{a_1}^2 & \sigma_{a_1 a_2} & \cdots & \sigma_{a_1 a_8} \\ \sigma_{a_1 a_2} & \sigma_{a_2}^2 & \cdots & \sigma_{a_2 a_8} \\ \vdots & \vdots & \ddots & \vdots \\ \sigma_{a_1 a_8} & \sigma_{a_2 a_8} & \cdots & \sigma_{a_8}^2 \end{bmatrix} \text{ represents matrix of genetic (co)variance between traits 1 to 8;}$$

$\sigma_{a_h}^2$ represents additive genetic variance for trait h ; $\sigma_{a_h a_{h'}}$ represents additive genetic covariance between traits h and h' ; $R = R_0 \otimes A$ represents residual variance matrix;

$$R_0 = \begin{bmatrix} \sigma_{e_1}^2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \sigma_{e_2}^2 & \sigma_{e_2 e_3} & \sigma_{e_2 e_4} & \sigma_{e_2 e_5} & 0 & 0 & 0 \\ 0 & \sigma_{e_2 e_3} & \sigma_{e_3}^2 & \sigma_{e_3 e_4} & \sigma_{e_3 e_5} & 0 & 0 & 0 \\ 0 & \sigma_{e_2 e_4} & \sigma_{e_3 e_4} & \sigma_{e_4}^2 & 0 & 0 & 0 & 0 \\ 0 & \sigma_{e_2 e_5} & \sigma_{e_3 e_5} & 0 & \sigma_{e_5}^2 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \sigma_{e_6}^2 & \sigma_{e_6 e_7} & \sigma_{e_6 e_8} \\ 0 & 0 & 0 & 0 & 0 & \sigma_{e_6 e_7} & \sigma_{e_7}^2 & \sigma_{e_7 e_8} \\ 0 & 0 & 0 & 0 & 0 & \sigma_{e_6 e_8} & \sigma_{e_7 e_8} & \sigma_{e_8}^2 \end{bmatrix} \text{ represents matrix of residual}$$

variance of traits 1 to 8; $\sigma_{e_h}^2$ is the residual variance for trait h ; $\sigma_{e_h e_{h'}}$ is the residual covariance between traits h and h' ; ν_a and ν_e (degrees of freedom of the inverted Wishart distributions) and S_a and S_e (8×8 matrices of (co)variance components obtained from preliminary analyses) are the hyper-parameters of inverted Wishart distributions of genetic and residual (co)variances; and the other terms are the same as those described above. The complete conditional posterior distributions are available from Sorensen and Gianola (2002).

Gibbs chains of 410,000 iterations were generated for each parameter, with a burn-in period of 10,000 iterations and a sampling interval of 200 iterations in GIBBS1F90 program (Misztal et al., 2014). Genetic and residual variances for FW, ADG, SC and AFC in commercial animals on pasture and FW, ADG and SC in commercial animals in feedlots shown in this paper were obtained from means of 12,000 samples obtained by six multiple-trait analyses. Convergence diagnostics were performed following Geweke's (1992) and Heidelberger and Welch's (1983) techniques, and visual analyses of trace plots were performed using the Bayesian Output Analysis (Smith, 2005) program in R software 3.2.3 (2015).

Samples of posterior distributions for efficiency of correlated response (ECR), considering the same intensity of selection for traits in performance-tested and commercial animals, were obtained by the equation available in Falconer and Mackay (1996):

$$ECR_{hh'} = \frac{\Delta G_{hh'}}{\Delta G_h} = r_{a_{hh'}} \frac{h_{h'}}{h_h},$$

where $\Delta G_{hh'}$ is the expected genetic gain per generation for trait h in commercial animals when selection was applied for trait h' in performance-tested animals; ΔG_h is the expected genetic gain per generation for trait h in commercial animals; h' is the trait under selection in performance-tested animals; h is the indirectly selected trait in commercial animals; $r_{a_{hh'}}$ is the genetic correlation between traits h and h' ; and $h_{h'}$ and h_h are square root of heritabilities for traits h' and h , respectively.

In addition to the analyses previously described, two multiple-trait analyses were done in which FW or ADG in performance-tested animals on pasture were defined as trait 1, FW and ADG in male commercial animals on pasture were defined as traits 2 and 3, respectively, and FW, ADG and AFC in female commercial animals on pasture were defined as traits 4, 5 and 6, respectively. These analyses were performed to estimate genetic correlations between the same trait on young bulls and heifers. Furthermore, another two analyses for the same traits measured in performance-tested and commercial animals in feedlots were also done. A single-trait analysis for AFC was run to compare the results from single and multiple-trait analyses for this trait.

4.3 RESULTS

4.3.1 Genetic variation for growth and reproductive traits

Posterior means and highest posterior density intervals of variances and heritabilities for growth and reproductive traits in performance-tested and commercial young bulls and heifers are shown in Table 4.3. The posterior means of the additive genetic variances for FW and ADG were greater for performance-tested young bulls than for commercial animals on pasture or in feedlots (Table 4.3).

Table 4.3. Variance components^a for growth and reproductive traits in performance-tested and commercial young bulls and heifers on pasture and feedlot

Trait ^b	σ_a^2	σ_e^2	h^2
Performance test on pasture			
FW	421.03 (380.00; 461.80)	514.38 (487.00; 547.60)	0.45 (0.41; 0.49)
ADG	0.019 (0.016; 0.022)	0.053 (0.051; 0.055)	0.26 (0.23; 0.30)
SC	3.34 (2.94; 3.69)	3.05 (2.79; 3.33)	0.52 (0.47; 0.57)
Commercial on pasture			
FW	322.26 (295.70; 345.30)	721.84 (702.80; 739.90)	0.31 (0.29; 0.33)
M_FW	321.08 (281.90; 358.30)	887.12 (857.30; 916.10)	0.27 (0.24; 0.29)
F_FW	264.14 (238.10; 286.90)	604.12 (585.20; 623.30)	0.30 (0.27; 0.33)
ADG	0.010 (0.009; 0.011)	0.051 (0.050; 0.055)	0.16 (0.14; 0.18)
M_ADG	0.012 (0.011; 0.014)	0.058 (0.057; 0.060)	0.18 (0.15; 0.20)
F_ADG	0.009 (0.008; 0.010)	0.044 (0.042; 0.045)	0.17 (0.15; 0.20)
SC	2.58 (2.20; 2.91)	3.86 (3.59; 4.13)	0.40 (0.35; 0.45)
AFC	3.65 (1.93; 4.36)	15.50 (14.69; 16.91)	0.18 (0.10; 0.22)
AFC ^c	1.68 (1.20; 2.16)	16.96 (16.33; 17.57)	0.09 (0.06; 0.11)
Performance test on feedlot			
FW	756.70 (626.30; 895.80)	689.82 (590.40; 780.30)	0.52 (0.45; 0.60)
ADG	0.064 (0.048; 0.082)	0.181 (0.168; 0.195)	0.26 (0.20; 0.32)
SC	4.27 (3.64; 4.88)	2.49 (2.07; 2.97)	0.63 (0.56; 0.70)
Commercial on feedlot			
FW	426.53 (308.00; 586.90)	860.56 (749.80; 976.40)	0.33 (0.24; 0.44)
M_FW	355.59 (298.10; 432.20)	984.17 (915.50; 1,060.00)	0.27 (0.22; 0.31)
F_FW	473.95 (319.40; 645.20)	687.18 (549.70; 803.20)	0.41 (0.28; 0.53)
ADG	0.015 (0.010; 0.019)	0.064 (0.060; 0.070)	0.19 (0.13; 0.24)
M_ADG	0.013 (0.008; 0.018)	0.069 (0.065; 0.075)	0.16 (0.09; 0.22)
F_ADG	0.013 (0.007; 0.018)	0.060 (0.054; 0.066)	0.17 (0.09; 0.23)
SC	3.62 (2.65; 4.63)	4.16 (3.39; 4.99)	0.46 (0.35; 0.57)

Lower and upper limits of the highest posterior density intervals with 90% of the samples are listed between brackets.

^aPosterior means of σ_a^2 = additive genetic variance, σ_e^2 = residual variance, and h^2 = heritability.

^bFW = final weight, M_FW = male FW, F_FW = female FW, ADG = average daily gain, M_ADG = male ADG, F_ADG = female ADG, SC = scrotal circumference, and AFC = age at first calving.

^cResults from single trait analysis. Variances for AFC were multiplied by 10^{-3} .

The posterior means of the additive genetic variance for SC was greater for performance-tested young bulls on pasture than for commercial animals on pasture. However, the additive genetic variances for SC were similar between young bulls in performance tests and commercial herds, both in feedlots (Table 4.3). In addition, residual variances for FW and SC were smaller for performance-tested young bulls than for commercial animals, and posterior mean of residual variance for ADG was greater for performance-tested animals in feedlots than for commercial animals in feedlots (Table 4.3). These results lead to greater

estimates of heritabilities for traits for performance-tested young bulls than for commercial animals (Table 4.3).

The posterior means of the additive genetic and residual variances for FW and ADG were greater for males than for females in commercial herds on pasture (Table 4.3). Estimates of the residual variances for FW and ADG were greater for males than for females in commercial herds in feedlots (Table 4.3). The heritabilities for FW and ADG were similar between males and females in commercial herds on pasture (Table 4.3). The heritability for FW was greater for females than for males in commercial herds in feedlots, but highest posterior density intervals overlapped (Table 4.3). The heritabilities for ADG were similar between males and females in commercial herds in feedlots (Table 4.3).

The additive genetic variance and heritability for AFC were smaller for single trait analyses than for multiple-trait analyses (Table 4.3).

4.3.2 Genetic correlation between male and female traits

The posterior means (and lower and upper limits of the highest posterior density intervals with 90% of samples, between brackets) of genetic correlations between male and female FW and ADG in commercial herds on pasture were 0.96 (0.94; 0.98) and 0.75 (0.58; 0.88), respectively. The genetic correlations between male and female FW and ADG in commercial herds in feedlots were 0.96 (0.93; 0.99) and 0.74 (0.63; 0.85), respectively.

4.3.3 Genetic correlation

The genetic correlations between ADG and SC in performance-tested young bulls on pasture with AFC in heifers on pasture were negative (Table 4.4). However, genetic correlations between FW in performance-tested young bulls on pasture, FW, ADG and SC in performance-tested young bulls in feedlots with AFC were similar to zero (Table 4.4).

The selection for ADG and SC in performance-tested young bulls on pasture will result in reduced AFC in commercial heifers but the selection for FW in performance-tested young bulls on pasture or growth and SC in performance-tested young bulls in feedlots will not change AFC in commercial heifers on pasture (Table 4.4). The posterior means of the genetic correlations between FW, ADG and SC in performance-tested and commercial animals were positive (Table 4.4), indicating that selection for either of these traits in performance-tested young bulls will result in improved growth and SC in commercial animals.

Table 4.4 Genetic correlation between growth and reproductive traits^a in performance-tested young bulls on pasture and feedlot (columns) with growth and reproductive traits in commercial young bulls and heifers on pasture and feedlots (lines)

		Performance test							
		Pasture			Feedlot				
		FW	ADG	SC	FW	ADG	SC		
Commercial	Pasture	FW	0.91 (0.86; 0.96)	0.63 (0.54; 0.78)	0.37 (0.27; 0.46)	0.87 (0.82; 0.91)	0.60 (0.47; 0.71)	0.53 (0.44; 0.63)	
		ADG	0.69 (0.62; 0.76)	0.84 (0.78; 0.90)	0.27 (0.18; 0.37)	0.40 (0.30; 0.51)	0.39 (0.27; 0.52)	0.24 (0.11; 0.36)	
		SC	0.32 (0.22; 0.40)	0.27 (0.16; 0.37)	0.94 (0.92; 0.97)	0.28 (0.16; 0.40)	0.17 (0.00; 0.33)	0.80 (0.73; 0.88)	
		AFC	-0.19 (-0.38; 0.09)	-0.26 (-0.48; 0.06)	-0.23 (-0.41; 0.05)	0.02 (-0.17; 0.18)	-0.06 (-0.29; 0.10)	-0.11 (-0.35; 0.13)	
		Feedlot	FW	0.66 (0.54; 0.78)	0.33 (0.17; 0.54)	0.25 (0.10; 0.38)	0.88 (0.83; 0.94)	0.65 (0.52; 0.77)	0.33 (0.18; 0.47)
			ADG	0.54 (0.38; 0.71)	0.39 (0.23; 0.56)	0.23 (0.03; 0.42)	0.72 (0.60; 0.85)	0.58 (0.40; 0.79)	0.26 (0.12; 0.40)
	SC		0.12 (-0.10; 0.34)	0.12 (-0.10; 0.28)	0.73 (0.63; 0.83)	0.49 (0.38; 0.61)	0.56 (0.45; 0.70)	0.67 (0.50; 0.83)	

Lower and upper limits of the highest posterior density intervals with 90% of the samples are listed between brackets.

^aFW = final weight, ADG = average daily gain, SC = scrotal circumference, and AFC = age at first calving.

The posterior mean of the genetic correlation between FW in performance-tested young bulls on pasture with FW in commercial animals on pasture was higher than the genetic correlation between FW in performance-tested young bulls on pasture with FW in commercial animals in feedlots (Table 4.4). The same results were observed for ADG and SC (Table 4.4). These differences were not observed for genetic correlations between FW, ADG and SC in performance-tested young bulls in feedlots with FW, ADG and SC in commercial animals on pasture or in feedlots (Table 4.4).

4.3.4 Efficiency of correlated responses

Table 4.5 presents the efficiencies of correlated responses for FW, ADG, SC and AFC in commercial animals when FW, ADG and SC were selected in performance-tested young bulls. The correlated responses for FW, ADG and SC in commercial animals on pasture when FW, ADG and SC were selected in performance-tested young bulls on pasture were similar or greater than the direct responses for FW, ADG and SC in commercial animals on pasture (Table 4.5). The correlated responses for FW in commercial animals (on pasture or in

feedlots) when FW was selected in performance-tested young bulls in feedlots were similar or greater than the direct responses for FW in commercial animals (on pasture or in feedlots) (Table 4.5).

Table 4.5. Efficiency of correlated responses for growth and reproductive traits^a in commercial young bulls and heifers on pasture and feedlot (lines) when the selection is applied for increased growth and reproductive traits in performance-tested young bulls on pasture and feedlots (columns)

		Performance test						
		Pasture			Feedlot			
		FW	ADG	SC	FW	ADG	SC	
Commercial animals	Pasture	FW	1.10 (1.03; 1.19)	0.58 (0.48; 0.68)	0.48 (0.35; 0.60)	1.12 (1.03; 1.22)	0.55 (0.43; 0.67)	0.74 (0.60; 0.90)
		ADG	1.16 (1.00; 1.13)	1.08 (0.94; 1.19)	0.49 (0.32; 0.67)	0.71 (0.54; 0.89)	0.50 (0.34; 0.68)	0.46 (0.24; 0.72)
		SC	0.34 (0.24; 0.43)	0.22 (0.13; 0.31)	1.08 (1.01; 1.16)	0.32 (0.17; 0.44)	0.14 (0.02; 0.27)	1.00 (0.90; 1.13)
	Feedlot	AFC	-0.33 (-0.68; 0.44)	-0.33 (-0.63; 0.03)	-0.44 (-0.85; 0.05)	0.04 (-0.33; 0.31)	-0.07 (-0.36; 0.14)	-0.20 (-0.73; 0.20)
		FW	0.78 (0.47; 0.99)	0.30 (0.09; 0.52)	0.32 (0.16; 0.49)	1.11 (0.98; 1.25)	0.59 (0.46; 0.75)	0.46 (0.24; 0.65)
		ADG	0.84 (0.56; 1.19)	0.47 (0.26; 0.71)	0.44 (0.06; 0.81)	1.25 (1.01; 1.53)	0.70 (0.38; 0.95)	0.50 (0.20; 0.84)
SC	0.12 (-0.09; 0.32)	0.09 (-0.06; 0.22)	0.78 (0.64; 0.96)	0.50 (0.37; 0.65)	0.41 (0.29; 0.53)	0.76 (0.50; 0.99)		

Lower and upper limits of the highest posterior density intervals with 90% of the samples are listed between brackets.

^aFW = final weight, ADG = average daily gain, SC = scrotal circumference, and AFC = age at first calving.

The correlated response for SC in commercial animals on pasture when SC was selected in performance-tested young bulls in feedlots was similar to the direct response for SC in commercial animals on pasture (Table 4.5). The correlated responses for ADG in commercial animals in feedlots when ADG was selected in performance-tested young bulls on pasture or in feedlots were similar (Table 4.5). And the correlated responses for SC in commercial animals in feedlots when SC was selected in performance-tested young bulls on pasture or in feedlots were also similar (Table 4.5).

4.4 DISCUSSION

4.4.1 Genetic variation for growth and reproductive traits

The heritabilities, correlations and response to selection for growth and SC in performance-tested young bulls on pasture and feedlot have been discussed previously (Raidan et al., 2015). The discussion about these genetic parameters in commercial animals on pasture and feedlots is quite the same. In summary, the response to selection will be greater in feedlots than on pasture (if selection intensities were the same) because the feeding conditions in feedlots are better than the feeding conditions on pasture and they allow a higher expression of genetic differences between animals (Hammond, 1947; Kearney et al., 2004).

The genetic variances and heritabilities for growth and SC are greater for performance-tested young bulls than for commercial animals (Table 4.3). Genetic differences are greater for young bulls in performance tests than for commercial animals because the changes in management conditions are less frequent, and the process of data recording is stricter in performance tests than in commercial conditions (Fragomeni et al., 2013). The number of young bulls in each performance test was greater than the number of animals in each contemporary group of commercial herds; this condition contributes to having better estimates of the solutions for systematic effects included in the statistical models, and to keep temporary random effects smaller in performance tests than in commercial herds. The residual variance for ADG is greater for performance-tested young bulls in feedlots than for commercial animals in feedlots because the mean ADG is more than 50% greater in performance tests in feedlots than elsewhere.

The AFC records probably came from a selected group of heifers because those females with low weaning weight could be culled at weaning and some heifers with low body weight at yearling did not get pregnant during the first breeding season. Thus, the posterior means for genetic variance and heritability from single-trait analyze are the smallest. However, the multiple-trait analyses were effective to reduce the bias from selection, as previously stated by Schaeffer (1984). Additionally, posterior mean of heritability for AFC of commercial animals on pasture obtained by multiple-trait analysis was similar to the mean heritability of 0.17 obtained from three different samples of Nellore heifers (Boligon et al., 2010; Regatieri et al., 2012; Eler et al., 2014).

4.4.2 Genetic correlation between male and female traits

Posterior means of heritabilities for growth traits were similar between males and females and genetic correlations between male and female growth traits were high (> 0.74). These results agree with those by Garrick et al. (1989), Rodríguez-Almeida et al. (1995) and Van Vleck and Cundiff (1998). A large fraction of additive genes for growth traits has the same effect with regard to controlling variation in each of the sex subclasses (Garrick et al., 1989), and there is no evidence of genotype x sex interaction in commercial herds.

4.4.3 Genetic correlation

The selection for increased ADG and SC in performance-tested young bulls on pasture will result in reduced AFC. The estimates of genetic correlations between ADG and AFC ranged from -0.38 to -0.32 (Castro-Pereira et al., 2007 and Boligon et al., 2010). The estimates of genetic correlations between SC (at 12 or 18 months of age) and AFC ranged from -0.42 to -0.22 (Castro-Pereira et al., 2007 and Terakado et al., 2015). These results indicate that additive genes for ADG and SC could be connected somehow to those genes responsible for AFC. In fact, Utsunomiya et al. (2014) and Costa et al. (2015) found significant single nucleotide polymorphisms (SNPs) on chromosomes 10 and 14 that affect both SC and AFC in Nellore cattle. There is at least one SNP close to positions 78.5 to 79.85 Mb on chromosome 10, and another SNP close to positions 23.4 to 33.85 Mb on chromosome 14 that affects both SC and AFC (Utsunomiya et al., 2014 and Costa et al., 2015).

Posterior mean of genetic correlation between FW in performance-tested young bulls on pasture with AFC was negative (Table 4.4), but the posterior density interval included zero. The genetic correlation between growth of performance-tested young bulls and growth of commercial young bulls and heifers on pasture was sufficiently high to consider these traits in different environments as only one trait. The results presented in Table 4.4 suggest that AFC is more strongly related to ADG than to FW. The relationships between growth rate, age and live weight at puberty are very complex and it is virtually impossible to separate the effects of growth rate per se from those of live weight and/or age (Lawrence, 2002). However, the genetic correlations between ADG and maturation rate with AFC (-0.32 and -0.83, respectively) are stronger than the genetic correlations between FW and weight at maturity with AFC (-0.26 and 0.52, respectively) (Boligon et al., 2010 and Gaviolli et al., 2012). In addition, the selection for high growth rate results in a younger and heavier selected population at puberty (Foxcroft, 1980). A high growth rate before puberty would involve a considerably greater rate of adipose tissue growth than in case of a low growth rate

(Lawrence, 2002), and this change in body composition can be an effective trigger for puberty (Foxcroft, 1980). The control of reproduction involves a wide variety of interacting mechanisms and it is undoubtedly premature to suggest that there is only one mechanism involved in the onset of puberty.

The selection for increased FW, ADG and SC in performance-tested young bulls in feedlots will not change AFC (Tables 4.4 and 4.5). The estimated genetic correlations between midtest body weight and ADG in performance-tested young bulls in feedlots with AFC were -0.18 ± 0.13 and 0.21 ± 0.15 , respectively (Crowley et al., 2011a). The large standard errors associated with these genetic correlations made it difficult to generate definitive conclusions on the implication of the selection for increased growth in performance-tested young bulls in feedlots on AFC. However, the results of the selection experiment presented by Mercadante et al. (2003) confirmed that genetic correlation between FW in performance-tested young bulls in feedlots (378 days of age) and days to calving of the first mating, an indicative trait of AFC (Forni et al., 2005), in beef cattle is almost zero. Mercadante et al. (2003) estimated significant genetic trends of 1.78 ± 0.20 kg/year and 2.39 ± 0.20 kg/year for FW and non-significant genetic trends of 0.03 ± 0.16 days/year and 0.19 ± 0.17 days/year for days to calving of the first mating in two lines selected for increased FW, respectively. Afterward, Monteiro et al. (2013) showed that selection for increased FW did not change ovarian or endometrial development, not manifestation of puberty at 24 months of age in heifers. The selection for increased growth in performance-tested young bulls in feedlots will not change AFC in commercial heifers.

As stated before, AFC is more strongly related to ADG than to FW, but genetic correlation between ADG of performance-tested young bulls in feedlots with ADG of commercial young bulls and heifers on pasture is only moderate (0.39, Table 4.4). Consequently, the ADG in performance-tested young bulls in feedlots is not an efficient selection criterion for indirect improvement of ADG and AFC in commercial heifers on pasture.

Genetic correlations between ADG and FW in performance-tested young bulls on pasture (0.74) and feedlots (0.67) are high (Raidan et al., 2016), but the selection for one or another had different consequences in commercial herds. Heritability is greater for FW than for ADG (Table 4.3), changes for FW or ADG in commercial animals can be achieved when selection is applied for FW or ADG (Tables 4.4 and 4.5), but selection for increased ADG will result in reduced AFC whereas selection for increased FW will not. FW is more correlated to body weight at the beginning of performance tests than ADG (Neves et al., 2014 and Tineo et

al., 2016), and currently there is no limit for differences in body weight at the beginning of performance tests. Consequently, FW is more affected by body weight at the beginning of the test and herd-of-origin effects than ADG. FW might be more correlated to adult body weight than ADG and increased adult body weight will result in increased energy requirements for the maintenance of cows (NRC, 2000). These results suggest that ADG is better than FW as a post-weaning selection criterion.

Genetic correlation between the same trait in different environments has been one of the parameters used for indicating the existence of genotype x environment interaction. Falconer (1952) suggested that genetic correlation between the same trait in different environments smaller than unity is an evidence of genotype x environment interaction. Additionally, James (1961) and Mulder et al. (2006) showed that it is important to have environment-specific breeding programs of progeny testing when the genetic correlations between the same trait in different environments are smaller than the thresholds of 0.70 and 0.61, respectively.

The genetic correlations between the same trait measured in performance tests or commercial herds were smaller than unity, but the upper limits of the highest posterior density intervals with 90% of the samples were 0.79 or greater (Table 4). Some authors just look at the genetic correlations between the same trait in different environments to discuss about the existence of genotype x environment interaction (De Mattos et al., 2000; Kearney et al., 2004; Diaz et al., 2011; Willians et al., 2012a and 2012b). However, our additional results (e.g. the diagonal values in Table 4.5) support the hypothesis that there is no practical effect of genotype x environment interaction for growth and SC for performance tests and commercial cattle. The heritabilities for traits in performance-tested young bulls were greater than the heritabilities for the same traits in commercial animals (Table 4.3), and the genetic correlations between these traits were large enough (Table 4.4) to offset the effect of genotype x environment interaction.

4.4.4 Efficiency of correlated responses and implications for breeding

The performance test can be used as a tool for the evaluation and selection of bulls for commercial herds. Furthermore, the results obtained in the present study and those obtained by Falconer (1960) and Mascioli (2000) showed that pasture, when compared to feedlot, is the best environment for the evaluation and selection of Nellore young bulls. Selection would be more efficient in an environment that allows the maximum expression of genetic differences (Hammond, 1947; Kearney et al., 2004 and Raidan et al., 2015). However, Falconer and

Latyszewski (1952) affirmed that the improvement made by selection for growth traits on a high plane of nutrition did not carry over when the animals were transferred to a low plane of nutrition, but the improvement made on the low plane of nutrition was retained when the animals were transferred to a high plane of nutrition. Falconer (1960) obtained direct and correlated responses for growth traits of mice on two planes of nutrition. The animals selected on low plane of nutrition were heavier, had less fat and more protein and females were better dams than animals selected in the high plane of nutrition when the two groups were raised on the high plane of nutrition. Thereby, the selection should be made under conditions least favorable to expression of the trait. This author observed the following differences in carcass composition: mice whose growth had been increased by selection on low plane were leaner than those whose growth had been increased by selection on high plane of nutrition. These results indicate that growth traits of mice on a high or low plane of nutrition were reached by different physiological pathways (Falconer, 1960).

Mascioli (2000) conducted progeny tests on pasture and in feedlots with Canchim young bulls. These bulls were ranked as superior, intermediate and inferior according to their FW in performance tests on pasture and in feedlots (approximately 400 d old), posteriorly, their progenies were raised on pasture and feedlot systems. No effect of bull rank on feedlot the weaning weight and post-weaning growth of the progenies was observed. However, the progenies of bulls ranked as superior on pasture were heavier than other classes for birth weight, weaning weight and weight at 12 months. Mascioli (2000) concluded that the selection of Canchim young bulls in favorable environments (feedlots) did not produce the same response to selection in restricted environments (pasture). Similarly, the results presented in Table 5 support the hypothesis that selection for ADG and SC of performance-tested animals on pasture is better than selection for ADG and SC of performance-tested animals in feedlots to improve the means for growth and reproductive traits in commercial animals on pasture or in feedlots.

4.5 CONCLUSIONS

Heritabilities for growth and scrotal circumference are greater in performance-tested young bulls than in commercial young bulls and heifers.

The evaluation and selection for increased growth and scrotal circumference of young bulls in performance tests is efficient to improve growth, scrotal circumference and age at first calving in commercial animals.

Average daily gain is better than final weight as a post-weaning selection criterion in performance tests.

The evaluation and selection of young bulls in performance test on pasture is more efficient than evaluation and selection of young bulls in performance tests in feedlots.

5.0 CONSIDERAÇÕES FINAIS

O Brasil é um país de dimensões continentais com variações climáticas, econômicas e culturais que culminam em grande diversidade de sistemas de produção de carne bovina. Isso estimula a investigação da presença de IGA. Nesse estudo, identificamos a IGA para características de crescimento de bovinos de corte mensuradas a pasto e em confinamento. Entretanto não foi identificada IGA para perímetro escrotal no pasto ou em confinamento. Observamos que as características de menor herdabilidade são mais susceptíveis aos impactos da IGA. Esses impactos foram identificados como mudanças nas variâncias e covariâncias, genéticas e residuais, e respostas, diretas e indiretas, à seleção para características de crescimento. Adicionalmente, podemos citar a ocorrência de alterações nas classificações dos animais em função das diferenças esperadas na progênie para peso final e ganho médio diário em peso obtidas a pasto ou em confinamento.

É importante destacar que quando a variabilidade genética é baixa e a diferença ambiental é alta, como pode ocorrer para animais criados a pasto e em confinamento, a presença da IGA poderá ser importante para definir as condições de ambiente em que os animais deverão ser selecionados. Nesse sentido, demonstramos que a intensidade de seleção é um importante parâmetro para estudo da interação genótipo x ambiente. Nesse estudo, observamos que quando a intensidade de seleção no pasto é maior, esse ambiente pode ser utilizado para seleção de reprodutores a serem utilizadas em ambientes mais favoráveis, como o confinamento. Dessa forma, é possível selecionar reprodutores geneticamente superiores para produção de progênie a pasto ou em confinamento a partir de ambientes que proporcionem maior intensidade de seleção. É esperado que sistemas de produção a pasto, de menor custo de produção, possibilitem avaliação de maior número de animais, o que pode resultar em maior intensidade de seleção.

Adicionalmente, não identificamos IGA para características de crescimento e reprodução entre bovinos Nelore criados em testes de desempenho individual e rebanhos comerciais, ambos a pasto ou em confinamento. A padronização do ambiente em testes de desempenho individual contribuiu para obtenção de maiores herdabilidades nesse ambiente. Ainda, a seleção para características de crescimento e perímetro escrotal de tourinhos testados a pasto foi mais eficiente para melhorar o desempenho para características de crescimento, perímetro escrotal e idade ao primeiro parto de animais criados no rebanho comercial a pasto ou em confinamento, quando comparada a seleção de tourinhos testados em confinamento.

Assim, o teste de desempenho individual a pasto permite obter progresso genético nos sistemas comerciais de produção de bovinos de corte e deve ser utilizado como ambiente para seleção de reprodutores.

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7.0 ANEXO A

Table A7.1. Number of observations for final weight and ADG of Nellore young bulls in pasture or in feedlots performance tests across states

State	Pasture		Feedlot		Pasture and feedlot	
	Young bulls	Sires	Young bulls	Sires	Sires	Progenies
AC	25	17	-	-	-	-
BA	1,223	276	-	-	-	-
ES	600	136	18	7	6	86
GO	2,263	396	829	203	115	2,147
MA	94	32	-	-	-	-
MG	5,398	524	780	142	73	1,996
MS	1,494	212	451	141	67	1,110
MT	4,059	522	3,027	261	137	3,933
PA	1,385	322	69	20	17	265
PR	1,134	120	662	70	33	792
RO	1,009	156	-	-	-	-
RS	-	-	14	10	-	-
SP	3,771	450	2,253	221	90	3,525
TO	2,455	358	-	-	-	-
Total*	24,910	2,047	8,103	688	279	13,854

*Total number of sires with progeny in each type performance test.

Table A7.2. Number of observations for scrotal circumference of Nellore young bulls in pasture or in feedlots performance tests across states

State	Pasture		Feedlot		Pasture and feedlot	
	Young bulls	Sires	Young bulls	Sires	Sires	Progenies
AC	25	16	-	-	-	-
BA	1,001	276	-	-	-	-
ES	347	136	-	-	-	-
GO	1,246	253	572	143	88	1,254
MA	93	32	-	-	-	-
MG	3,124	369	498	66	45	1,206
MS	769	115	383	136	36	581
MT	2,566	339	2,326	197	93	2,614
PA	997	230	69	20	16	215
PR	557	72	38	10	8	84
RO	678	102	-	-	-	-
RS	-	-	-	-	-	-
SP	1,942	255	790	138	49	1,031
TO	1,543	235	-	-	-	-
Total*	14,888	1,347	4,676	469	179	6,985

*Total number of sires with progeny in each type performance test.