UNIVERSIDADE ESTADUAL PAULISTA - UNESP

CÂMPUS DE JABOTICABAL

IMPACTO GENÉTICO DA SELEÇÃO DE LONGO PRAZO PARA PESO CORPORAL E CONTROLE GENÔMICO DE CARACTERÍSTICAS DE CRESCIMENTO E CARCAÇA EM BOVINOS CARACU

Viviane Andrade Ligori

Zootecnista

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Registro de Impacto

O presente estudo amplia o conhecimento sobre a base genética da raça Caracu e oferece ferramentas para programas de melhoramento que conciliem crescimento, qualidade da carne e adaptação ao clima tropical. Os resultados contribuem para produção pecuária mais eficiente, sustentável e alinhada a desafios globais de segurança alimentar e conservação ambiental.

Impact Statement

This study expands knowledge about the genetic basis of the Caracu breed and provides tools for breeding programs that balance growth, meat quality, and adaptation to the tropical climate. The results contribute to more efficient and sustainable livestock production, aligned with global food security and environmental conservation challenges.

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DADOS CURRICULARES DO AUTOR

Viviane Andrade Ligori, filha de Carlos Alberto Ligori e Susana Marques de Andrade Ligori. Nascida em 08 de maio de 1994 na cidade de São Paulo, estado de São Paulo, Brasil. Concluiu juntamente com o ensino médio o curso técnico em Análises Química, pelo SENAI Fundação Zerrenner. Iniciou o curso de Bacharelado em Zootecnia no Instituto Federal de Educação, Ciência e Tecnologia (IFSULDEMINAS), *Campus* Machado *campus* em março de 2015, obtendo o título de Bacharel em Zootecnia em julho de 2019, sob orientação da Profa. Dra. Daiane Moreira Silva. Durante a graduação, foi bolsista de iniciação científica (FAPEMIG), sob orientação da Profa. Dra. Lêda Gonçalves Fernandes. Em agosto de 2019, iniciou o curso de Mestrado em Produção Animal Sustentável pelo Programa de Pós-Graduação do Instituto de Zootecnia (IZ), sob orientação da Profa. Dra. Lenira El Faro Zadra, e coorientação da Dra. Maria Gabriela Campolina Diniz Peixoto, obtendo título de Mestre em Produção Animal Sustentável em julho de 2021. Em agosto de 2021, iniciou o curso de Doutorado no Programa de Pós-Graduação em Ciência Animal da Universidade Estadual Paulista "Júlio de Mesquita Filho – Faculdade de Ciências Agrárias e Veterinárias (FCAV/UNESP), *campus* Jaboticabal, sob orientação da Profa. Dra. Lenira El Faro Zadra, e coorientação da Profa. Dra. Maria Eugênia Zerlotti Mercadante. Fez o doutorado sanduíche na “Auburn University”, em Auburn-AL, nos Estados Unidos da América, de outubro de 2024 à março de 2025, sob orientação do Prof. Dr. Wellison Jarles da Silva Diniz. Foi bolsista CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) durante a realização dos cursos de Mestrado, Doutorado e período sanduíche.

EPÍGRAFE

“Lembre-se de quem você é.”
(Mufasa, O Rei Leão)

“Aventure-se no desconhecido.”
(Frozen II)

“A flor que desabrocha na adversidade é a mais rara e bela de todas.”
(Imperador da China, Mulan)

“Se você pode sonhar, você pode fazer.”
(Walt Disney)

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SUMÁRIO

IMPACTO GENÉTICO DA SELEÇÃO DE LONGO PRAZO PARA PESO CORPORAL E CONTROLE GENÔMICO DE CARACTERÍSTICAS DE CRESCIMENTO E CARCAÇA EM BOVINOS CARACU

RESUMO – O Caracu é uma raça taurina adaptada ao Brasil, com mais de 40 anos de seleção para peso corporal (BW) e registros de desempenho ao longo de várias gerações. O objetivo desta tese foi avaliar o impacto genético da seleção de longo prazo para BW e investigar, por meio de abordagens quantitativas e genômicas integradas, o controle genético e regulatório de características de crescimento e carcaça. No primeiro estudo, foram estimados parâmetros genéticos de crescimento, carcaça e reprodução em 4.783 animais, incluindo 829 genotipados com o painel GGP Bovine 100K. Correlações genéticas favoráveis foram observadas entre BW e área de olho de lombo (REA; 0,51±0,11), relação altura/largura do Longissimus (HWR; 0,45±0,17) e perímetro escrotal (SC; 0,24±0,13), indicando ganhos indiretos em carcaça e fertilidade masculina. BW apresentou correlação desfavorável com dias ao parto (DC; 0,48±0,15), mostrando a necessidade de seleção equilibrada para preservar a eficiência reprodutiva feminina. No segundo estudo, investigou-se a base genômica de BW e características de carcaça em 862 animais usando WssGBLUP e AWM-PCIT. As dez janelas genômicas de maior efeito explicaram 21,36% a 31,74% da variância genética, destacando BTA18 (BW), BTA2 (REA), BTA21 (HWR), BTA1 (BFT) e BTA11 (RFT). Análises funcionais indicaram processos de desenvolvimento tecidual, metabolismo lipídico e remodelamento, e a análise de redes gênicas identificou quatro genes centrais (ZEB2, LTF, IRX3 e LHX1), evidenciando a regulação complexa do crescimento e composição de carcaça. Estes resultados fornecem subsídios para programas de melhoramento genético sustentáveis em Caracu, permitindo otimizar simultaneamente crescimento, qualidade de carcaça e eficiência reprodutiva.

Palavras-chave: AWM, parâmetros genéticos, rede gênica, seleção indireta, WssGBLUP.

GENETIC IMPACT OF LONG-TERM SELECTION FOR BODY WEIGHT AND GENOMIC CONTROL OF GROWTH AND CARCASS TRAITS IN CARACU CATTLE

ABSTRACT- The Caracu is a taurine breed adapted to Brazil, with over 40 years of selection for body weight (BW) and performance records spanning several generations. The objective of this thesis was to evaluate the genetic impact of long-term selection for BW and to investigate, through integrated quantitative and genomic approaches, the genetic and regulatory control of growth and carcass traits. In the first study, genetic parameters of growth, carcass, and reproduction were estimated in 4,783 animals, including 829 genotyped with the GGP Bovine 100K panel. Favorable genetic correlations were observed between BW and rib eye area (REA; 0.51±0.11), longissimus height-to-width ratio (HWR; 0.45±0.17), and scrotal circumference (SC; 0.24±0.13), indicating indirect gains in carcass and male fertility. BW showed an unfavorable correlation with days to calving (DC; 0.48 ± 0.15), demonstrating the need for balanced selection to preserve female reproductive efficiency. In the second study, the genomic basis of BW and carcass traits was investigated in 862 animals using WssGBLUP and AWM-PCIT. The ten genomic windows with the greatest effect explained 21.36% to 31.74% of the genetic variance, highlighting BTA18 (BW), BTA2 (REA), BTA21 (HWR), BTA1 (BFT), and BTA11 (RFT). Functional analyses indicated processes of tissue development, lipid metabolism, and remodeling, and gene network analysis identified four central genes (ZEB2, LTF, IRX3, and LHX1), evidencing the complex regulation of growth and carcass composition. These results provide support for sustainable genetic improvement programs in Caracu, allowing for the simultaneous optimization of growth, carcass quality and reproductive efficiency.

Keywords: AWM, gene network, genetic parameters, indirect selection, WssGBLUP.

CAPÍTULO 1 – CONSIDERAÇÕES GERAIS

1. INTRODUÇÃO

A pecuária desempenha papel de relevância para a segurança alimentar e economia brasileira (MAPA, 2020). A crescente demanda global por proteína de origem animal, aliada à pressão por práticas mais eficientes e sustentáveis, tem impulsionado o aprimoramento genético de rebanhos para maximizar a produtividade, qualidade da carne e adaptação ao clima tropical (Lancaster et al., 2009).

O peso corporal foi o principal critério de seleção nos rebanhos de corte, por apresentar herdabilidade moderada a alta e forte correlação com características de desempenho e rendimento de carcaça (Ferreira e Borjas, 2008). Porém, a seleção intensiva e de longo prazo para peso corporal pode afetar negativamente outras características de interesse econômico, como a qualidade da carne, eficiência reprodutiva e a adaptabilidade, exigindo estratégias de seleção mais equilibradas.

A raça Caracu (*Bos taurus taurus*) destaca-se como um recurso genético valioso no contexto da bovinocultura nacional. Diferentemente dos demais taurinos, é uma raça adaptada ao clima tropical, a qual apresenta características desejáveis de rusticidade, produtividade e qualidade de carne (Lima et al., 1992). Com o intuito da conservação da raça, desde 1976, o Instituto de Zootecnia conduz um programa de seleção para peso corporal, proporcionando uma base sólida para investigar os efeitos da seleção de longo prazo nessa população (Lima et al., 1992; Pereira et al., 2005). Apesar da relevância dessa raça, ainda são escassos os estudos que avaliam os impactos genéticos da seleção para peso corporal sobre outras características economicamente importantes. Além disso, poucos estudos integram abordagens genômicas avançadas para explorar os mecanismos moleculares subjacentes a essas características, especialmente em raças adaptadas ao trópico.

Essa tese foi estruturada em dois estudos complementares sobre a raça Caracu. O primeiro investigou os parâmetros genéticos para peso corporal, características de carcaça e eficiência reprodutiva, com o objetivo de avaliar os efeitos diretos e indiretos

da seleção para crescimento. O segundo estudo aplicou metodologias de genômica integrativa, como WssGBLUP e AWM-PCIT, para identificar regiões genômicas e redes regulatórias associadas ao controle poligênico de características produtivas, revelando potenciais genes com efeitos pleiotrópicos.

2. OBJETIVO

2.1 Objetivo geral

Avaliar o impacto genético da seleção de longo prazo para peso corporal e investigar, por meio de abordagens quantitativas e genômicas integradas, o controle genético e regulatório de características de crescimento e carcaça em bovinos da raça Caracu.

2.2 Objetivos específicos

- Estimar parâmetros genéticos (herdabilidades e correlações genéticas) para peso corporal, características de carcaça e medidas de eficiência reprodutiva, a fim de avaliar os impactos indiretos da seleção para peso corporal.
- Avaliar a possibilidade de continuidade da seleção para peso corporal sem comprometer características economicamente importantes, como qualidade da carcaça e fertilidade.
- Identificar regiões do genoma associadas ao peso corporal, área de olho de lombo, relação altura/largura do músculo Longissimus dorsi, espessura de gordura subcutânea e espessura de gordura na garupa.
- Anotar e interpretar funcionalmente genes candidatos, com base em regiões genômicas de maior efeito e identificar vias biológicas relevantes envolvidas nos processos de crescimento e deposição muscular e adiposa.
- Construir redes de interação gênica por meio da abordagem AWM-PCIT, e destacar genes reguladores centrais e módulos com ação pleiotrópica sobre características produtivas.

3. REVISÃO DE LITERATURA

3.1 Importância econômica e desafios da pecuária brasileira

A pecuária desempenha papel de relevância para a economia brasileira, representando uma arrecadação de 252,27 bilhões de reais em meados de 2020, destes, 110 bilhões de reais equivalem a produção de bovinos, constituída por mais de 213 milhões cabeças (MAPA, 2020). Devido a melhor adaptação dos animais zebuínos (*Bos taurus indicus*) às condições tropicais, estes correspondem a 80% do rebanho nacional (Menezes, 2016). Além disso, de acordo com o relatório do *World Population Review* (2020), cerca de 225 mil pessoas são adicionadas à população mundial por dia. Esse aumento populacional gera a necessidade de novas tecnologias e abordagens na produção de alimentos que aumentem sua eficiência produtiva, e para que a oferta de alimentos seja compatível com a demanda. Associado a esse fato, a procura pela produção sustentável de alimentos tem crescido e incentivado uma reestruturação no setor de produção de carne bovina para obter produtos de melhor qualidade sem aumentar os custos de produção ao mesmo tempo que promovendo o bem estar dos animais. Dessa forma, o melhoramento genético busca melhorar a produtividade econômica das futuras gerações de espécies domésticas.

Apesar dos altos números de produção, dada a quantidade de animais pertencentes ao rebanho de corte brasileiro, o país ainda necessita incrementar os índices de produtividade. Dessa maneira, a produção animal tem sido influenciada por diversos fatores ao longo dos anos, o que impulsiona a investigação que minimize os prejuízos e maximize a eficiência produtiva. Portanto, para modificar o cenário produtivo e maximizar a lucratividade da bovinocultura de corte é fundamental que haja concomitante evolução de características de interesse econômico, respaldadas pelo melhoramento animal e controle de gastos com insumos para nutrição (Lancaster et al., 2009). Assim, a combinação de fatores genéticos e de manejo adequados pode permitir ao Brasil incrementar a produção de carnes diferenciadas segundo as diversas demandas dos vários mercados (Buainain e Batalha, 2007).

Neste contexto, uma alternativa para promover incrementos é a condução de programas de melhoramento animal, para a avaliação genética de bovinos de corte, que,

nas últimas duas décadas têm sido estabelecidos para o melhoramento de características de importância econômica, como as de crescimento, reprodutivas e morfológicas (Osso, 2016; Silva et al., 2020). As raças destinadas à produção de carne apresentam características fisiológicas e morfológicas diferentes em decorrência da região em que habitam, sendo que muitos autores buscam identificar raças mais adaptadas a determinado ambiente comparando animais zebuínos com taurinos (Renaudeau et al., 2012; Kumar et al., 2018; Veissier et al., 2018). Dessa forma, a raça Caracu, tornou-se adaptada às mais diversas condições locais, além de desenvolver características que permitiram aos animais sobreviver com dietas menos exigentes nutricionalmente, expostos a ectoparasitas e a elevadas temperaturas ambientais (Spritze et al., 2003).

3.2 Origem, evolução e importância da raça Caracu

A raça Caracu (*Bos taurus taurus*) foi formada ao longo de aproximadamente 400 anos, após cruzamentos descontrolados entre animais europeus trazidos pelos colonizadores, com forte contribuição de raças portuguesas/ibéricas, (Bicalho, 1985). Segundo ATHANASSOF (1957), o gado Caracu é oriundo das raças Minhota e Alentejana (tronco Aquitânico); BICALHO (1985) acrescenta que a raça Mertolenga também pode ter participado de sua formação, embora não existam registros da entrada de animais desta raça no Brasil; e, conforme PRIMO (2000), as raças Alentejana, Arouquesa, Barrosa, Minhota e Mirandesa foram responsáveis pela formação das raças Caracu e Curraleiro. Esses animais passaram por intenso processo de seleção natural devido às adversidades do clima tropical, bem como a alimentação escassa e a presença de parasitas (Lima et al., 1992). No início do século XX, algumas iniciativas, como o estabelecimento de um programa de melhoramento genético da raça realizado pelo Instituto de Zootecnia (IZ) da Secretaria da Agricultura e Abastecimento do Estado de São Paulo, aliado à criação do livro de registros, estabeleceram o padrão racial e promoveram o desenvolvimento da raça que atingiu seu ápice em 1940 e se tornou uma das raças mais expressivas da pecuária brasileira devido, principalmente a sua tripla aptidão (carne, leite e trabalho) e qualidades zootécnicas (Trovo e Duarte, 1981; Mercadante, 2005). Porém, a raça quase foi extinta na década de 60 devido à alta endogamia, à introdução de raças zebuínas e ao fechamento do livro de registros.

No entanto, em 1976 o Instituto de Zootecnia reativou o programa de seleção da raça Caracu visando a conservação desse material genético adaptado, o qual deu origem ao rebanho atual da Estação Experimental de Zootecnia de Sertãozinho – SP (Lima et al., 1992; Pereira et al., 2005). Neste programa os touros são selecionados para peso a um ano, ajustado para 378 dias, que é obtido ao final de um teste de desempenho de 168 dias, conduzido em confinamento, já as novilhas de reposição são selecionadas para alto peso corporal corrigido para 550 dias à pasto (Bonilha et al., 2008).

A partir de 1980, houve aumento de rebanhos da raça Caracu no Brasil, com a formação de nova associação de criadores (1980) e reabertura do Livro de Registros em 1983, marcando a recuperação e expansão da raça (Anon, 1989; Lima et al., 1990). Atualmente, segundo a ABC Caracu (2021), há cerca de 98 rebanhos. A raça Caracu é, por sua história e características, um patrimônio da pecuária nacional, uma vez que sustentou a produção brasileira antes da introdução dos zebuínos e, atualmente apresenta o maior rebanho efetivo para exploração pecuária entre as raças denominadas crioulas (ABC Caracu, 2021). Apesar de se tratar de uma raça taurina, os animais Caracu apresentam uma excelente adaptação ao clima tropical e subtropical brasileiro, possuindo características de qualidade de carne de animais taurinos (maciez), combinada com a habilidade de se desenvolver em qualquer região do país, característica típica dos zebuínos (McManus et al., 2010).

Alguns autores no Brasil tem avaliado o desempenho da raça Caracu para características relacionadas ao peso de carcaça (Bonilha et al., 2012; Cyrillo et al., 2012), produção e qualidade da carne (Lara et al., 2011; Ito et al., 2012), crescimento (Moreira et al., 2016), peso em diferentes idades (Gesualdi Júnior et al., 2006; Pereira et al., 2006), reprodução (Pagoto et al., 2023; Mattar et al., 2007; Queiroz et al., 2007), estresse térmico (Abduch 2021; Pires, 2021), produção de leite (Nascimento et al., 2019), e resiliência (Rodrigues et al., 2024). Apesar de sua relevância, o melhoramento genético para as características de carcaça e reprodutivas têm sido escassos/inexistentes para a raça Caracu.

3.3 Seleção de longo prazo para peso corporal: fundamentos e impactos

Durante muito tempo, o peso corporal foi tratado como o principal objetivo de seleção dos programas de melhoramento genético em bovinos de corte (Ferreira e Borjas, 2008). A seleção de longo prazo para essa característica tornou-se uma das estratégias mais utilizadas para impulsionar a produtividade nos rebanhos, buscando, geração após geração, animais que crescessem mais e mais rápido. Essa escolha foi baseada na alta variabilidade genética e pela herdabilidade moderada a alta observada em características como peso ao nascimento, peso à desmama e peso ao abate, o que possibilitou avanços genéticos consistentes ao longo do tempo (Ferreira e Borjas, 2008).

Uma das grandes vantagens de selecionar animais com maior peso corporal está no impacto direto na eficiência produtiva dos sistemas de carne. Animais que crescem mais tendem a apresentar melhor rendimento de carcaça, maior ganho de peso diário e, consequentemente, podem contribuir para uma maior rentabilidade na atividade pecuária. Estudos demonstram que a seleção para maior peso corporal pode ser acompanhada de melhorias indiretas em características economicamente importantes, como área de olho de lombo e conformação muscular, especialmente quando índices de seleção multicaracterísticas são empregados (Amorim et al., 2023; Bonilha et al., 2007).

Por outro lado, quando a seleção para peso corporal é feita de forma intensiva e mantida por muitas gerações, podem surgir alguns desafios importantes. Um deles é o aumento da consanguinidade dentro da população, o que, consequentemente, reduz a diversidade genética disponível e pode levar à chamada depressão endogâmica, uma queda no desempenho dos animais causada pelo acúmulo de genes desfavoráveis (Amaral et al., 2019). Além disso, é preciso estar atento aos efeitos pleiotrópicos, quando um mesmo gene afeta várias características ao mesmo tempo (Buss et al., 2023). Isso significa que ao selecionar animais para crescimento, podemos acabar influenciando negativamente outras características, como as características de carcaça, fertilidade, a conversão alimentar entre outras.

Outro ponto que merece atenção são as correlações genéticas desfavoráveis com outras características importantes para os sistemas de produção de carne. Focar exclusivamente no aumento do peso corporal pode acabar gerando animais muito

pesados na fase adulta, o que exige maior consumo de alimento e, por consequência, eleva os custos de manutenção, especialmente das fêmeas em reprodução (Menegaz et al., 2008; Ferreira et al., 1998). E também, aumentar o peso dos bezerros ao nascimento, pode aumentar a incidência de distocia no rebanho (Gasparelli et al., 2009; Pilau et al., 2009). Além disso, animais podem ter menor capacidade de adaptação a sistemas de produção mais rústicos ou extensivos, onde os recursos são mais limitados. Por isso, é fundamental adotar estratégias de seleção para evitar o aumento da frequência de características não desejadas, e o controle cuidadoso da consanguinidade.

3.4 Arquitetura genética das características de crescimento e carcaça em bovinos

Compreender a base genética das características de interesse zootécnico é um dos pilares do melhoramento animal moderno. Independente da característica, conhecer os fatores genéticos que controlam essas variáveis permite tomar decisões mais acertadas na seleção, otimizando os ganhos ao longo das gerações. Sem esse conhecimento, há o risco de focar apenas em resultados imediatos, sem considerar efeitos colaterais que podem comprometer a saúde, a adaptabilidade ou o equilíbrio do sistema produtivo (Euclides Filho, 1999).

Para isso, recorremos a alguns parâmetros fundamentais da genética quantitativa. A herdabilidade indica a proporção da variação de uma característica que pode ser atribuída à genética, em oposição aos efeitos ambientais. Quanto maior a herdabilidade, maior é a resposta esperada à seleção. Outro parâmetro chave são as correlações genéticas, que mostram como duas características se relacionam do ponto de vista genético (Euclides Filho, 1999).

As características associadas ao crescimento do animal são essenciais para determinar o sucesso da eficiência econômica de qualquer sistema de produção de bovinos de corte. As características de peso ou ganho de peso em diferentes idades são frequentemente utilizadas como critérios de seleção, pois são de fácil mensuração, apresentam média a alta herdabilidade, o que permite obter resposta à seleção, além de moderada a alta correlação genética com características de peso de carcaça (Laureano et al., 2011; Razook et al., 2001).

A medida de peso ao nascimento é a informação mais precoce da vida do indivíduo. Segundo Bunter et al. (2014), bezerros com extremos pesos ao nascimento tendem a apresentar maior mortalidade, o que causa um grande impacto econômico aos criadores. Enquanto um baixo peso ao nascimento está associado a um baixo vigor do bezerro, (Pires et al., 2020), um peso ao nascimento muito elevado está associado a maior risco de distocia devido a uma desproporção entre o tamanho do bezerro e o canal do parto (Pond e Bell, 2004). O peso ao nascimento apresenta valores de herdabilidade variando de 0,25 a 0,38 (Boligon et al., 2009; Chud et al., 2014; Kamprasert et al., 2019; Pereira et al., 2008), o que permite obter ganhos genéticos significativos mediante seleção. No entanto, o peso ao nascimento apresenta moderada a alta correlação genética com as características de peso até os dois anos de idade (Boligon et al., 2009). Sendo assim, a seleção para aumento de pesos em idades jovens pode levar a um aumento no peso ao nascimento, devendo ser feita de forma criteriosa.

Os pesos da fase maternal, aferidos em idades entre o nascimento e a desmama, avaliam não somente a capacidade de crescimento do animal, mas também a habilidade materna da mãe. O peso à desmama apresenta valores de herdabilidade direta variando entre 0,23 e 0,33 (Boligon et al., 2010; Laureano et al., 2011; Pereira et al., 2008), indicando possibilidade de resposta à seleção. Além disso, essas características apresentam correlações genéticas altas e positivas com os pesos em idades subsequentes (Boligon et al., 2010; Yokoo et al., 2007), indicando que essas características são controladas por genes em comum. Pereira et al. (2008) estudaram animais nascidos entre 1979 e 2002 do rebanho Caracu da Estação Experimental de Zootecnia de Sertãozinho e encontraram uma correlação genética de 0,90 entre o peso à desmama e o peso ao sobreano.

Os pesos ao ano e ao sobreano, mensurados por volta dos 13 e 18 meses de idade, permitem avaliar o potencial genético de crescimento do indivíduo após a desmama. Além disso, são mensurados em idade próxima da fase reprodutiva, o que contribui para que essas características sejam amplamente utilizadas como critérios de seleção. Apresentam valores de herdabilidade variando entre 0,24 e 0,37 (Boligon et al., 2010; Laureano et al., 2011; Pereira et al., 2005) e são geneticamente correlacionados

com pesos na idade adulta (Boligon et al., 2009). Isto significa que a seleção para aumento de peso em idades jovens pode levar a um aumento excessivo no tamanho dos animais na idade adulta, incrementando os custos de alimentação das matrizes, além de comprometer características reprodutivas e de sobrevivência (Baker et al., 1988; Vargas et al., 1999).

As características de carcaça têm sido cada vez mais valorizadas nos programas de seleção, pois estão intimamente relacionadas com o valor da carcaça e com a qualidade da carne (Wheeler et al., 1994). Podem ser avaliadas no animal *in vivo* através de ultrassonografia, ou após o abate na carcaça resfriada. A área do olho de lombo, definida como a área em cm² do músculo *longissimus dorsi*, é um indicador da composição da carcaça e está relacionada ao grau de musculosidade do animal (Boggs e Merkel, 1993). Já a espessura de gordura subcutânea, medida sobre o músculo *longissimus dorsi*, é um eficiente indicador do grau de acabamento da carcaça (Hedrick, 1983). Essas características apresentam valores de herdabilidade variando em torno de 0,23 a 0,33 (Caetano et al., 2013; Kluska et al., 2018), possibilitando obter resposta à seleção. Além disso, possuem correlação genética favorável com outras características. Caetano et al., (2013) estudaram bovinos da raça Nelore e relataram correlação de -0,35 entre gordura subcutânea e idade ao primeiro parto, indicando relação entre deposição de gordura e precocidade sexual. Os mesmos autores também encontraram correlação genética positiva entre a área do olho de lombo e características de crescimento. Apesar da importância, trabalhos estimando parâmetros genéticos para características de carcaça de bovinos da raça Caracu ainda são escassos.

3.5 Melhoria genética e integração de ferramentas genômicas

Com o desenvolvimento da genética e estatística quantitativa, o método da melhor predição linear imparcial (Best linear unbiased prediction; BLUP) proposto inicialmente por Henderson (1949) tornou-se o método mais amplamente aceito para avaliação genética de animais domésticos. O método BLUP evoluiu muito ao longo dos anos em termos de aplicação em modelos para avaliação genética, e permite estimar valores genéticos dos animais a partir de informações fenotípicas e de genealogia. No entanto, esse processo de seleção é lento e de alto custo, pois para a obtenção do fenótipo é

necessário aguardar o crescimento do animal e de sua progênie. Neste sentido, a disponibilidade e o uso de tecnologias genômicas pode potencialmente acelerar o progresso genético e aumentar a lucratividade da atividade, em consequência do aumento na eficiência de seleção e redução no intervalo de gerações. Além disso, a genômica facilita a avaliação de características de difícil ou de alto custo de mensuração.

Uma das ferramentas genômicas mais amplamente utilizadas atualmente para detectar variações no DNA são os polimorfismos de nucleotídeo único (SNP). Abundantes em todo o genoma (Schork et al., 2000), os SNPs apresentam potencial para uma análise automatizada de alto rendimento a custo moderado (Aguilar et al., 2019). Dentre as principais aplicações do uso de SNPs na área do melhoramento animal, se destaca a seleção genômica (SG), que visa utilizar a informação genômica para avaliar o potencial genético dos indivíduos. O método BLUP genômico (GBLUP), proposto por

VanRaden (2008), permite estimar os efeitos dos SNPs e o valor genético-genômico (GEBV) de animais genotipados através de uma matriz de parentesco genômico, representada por G. Como várias etapas são necessárias para calcular o GEBV, esse método é chamado de multi passos. No entanto, este apresenta algumas desvantagens: GEBVs são gerados apenas para modelos simples (unicaracterística e modelos não-maternos); apenas animais genotipados são incluídos no modelo; requer o uso de pseudo-fenótipos, que são complicados de se obter (Legarra et al., 2014). Com a intenção de resolver esses problemas, Misztal et al. (2009) propôs um método que combina fenótipos, pedigree e genótipos em uma única avaliação. Este método é denominado BLUP genômico de passo único (ssGBLUP) e envolve a substituição da matriz de parentesco do BLUP tradicional por uma matriz que combina pedigree e parentesco genômico, representada por H. De acordo com Legarra et al. (2014), a capacidade do ssGBLUP em utilizar as informações dos animais não-genotipados, a não dependência dos pseudo-fenótipos, são fatores responsáveis por ganhos de acurácia.

Outra importante aplicação da informação genômica são os estudos de associação genômica ampla (GWAS). O principal objetivo da realização de GWAS é de detectar SNPs que estejam associados, por meio de desequilíbrio de ligação, a loci controladores de características quantitativas (QTL). Tanto o GBLUP quanto o ssGBLUP assumem

pesos iguais para todos os SNPs, uma suposição biologicamente incorreta (Meuwissen et al., 2001). Desta forma, Wang et al. (2012) propuseram um método de aplicar uma ponderação diferente para cada SNP ao formar a matriz de parentesco genômico sob o método ssGBLUP, chamado de ssGBLUP ponderado (WssGBLUP). Diversos autores relataram vantagens no uso de métodos baseados em WssGBLUP em comparação com ssGBLUP não ponderado, com aumento na acurácia dos GEBVs e dos efeitos dos SNPs (Lourenco et al., 2017; Mehrban et al., 2021; Teissier et al., 2018; Zhang et al., 2016). Essa metodologia consiste em estimar iterativamente diferentes ponderações para cada SNP a partir da porção de variância genética aditiva da característica estudada que é explicada pelo SNP, causando um aumento nos pesos dos SNPs com grandes efeitos e reduzindo aqueles com pequenos efeitos, regredindo-os à média.

As análises de GWAS em geral detectam os marcadores mais significativos. No entanto, muitas vezes são identificados apenas parte dos SNPs significativos, que respondem por uma pequena proporção das variantes genéticas, oferecendo uma compreensão limitada de características complexas (Peng et al., 2010). Outro desafio é conseguir distinguir as variantes verdadeiramente associadas da preponderância de variantes que não estão associadas, mas que atingem a significância ao acaso (Chasman, 2008). Nesse contexto, análises de enriquecimento oferecem uma estratégia baseada na avaliação de conjuntos de genes funcionalmente relacionados, ao invés de focar somente nos marcadores mais significativos (Chasman, 2008; Peng et al., 2010). Esta análise complementar permite detectar genes que explicam menor variação genética, mas que, de forma conjunta, exercem grande influência na característica estudada. Também é capaz de identificar vias biologicamente associadas aos fenótipos, fornecendo um melhor entendimento dos mecanismos moleculares envolvidos na característica avaliada.

Com os resultados do WssGBLUP, também é possível montar a Association Weight Matrix (AWM), a qual organiza os pesos dos SNPs em relações de associação entre genes. A AWM não só destaca os genes mais fortemente ligados à característica, mas também revela as conexões funcionais entre eles, ou seja, mostra como os efeitos genéticos estão correlacionados ao longo do genoma. Isso é muito importante, já que

características complexas raramente são controladas por genes isolados, mas sim pela interação de vários genes em redes regulatórias e metabólicas (Fortes et al., 2010).

Além disso, a AWM permite a identificação de genes centrais, os quais possuem muitas conexões e que exercem um papel central na regulação da característica. Esses genes são importantes porque podem ser alvos prioritários para seleção genética, estudos funcionais ou até mesmo para intervenções biotecnológicas. A AWM, assim, traz uma visão mais sistêmica da genética da característica, permitindo entender não só “onde” os efeitos estão no genoma, mas também como esses efeitos se organizam em rede para formar o fenótipo observado (Fortes et al., 2010).

Para explorar melhor os resultados do AWM, pode-se integra-los e formar redes gênicas, conseguindo explorar as interações de forma ainda mais detalhada. A inferência dessas redes pode ser feita, por exemplo, por meio do algoritmo PCIT (Partial Correlation and Information Theory), que permite identificar as correlações significativas entre pares de genes considerando a influência de um terceiro gene, o que melhora a precisão na definição das conexões reais (Reverter e Fortes, 2013).

Redes gênicas podem ser visualizadas e analisadas em softwares como o Cytoscape, permitindo a identificação de módulos funcionais e fatores de transcrição centrais por ferramentas como o MCODE. A AWM não apenas destaca genes com efeito significativo em múltiplas características, sugerindo papéis regulatórios importantes, mas também revela conexões biológicas consistentes com mecanismos moleculares conhecidos, fortalecendo a interpretação biológica dos resultados de GWAS (Reverter & Fortes, 2013). O método PCIT (Partial Correlation with Information Theory) aumenta a robustez na identificação de interações genéticas ao eliminar correlações indiretas (Reverter & Chan, 2008), destacando genes centrais relacionados a fenótipos complexos quando usado com AWM. Em bovinos de corte, redes baseadas em PCIT identificaram fatores de transcrição associados ao crescimento corporal (Mudadu et al., 2016) e à deposição de gordura intramuscular (Schettini et al., 2022), incluindo PPARG em módulos ligados ao desenvolvimento muscular e metabolismo lipídico. De forma complementar, análises de redes gênicas em dados de GWAS revelaram conexões funcionais entre genes envolvidos no metabolismo energético e na diferenciação de fibras

musculares, reforçando seu papel em características de carcaça como área de olho de lombo e espessura de gordura subcutânea (Frezarim et al., 2025). Esses achados evidenciam que a integração de AWM e PCIT permite priorizar candidatos biológicos relevantes para peso corporal e composição de carcaça, indo além da mera significância estatística em GWAS.

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CHAPTER 2 – IS IT POSSIBLE TO SELECT BODY WEIGHT WITHOUT COMPROMISING CARCASS TRAITS AND REPRODUCTIVE EFFICIENCY IN CARACU CATTLE? [1]

ABSTRACT- The Caracu is a taurine breed adapted to Brazil's climatic conditions and has been selected for 40+ years for Body Weight (BW), maintaining performance records across multiple generations in its database. However, selecting young animals for BW can result in excessive growth, potentially impacting carcass and reproductive traits. This study aimed to estimate genetic correlations and, based on these estimates, evaluate how selection for BW (adjusted to 378 and 550 days of age for males and females, respectively) has influenced carcass traits and reproductive efficiency in this breed. The dataset contained records for BW (kg), Ribeye area (REA, cm²), Height-to-width ratio of the Longissimus dorsi muscle (HWR), Backfat thickness (BFT, mm), Rump fat thickness (RFT, mm), Yearly scrotal circumference (SC, cm), and Days to calving (DC, days) from animals born between 1966 and 2022. (Co)variance components were estimated by Bayesian inference using two-trait animal models. Analyses were conducted to estimate genetic parameters for pairs of traits, including BW with carcass traits (BW×REA, BW×HWR, BW×BFT, and BW×RFT) and BW with reproductive traits (BW×DC and BW×SC). Additionally, analyses were performed for pairwise combinations among carcass traits (REA×HWR, REA×BFT, REA×RFT, HWR×BFT, HWR×RFT, and RFT×BFT) and between reproductive traits (DC×SC). The relationship matrix included 4,783 animals, of which 829 were genotyped with the GGP Bovine 100K SNP panel. Favorable genetic correlations (rg) were observed between BW and REA (0.51±0.11), HWR (0.45±0.17), SC (0.24±0.13), and RFT (0.15±0.21), with the latter being favorable but low. On the other hand, unfavorable genetic correlations were observed between BW

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and BFT (-0.07±0.21), which was unfavorable but close to zero relationship, and between BW and DC (0.48±0.15). The significance of carcass and reproductive traits is underscored by the favorable, rg between BW and the carcass traits REA (BW×REA) and HWR (BW×HWR), while a high, unfavorable rg was observed between BW and DC cows. These findings emphasize the importance of carefully balancing genetic selection to optimize growth, carcass quality, and adequate reproduction in Caracu cattle.

Key-Words: Body weight, genetic correlation, ribeye area, height-to-width ratio, fat thickness, days to calving, scrotal circumference, genetic improvement.

1. INTRODUCTION

The Caracu breed (*Bos taurus*), originated in Brazil through uncontrolled crossbreeding of European cattle, and has been shaped by natural selection since the 16th century (Lima et al., 1992). These animals have faced challenges under tropical conditions, such as food scarcity and parasite exposure, which have contributed to their adaptability and resilience (McManus et al., 2010). Currently, Caracu is the Brazilian cattle breed with the largest herd among tropically adapted breeds, recognized for its resistance to harsh environmental conditions, productivity, and adaptability (Lima et al., 2020; Pires et al., 2021; Abduch et al., 2022; Pires et al., 2022). Derived from continental European breeds, Caracu is characterized by its large size and well-developed musculature, with lower fat levels compared to British breeds, which are smaller and can accumulate more fat (Marshall, 1994; Kause et al., 2015). Caracu animals exhibit a larger ribeye area (REA) and reduced fat deposition when compared to other tropically adapted breeds, such as Nellore (*Bos indicus*) (Gesualdi Júnior et al., 2006; Vittori et al., 2006).

Given the importance of weight gain in beef cattle selection, it is essential to assess how this selection impacts carcass and reproductive traits. Although weight gain is a primary target in beef production, focusing solely on this trait may compromise carcass quality and reproductive efficiency of the animals. It is therefore necessary to establish a balance between body weight and other key traits such as carcass conformation, meat yield, and fertility to optimize production and maintain livestock profitability. Yearling

weights are typically measured at approximately 13 and 18 months of age, respectively, and are important selection criteria due to their genetic correlation with mature weight, as reported in previous studies with the Nelore breed (Boligon et al., 2010). This correlation suggests that selecting animals for yearling weight can serve as an indirect way to improve mature weight without the need to wait for animals to reach full maturity. Heritability estimates for yearling weights range from 0.24 to 0.37 (Pereira et al., 2006; Boligon et al., 2010; Laureano et al., 2011), demonstrating their moderate genetic control. However, the genetic potential for increased mature weight, inferred from yearling weight, may lead to higher feed costs and potential negative effects on reproductive and survival traits (Baker et al., 1988; Vargas et al., 1998).

The importance of carcass traits in breeding programs has grown due to their strong association with carcass value and meat quality (Ripoll & Panea, 2022). These traits can be assessed on live animals by ultrasound, or after slaughter on chilled carcasses. The REA, which represents the area in cm² of the *Longissimus dorsi* muscle and is a key indicator of carcass composition as it is directly linked to animal's muscle deposition (Boggs & Merkel, 1993). On the other hand, backfat thickness (BFT), is measured over the *longissimus dorsi* muscle, and is an effective indicator of the degree of carcass finishing (Hedrick, 1983).

Reproductive traits are fundamental for the efficiency, productivity, and profitability of beef cattle herds (Jiménez et al., 2023). The heritability of scrotal circumference (SC), an easily measured trait, ranges from 0.31 to 0.46, indicating significant genetic contribution (Laureano et al., 2011; Buzanskas et al., 2017; Carvajal, 2017). While direct selection for SC may not yield immediate economic benefits (Bergmann, 1993), it correlates with other difficult-to-measure reproductive traits such as semen volume and age at first calving and also shows associations with growth and carcass traits (Barrera Carvajal, 2017). Days to calving (DC) directly influences productivity, as a reduction in DC increases the calving rate per cow and reduces production costs (Mercadante et al., 2013). However, when exploring the particularities of the Caracu breed, the impact of selection for yearling weight on reproductive and carcass traits remains unknown. While genetic relationships among these traits have been studied in other taurine and zebuine

breeds, limited information is available for Caracu cattle. Therefore, the aim of this study was to estimate genetic correlations and, based on these estimates, evaluate how selection for BW (adjusted to 378 and 550 days of age for males and females, respectively) has influenced carcass traits and reproductive efficiency of Caracu cattle.

2. MATERIAL AND METHODS

2.1 Animals and data collection

This study utilized data from the Caracu Selection Program of the Beef Cattle Research and Development Center, Animal Science Institute (IZ), Sertãozinho, SP, Brazil. The dataset comprised records of animals born from 1966 to 2022. Male animals were selected based on the highest expected selection differential for weight at the end of the performance test, within a contemporary group. The test comprises a 56-day adaptation period followed by a 112-day assessment period, with weights adjusted to 378 days of age (W378). Females were selected based on the highest expected selection differential for weights adjusted to 550 days (W550).

Days to calving (DC) was calculated as the difference between the calving date and the breeding season entry date; when fixed time artificial insemination (FTAI) was performed , it was obtained as the difference between the calving date and the date of first insemination. Females that failed to conceive were assigned the highest DC value within the breeding group (when natural mating was performed, the year of mating was considered; when FTAI was performed, the date of first insemination was considered) plus an additional 21 days as a penalty (Garcia et al., 2016; Johnston & Bunter, 1996).

At 7 months of age males were subjected to a weight gain test (for 168 days), while females remained on pasture until 18 months of age. At the end of the weight gain test, males were weighed, and weights were adjusted to 378 days of age (W378). On this occasion, SC was measured with a tape measure, and carcass measurements were obtained, as Ribeye area (REA), Height-to-width ratio of the *Longissimus dorsi* muscle (HWR), Backfat thickness (BFT) and Rump fat thickness (RFT). Female measurements were obtained, at 18 months of age (because of the grazing regimen), and at that age

females were weighed, and weights were adjusted to 550 days of age (W550). Carcass measurements were also obtained at the same age. For the analyses, W378 in males and W550 in females were considered the same trait (Ceacero et al., 2016), defined as body weight (BW) (Table1).

The pedigree file contained 4,783 animals; of these, 862 were genotyped with the GGP Bovine 100K SNP panel (NEOGEN, Lincoln, NE, USA). Quality control of the genomic data was performed by maintaining only autosomal single-nucleotide polymorphisms (SNP) with a minor allele frequency > 0.05, departure of heterozygous from Hardy-Weinberg equilibrium < 0.15, an SNP call rate > 90%, and a sample call rate > 90%, using preGSf90 program (Misztal et al., 2014). After quality control, 829 genotyped animals and 76,607 SNP were retained for further analysis.

Table 1. Data structure for growth, carcass, and reproductive traits of Caracu cattle

	Trait[1]						
	Growth	Carcass				Reproductive	
	BW	REA	HWR	BFT	RFT	SC	DC
Number of animals with records	3,496	1,291	762	1,300	1,312	973	5,939
Number of females with records	1,689	581	325	589	592	0	1,155
Number of males with records	1,807	710	437	711	720	973	0
Number of sires	155	87	49	86	87	89	164
Number of dams	1,014	516	335	513	518	472	645
Number of females in the pedigree	5,738	5,738	5,738	5,738	5,738	5,738	5,738
Number of sires in the pedigree	6,558	6,558	6,558	6,558	6,558	6,558	6,558
Number of dams in the pedigree	1,318	1,318	1,318	1,318	1,318	1,318	1,318
Number of parents in the pedigree	274	274	274	274	274	274	274
Number of contemporary groups	247	99	58	99	99	65	293

[1]BW = body weight; REA = ribeye area; HWR = height-to-width ratio of *Longissimus dorsi* muscle; BFT = backfat thickness; RFT = rump fat thickness; SC= scrotal circumference at yearling; DC = days to calving.

2.2 Statistical analysis

(Co)variance components for all traits were obtained by Bayesian inference using a single-trait (for heritabilities) and a two-trait (for correlations) animal model that always included BW, i.e., BW with carcass traits (REA, HWR, BFT, and RFT) and BW with reproductive traits (SC and DC). Bayesian methods were chosen for their ability to provide credible intervals and robust estimates, especially advantageous in datasets with limited size (van de Schoot et al., 2021). Gibbs sampling was performed using the gibbsf90+ program (Misztal et al., 2014), as well as the genetic correlations between carcass traits and between reproductive traits. The general model can be written as:

$$\mathbf{y = Xb + Z_1a + Z_2p + e},$$

where: **y** is the vector of observations (BW, REA, HWR, BFT and RFT); **b** is the vector of fixed effects of the contemporary group and covariate (defined later); **a** is the vector of animal additive genetic effects; **p** is the vector of animal permanent environmental effects; $\mathbf{Z_1}$ and $\mathbf{Z_2}$ are incidence matrices that relate **a** and **p** to **y**, and **e** is the vector of random residuals. The following (co)variance structure was assumed:

$$\mathrm{Var}\begin{bmatrix}\mathbf{a}\\ \mathbf{p}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{G_0}\otimes\mathbf{H} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{G_1}\otimes\mathbf{I_1} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{R_0}\otimes\mathbf{I_2}\end{bmatrix},$$

Where: $\mathbf{G_0}$ is the animal additive genetic (co)variance matrix among traits; **H** is the relationship matrix that combines pedigree and genomic information (Aguilar et al, 2010; Christensen and Lund 2010); $\mathbf{G_1}$ is the permanent environmental (co)variance matrix among traits; $\mathbf{I_1}$ is an identity matrix of the order equal to the number of dams with offspring; $\mathbf{R_0}$ is the residual (co)variance matrix; and $\mathbf{I_2}$ is an identity matrix of the order equal to the number of animals with records. The genomic relationship matrix used in matrix **H** construction, was obtained using the Method 1 of VanRaden (2008).

The model for BW, REA, HWR, BFT, and RFT included random animal additive genetic effects, as well as the fixed effects of contemporary group (year of birth, month of birth, sex), the linear effect of the animal's age at weighing or carcass evaluation, and the linear and quadratic effects of the dam's age at calving. The effects included in the model

for SC were similar, except for the exclusion of sex in the contemporary group. For the analysis of DC, the model included random animal additive genetic effects and animal permanent environmental effects, together with the fixed effects of contemporary group (when natural mating was performed, the sire and year of mating was included in the CG; when FTAI was performed, the date of first insemination was included in the GC)) and previous pregnancy (pregnant (1) or not pregnant (0)), in addition to linear and quadratic effects of the female's age at entry into the breeding season or first FTAI.

A total of 300,000 samples, with a burn-in period of 100,000 samples and a thinning interval of 10 samples, were considered. The convergence of the chains was checked using Geweke convergence diagnostic (Geweke, 1992).

Genetic trends were assessed using solutions of animal additive genetic effects. The genetic basis was defined using animals born in a specific base year (in this case equals to 1977), and all animals in the population were deviated from the average breeding value of this base. To estimate the annual genetic gain, a linear regression of the genomic estimated breeding values (GEBV) for all animals was performed on the coded year of birth (1, 2, ..., n) using PROC REG in the SAS statistical program (SAS Institute, Cary, NC, USA). Although the regression was based on all individual GEBV, only the annual means were plotted for visualization purposes.

3. RESULTS

The means of each trait analyzed are presented in Table 2. These results provide a comprehensive overview of the carcass and reproductive traits in Caracu cattle, revealing variability within the population. The average BW was 319 kg, while REA had a mean of 49.2 cm². The HWR of the *longissimus dorsi* averaged 0.42, indicating balanced conformation. Fat deposition traits showed moderate averages, with BFT at 1.14 mm and RFT at 3.50 mm. Reproductive traits demonstrated consistency, with SC averaging 30.2 cm and DC at 337 days.

Table 2. Mean, standard deviation (SD) and minimum and maximum values of growth, carcass and reproductive traits of Caracu cattle

Trait[1]	Mean ± SD	Minimum	Maximum
BW (kg)	319.00 ± 56.70	89.90	503.00
REA (cm^2)	49.20 ± 11.40	19.60	78.70
HWR	0.42 ± 0.06	0.25	0.63
BFT (mm)	1.14 ± 0.87	0.00	6.09
RFT (mm)	3.50 ± 2.25	0.00	11.30
SC (cm)	30.20 ± 3.59	17.00	40.00
DC (days)	337.00 ± 36.60	244.00	419.00

[1]BW = body weight; REA = ribeye area; HWR = height-to-width ratio of *Longissimus dorsi* muscle; BFT = backfat thickness; RFT = rump fat thickness; SC = scrotal circumference at yearling; DC = days to calving.

BW showed an additive genetic variance mean of 301 ± 50.6, with an interval from 202 to 401, and a residual variance of 835 ± 37.7. REA presented an additive genetic variance of 10.5 ± 2.5, with an interval from 5.5 to 15.4, while the residual variance was 33.3 ± 2.1. HWR displayed a genetic variance of 0.0009 ± 0.0003 and an interval from 0.0004 to 0.001, with a residual variance of 0.0019 ± 0.0002. BFT showed a genetic variance of 0.07 ± 0.02, while RFT was 0.14 ± 0.05, both with moderate residual variances. SC revealed a genetic variance of 3.7 ± 0.78 and a residual variance of 4.5 ± 0.55. Finally, DC had a genetic variance of 61 ± 20.7, a permanent environmental variance of 95 ± 20, and a residual variance of 980 ± 20.9 (Table 3).

Table 3. Posterior mean estimates of genetic and residual variances for weight, carcass, and reproductive traits of Caracu cattle

Trait	σ^2_a	PSDI (95%)	σ^2_p	PSDI (95%)	σ^2_e	PSDI (95%)
BW	301.00 ± 50.60	202.00 to 401.00	-	-	835.00 ± 37.70	762.00 to 909.00
REA	10.50 ± 2.50	5.50 to 15.40	-	-	33.30 ± 2.10	29.00 to 37.50
HWR	0.0009 ± 0.0003	0.0004 to 0.001	-	-	0.0019 ± 0.0002	0.001 to 0.002
BFT	0.07 ± 0.02	0.03 to 0.12	-	-	0.44 ± 0.02	0.39 to 0.49
RFT	0.14 ± 0.05	0.04 to 0.23	-	-	0.78 ± 0.05	0.68 to 0.87
SC	3.70 ± 0.78	2.20 to 5.30	-	-	4.50 ± 0.55	3.40 to 5.60
DC	61.00 ± 20.70	21.00 to 102.00	95.00 ± 20.00	56.00 to 135.00	980.00 ± 20.90	939.00 to 1021.00

BW = body weight; REA = ribeye area; HWR = height-to-width ratio of *Longissimus dorsi* muscle; BFT = backfat thickness; RFT = rump fat thickness; SC = scrotal circumference at yearling; DC = days to calving; σ^2_a = additive genetic variance; σ^2_p = permanent environmental variance; σ^2_e = residual variance; PSDI (95%) = 95% posterior standard deviation interval.

The heritability (h^2) estimates for growth and carcass traits ranged from moderate (for BW, REA, and HWR) to low (for BFT and RFT) magnitudes. Genetic correlations (r_g) between BW and carcass traits were generally favorable, with magnitudes varying considerably (Table 4), except for BW×BFT. r_g estimates for BW×REA and BW×HWR were both favorable (0.51 ± 0.11 and 0.45 ± 0.17, respectively), suggesting some positive impact of BW selection on these traits. Conversely, the r_g between BW and BFT was unfavorable, but close to zero (-0.07 ± 0.21), while the r_g between BW and RFT was favorable but also low (0.15 ± 0.21).

Table 4. Posterior estimates of heritability (diagonal; from single-trait), genetic (above the diagonal) and phenotypic (below the diagonal) correlations (from two-trait), their respective standard deviations and 95% posterior standard deviation intervals (in parentheses) for body weight and carcass traits of Caracu cattle

	BW	**REA**	**HWR**	**BFT**	**RFT**
BW	**0.26 ± 0.04**	0.51 ± 0.11	0.45 ± 0.17	-0.07 ± 0.21	0.15 ± 0.21
	(0.19 to 0.34)	(0.29 to 0.74)	(0.12 to 0.78)	(-0.47 to 0.34)	(-0.26 to 0.55)
REA	0.54 ± 0.02	**0.24 ± 0.05**	0.93 ± 0.08	0.32 ± 0.21	0.08 ± 0.25
	(0.50 to 0.59)	**(0.14 to 0.34)**	(0.77 to 1.10)	(-0.11 to 0.74)	(-0.40 to 0.56)
HWR	0.24 ± 0.04	0.31 ± 0.05	**0.32 ± 0.08**	0.43 ± 0.21	0.41 ± 0.26
	(0.17 to 0.32)	(0.21 to 0.42)	**(0.16 to 0.48)**	(0.15 to 0.84)	(-0.09 to 0.91)
BFT	0.20 ± 0.03	0.19 ± 0.04	0.13 ± 0.04	**0.14 ± 0.04**	0.76 ± 0.16
	(0.14 to 0.26)	(0.11 to 0.26)	(0.05 to 0.20)	**(0.05 to 0.23)**	(0.45 to 1.07)
RFT	0.13 ± 0.03	0.11 ± 0.04	0.14 ± 0.04	0.29 ± 0.03	**0.15 ± 0.05**
	(0.07 to 0.19)	(0.03 to 0.18)	(0.05 to 0.22)	(0.23 to 0.35)	**(0.05 to 0.25)**

BW = body weight; REA = ribeye area; HWR = height-to-width ratio of *Longissimus dorsi* muscle; BFT = backfat thickness; RFT = rump fat thickness.

All correlations between carcass traits were favorable. Favorable relationships were observed between REA×HWR, HWR×BFT, HWR×RFT, and BFT×RFT, while favorable but weaker relationships were found between REA and subcutaneous fat thickness (BFT and RFT), with r_g with RFT being close to zero. All r_g estimates between growth and carcass traits showed high standard errors (Table 4).

h^2 estimate for SC was high. DC showed a low h^2 and low repeatability (0.14 ± 0.10). The r_g between BW and reproductive traits showed a favorable relationship with SC (BW×SC = 0.24), but an unfavorable relationship with DC (BW×DC = 0.48). The r_g between SC and DC was also unfavorable, but with low magnitude (-0.19 ± 0.26), with a high standard error (Table 5).

Table 5. Posterior estimates of heritability (diagonal), genetic correlation (above the diagonal) and phenotypic correlation (below the diagonal), and standard deviations and their respective 95% posterior standard deviation intervals (in parentheses) for weight at selection and reproductive traits of Caracu cattle

	BW	**SC**	**DC**
BW	**0.26 ± 0.04**	0.24 ± 0.13	0.48 ± 0.15
	(0.18 to 0.33)	(-0.01 to 0.49)	(0.19 to 0.77)
SC	0.41 ± 0.03	**0.45 ± 0.08**	-0.19 ± 0.26
	(0.36 to 0.46)	**(0.29 to 0.60)**	(-0.64 to 0.30)
DC	-0.13 ± 0.05	-	**0.05 ± 0.02**
	(-0.22 to -0.03)		**(0.02 to 0.09)**

BW = body weight; SC= scrotal circumference at yearling; DC = days to calving.

There was an increasing genetic trend over the years, for BW, REA, HWR, RFT, and SC (Figures 1 and 2). However, instability was observed in the mean GEBV for BFT and DC over the years. The estimated linear regression coefficients were of small magnitude for the carcass traits, but the linear effect of regression was significant for BW, REA, HWR, and RFT, indicating subtle genetic changes over the years. The linear regression coefficients were 0.860±0.012 kg/year for BW, 0.098±0.002 cm²/year for REA,

0.0006±0.00005/year for HWR, -0.0005±0.0001 mm/year for BFT, and 0.002±0.0001 mm/year for RFT (Figure 1). Positive genetic changes over time were also observed in the reproductive traits, with linear regression coefficients of 0.019±0.001 cm/year for SC and of 0.0011±0.00006 days/year for DC (Figure 2); however, the linear effect of the regression of GEBVs on year of birth was significant only for SC.

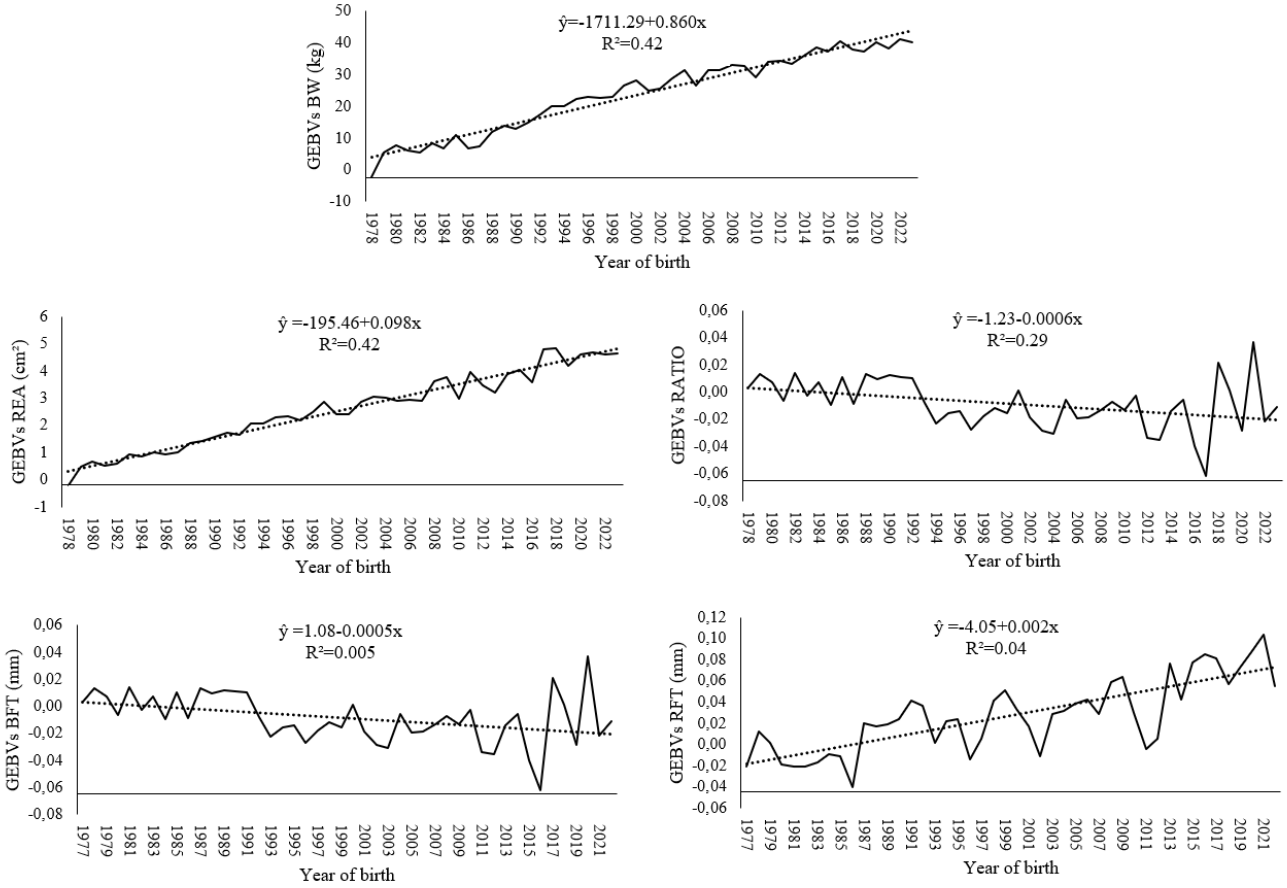

Figure 1. Genetic trends for growth and carcass traits of Caracu cattle. GEBV = genomic estimated breeding value; BW = body weight; REA = ribeye area; HWR = height-to-width ratio of *longissimus* muscle; BFT = backfat thickness; RFT = rump fat thickness; R^2 = coefficient of determination.

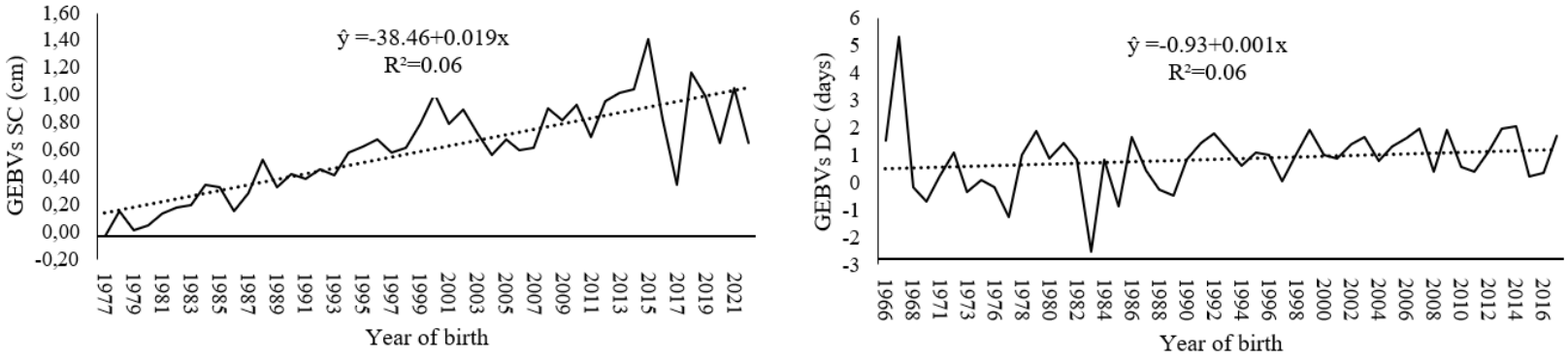

Figure 2. Genetic trends for reproductive traits of Caracu cattle. GEBV = genomic estimated breeding value; SC = scrotal circumference at yearling; DC = days to calving; R^2 = coefficient of determination.

4. DISCUSSION

Given the limited number studies on genetic parameters for carcass and reproductive traits in Caracu, our results will be compared to those of studies involving taurine and zebuine breeds.

The Caracu breed exhibits characteristics that reflect its selection for efficiency in lean meat production. Compared to taurine breeds, Caracu animals have a similar REA and HWR, indicating similar muscle growth. Previous studies have shown that taurine animals generally exhibit a greater REA, which is positively correlated with live weight (Hassen et al., 1999; Suguisawa, 2002; Koohmaraie et al., 2003), this favors muscle development in environments with abundant food resources and milder climates. On the other hand, zebuine breeds generally have intermediate values of REA, BFT and RFT when compared to other taurine breeds, which have a greater REA, and British taurine breeds (Lopes et al., 2008). Both Caracu and Zebu cattle are adapted to the tropical climate, i.e., they deposit less fat, while animals with greater fat deposition are genetically more susceptible to heat (Prayaga et al., 2009). However, since Caracu is derived from continental taurine breeds that naturally have less fat deposition, this breed exhibits less fat than zebuine cattle (Gesualdi Júnior et al., 2006; Vittori et al., 2006).

A greater SC may indicate greater reproductive potential and better adaptation to the conditions of tropical environments where heat stress can affect reproduction (Butler et al., 2019; Morrell et al., 2020 and Wahyudi et al., 2022). The DC, with a mean value of 337.46 days observed in this study, reflects the interval between insemination or service of the cow and subsequent calving. This value suggests that the reproductive performance of the herd aligns with acceptable ranges for efficient management. A shorter DC is known to reduce calving intervals and increase herd productivity (Morris et al., 2016). In the context of tropical climates, where environmental conditions can compromise reproductive efficiency, this result highlights the herd's ability to maintain satisfactory reproductive performance under such challenges, reinforcing the importance of tailored reproductive strategies.

The h^2 estimate for REA (0.24 ± 0.05) obtained in the present study (Table 4) had a magnitude similar to the estimates reported by Su et al. (2017) for Hereford and

Simmental animals (0.31 and 0.32) and by Weik et al. (2021) and Kemp et al. (2002) for Angus, Hereford, Charolais, and Simmental animals (0.36). This similarity suggests that the genetic control of REA in the Caracu breed, despite its adaptation to tropical environments, aligns closely with that of taurine breeds traditionally raised in temperate climates. For zebuine breeds raised in Brazil, similar h^2 estimates have been reported by Da Silva Neto et al. (2020), Marestone et al. (2022), and Barro et al. (2023) for Nellore animals (0.31 to 0.37), by Bessa et al. (2021) for Brahman animals (0.24), and by Pereira et al. (2023) for the Guzerat breed (0.27). These findings reinforce the idea that this tropical-adapted taurine population maintains genetic potential for muscle development comparable to other taurine breeds while also demonstrating some similarity with zebuine breeds, possibly due to shared adaptive pressures in tropical environments. The observed h^2 for HWR in the present study was moderate (0.32 ± 0.08) (Table 4). Marestone et al. (2022) reported a similar estimate for Nellore cattle (0.31), suggesting that heritability for HWR may also exhibit moderate values in other tropical-adapted breeds. However, further studies are needed to confirm whether this pattern holds across different populations and production systems.

Carcass fat deposition traits generally had lower h^2 estimates than other carcass traits (Table 4). Heritability estimates for RFT and BFT in the present study for Caracu are consistent with previous reports for these traits in zebuine breeds (Faria et al., 2015; Da Silva Neto et al., 2020; Bessa et al., 2021; Pereira et al., 2023). Notably, the studies by Faria et al. (2015), Da Silva Neto et al. (2020), and Bessa et al. (2021), which reported results similar to the present analysis, estimated variance components using Bayesian methods, as did our study. This approach differs from traditional methods used in other studies, such as Robinson et al. (1993) and Karsburg (2003), which reported low h^2 estimates for BFT in taurine breeds (0.05 and 0.13, respectively), and Arnold et al. (1991) and Weik et al. (2021), which found higher estimates (0.58 for BFT and 0.54 for RFT). Bayesian methodologies are particularly advantageous in studies of populations reared under variable and extensive systems, as they allow for more precise estimates by incorporating prior information and better accounting for the complex interplay between genetic and environmental factors. The Caracu breed, classified as a continental and

large-frame breed, is maintained in a low-input production system in the studied population. Animals are raised on pasture until weaning at 7 months of age. Females remain on pasture until 550 days of age, while males are confined until one year of age, at which point both groups are submitted to carcass ultrasound evaluation. This management, which is characterized by a variable nutrition environment and extensive rearing, increases the influence of environmental factors such as pasture quality and climate conditions on fat deposition traits. The transition of males to the feedlot is accompanied by an abrupt change in diet that, combined with accelerated growth during this phase, hinders the full genetic expression of fat deposition. These conditions increase environmental variability and reduce heritability estimates. Considering the natural selection of the Caracu breed for adaptation to the tropics, together with the artificial selection for BW gain evaluated in the present population, most of the energy generated by the production of VFAs is used for metabolic functions of muscle maintenance and growth, which may produce animals with a lower propensity to accumulate fat. In addition, the adaptive capacity may direct more energy to coping with adverse conditions such as climate and the presence of endo- and ectoparasites (Davide et al., 2019; Colelli et al., 2022).

In the present study, the h^2 estimated for SC was 0.47 ± 0.08 (Table 5). McAllister et al. (2011) and Russell et al. (2021) reported similar heritabilities (0.46 and 0.45, respectively) for Angus, Simmental, Red Angus, and South Devon cattle. Carvalho Filho et al. (2020) also estimated an h^2 for SC of 0.47 in Nellore animals. Days to calving is an important reproductive measure that indicates the interval between the time point when the cow enters the breeding season or is inseminated and subsequent calving. Thus, the shorter this interval, the more efficient reproduction (Morris et al., 2016). Heritability estimates for this trait similar to that of the present study (h^2 = 0.05 ± 0.02) have been reported by Mercadante et al. (2003); Olasege et al. (2021); Facy et al. (2022) and Da Silva Morales et al. (2024), with values of 0.08 and 0.10, 0.06, 0.13 and 0.07 to 0.17, respectively, in studies involving Nellore animals, composite bulls and Brahman animals. Since DC is a temporal trait, it may be more easily affected by factors linked to the environment such as reproductive cyclicity, nutrition, climate conditions, management,

health, and stress (Sartori & Guardieiro, 2010; Almeida et al., 2020; Fernandez-Novo et al., 2020). This indicates that the ability to transmit DC from one generation to another becomes limited, suggesting that the development and expression of this trait are more influenced by the environment than by genetics. For traits such as DC that possess repeated measurements over time, when h^2 and repeatability are low, as occurred in the present study (0.05 ± 0.02 and 0.14 ± 0.10, respectively, Table 5), and reported for Nellore cattle (repeatability of 0.11) by Da Silva Morales et al. (2024), the variation in the trait observed is more influenced by environmental or transient factors than by genetic and permanent environmental differences.

The h^2 for body weight of Caracu was investigated by Pereira et al. (2006, 2008), Portes et al. (2020) and Rodrigues et al. (2024). However, in contrast to our study in which male and female weights were considered a single trait, these authors individually used W365 for males and W550 for females when estimating h^2. Pereira et al. (2006) reported a medium h^2 for both weights (0.35 and 0.42, respectively), while Pereira et al. (2006) observed a medium h^2 for W365 (0.36) and a high h^2 for W550 (0.37). Rodrigues et al. (2024) also observed h^2 for W550 of 0.38. Despite the methodological differences, all studies involved the same herd, although in different years, thus expecting similar h^2 results for these weights.

The Caracu herd of the Animal Science Institute has been selected for yearling weight since 1978, over nine generations, to increase the size and live weight of the animals, which are directly related to muscle development. According to Pinheiro et al. (2012), cattle selected for higher yearling weight tend to have greater muscle mass, which contributes to a greater REA. A strong favorable genetic correlation (r_g) between BW and REA is therefore physiologically plausible because of the increased muscling associated with higher yearling weight. Furthermore, an increase in animal size may affect not only REA but also HWR. However, the relationship between BW and HWR may be less direct than the relationship between BW and REA since the last trait involves an increase in muscle size, while HWR is mainly linked to a change in the spatial distribution of the loin. Thus, a favorable but less pronounced genetic correlation between BW and HWR can be expected.

The r_g estimates of BFT and RFT with BW were low, with BFT showing an unfavorable relationship (-0.07 ± 0.21), but close to zero relationship, and RFT showing a favorable but low relationship (0.15 ± 0.21). This indicates that selection has a small effect on body fat deposition in the breed. However, the standard deviations were high, possibly because Caracu, as an adapted taurine breed, tends to accumulate less subcutaneous fat when compared to other taurine and to zebuine breeds (Vittori et al., 2007; Bonilha et al., 2014). This trait, combined with ultrasound image artifacts, may compromise the accuracy of subcutaneous fat measurements, increasing variation and affecting data consistency.

Both BW and SC are related to physiological development in cattle. Since many traits in these animals are influenced by a combination of genetic and environmental factors, it is plausible to assume that BW and SC have an underlying genetic basis. It is therefore possible that some of the same genes or genomic regions influence the expression of these traits, a fact that may explain the favorable correlation (0.24 ± 0.13) between them. In the case of SC, the estimated r_g is favorable since a greater SC is associated with better reproductive performance. On the other hand, the r_g between BW and DC is unfavorable since an increase in BW can result in longer DC, i.e., cows with a longer service period or even with calving failure, as cows that entered the breeding season and did not conceive received a registration of DC. However, the unfavorable r_g between BW and DC increased the gestation period due to the increase in birth weight. In Caracu, Portes et al. (2020) reported a favorable r_g (0.61 ± 0.09) between BW and birth weight, which may have generated this increase in the gestation period, affecting DC. In addition, larger calves may be associated with a longer gestation (Bourdon & Brinks, 1982), increasing DC.

The r_g between traits and their h^2 permit to predict the correlated genetic gain in a trait as a response to selection for another trait, as in the present study the selection for BW and the response in the other traits evaluated. Furthermore, the r_g between related traits may permit indirect selection for a target trait through selection for another correlated trait. Although most of the r_g estimates between BW and the other traits studied were favorable, the annual genetic gain (correlated response) in these traits was not high. On

the other hand, observation of the genetic trends over the years led us to conclude that indirect selection (correlated response) occurred in the desired direction for REA, HWR, BFT, RFT, and SC. However, the correlated response was undesirable for DC.

The choice of a two-trait analysis in this study was driven by the limitations of the dataset, particularly the sparse number of observations for some traits. While multi-trait models are known to provide more accurate estimates by simultaneously considering all genetic relationships, they require a robust dataset with sufficient connectivity between traits and animals. In this case, the two-trait approach ensured model convergence and maintained a higher degree of connectivity between contemporary groups, which was crucial for obtaining reliable genetic parameter estimates. Although this approach may not capture all pleiotropic effects or indirect selection responses across multiple traits, it provided biologically plausible results that align with the expected genetic architecture of the Caracu breed. Future studies with larger datasets should consider multi-trait analyses to further refine these estimates.

The direct response to selection for BW was effective, with an increase of 0.860 kg/year, corresponding to a gain of 0.30% per year. This finding indicates an increasing genetic trend over the years, with significant genetic changes in BW. Although moderate, the magnitude of gain suggests that selection for BW was successful in promoting consistent genetic improvements in the trait of the breed over time.

These results highlight the genetic potential of the Caracu breed for traits related to carcass and reproductive efficiency, even under tropical conditions. Based on the findings, it is recommended that selection strategies for this breed prioritize traits such as BW and SC, which exhibit favorable genetic trends and moderate to high h^2, ensuring sustained genetic progress. Moreover, the unfavorable r_g observed for DC underscore the importance of considering this trait when designing selection programs. This could involve the inclusion of reproductive efficiency traits as selection criteria to mitigate potential negative effects on calving intervals. Tailored selection strategies that balance productivity and adaptability traits are crucial to maintaining the dual-purpose characteristics of the Caracu breed while enhancing its suitability for tropical environments.

5. CONCLUSION

Thus, it is indeed possible to select for increased body weight in tropically adapted *Bos taurus* without compromising carcass traits or reproductive efficiency, provided that reproductive traits are carefully monitored. The genetic correlations indicated a favorable relationship between weight at selection and the carcass traits ribeye area and height-to-width ratio of *longissimus* muscle. However, the high unfavorable genetic correlation between body weight and days to calving highlights the need to monitor reproductive efficiency to avoid potential negative impacts from selecting for increased weight. Despite this, selection for body weight in the tropically adapted Caracu breed proved to be effective, leading to an annual gain of 0.30% in phenotypic average. This consistent genetic progress corroborates the hypothesis that selection for body weight can be pursued over time without detrimental effects. Furthermore, while selection for body weight promoted a favorable increase in ribeye area and height-to-width ratio of *longissimus* muscle, it did not significantly affect subcutaneous fat deposition. This demonstrates that the Caracu breed, with its tropical adaptability, maintains lower fat accumulation compared to other breeds.

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CHAPTER 3– INTEGRATIVE GENOMIC ANALYSIS OF GROWTH AND CARCASS TRAITS IN CARACU CATTLE USING AWM-WSSGBLUP AND GENE NETWORK APPROACHES

ABSTRACT- Caracu is a cattle breed adapted to tropical environments. Historically, selection prioritized body weight (BW), which may cause uneven genetic progress in traits such as fat deposition and muscle development. Despite advances, the genetic basis of these traits remains partially unknown. To address this, we characterized genomic regions, biological pathways, and regulatory networks controlling growth and carcass traits in Caracu cattle using WssGBLUP, Association Weight Matrix (AWM), and Partial Correlation and Information Theory (PCIT). Data from 3,496 animals, including 862 genotyped with the GGP Bovine 100K SNP panel, were analyzed for BW, ribeye area (REA), height-to-width ratio of *Longissimus dorsi* muscle (HWR), backfat thickness (BFT), and rump fat thickness (RFT). The top ten windows explained 27.79% (BW), 23.08% (REA), 21.67% (HWR), 31.74% (BFT), and 21.36% (RFT) of the total additive genetic variance and were mainly concentrated on BTA18, BTA2, BTA21, BTA1, and BTA11, respectively. Functional analyses revealed over-represented processes related to tissue development, metabolism, and immune response. The AWM-PCIT identified four hub genes (*ZEB2*, *LTF*, *IRX3*, and *LHX1*) with synergistic and antagonistic associations across traits, highlighting regulatory complexity in growth and carcass phenotypes. This integrative approach identifies key genomic regions, enriched pathways, and regulatory networks, supporting functional validation and balanced genomic selection in Caracu cattle.

Key-words: Candidate genes; Gene interaction; Genetic architecture; Genomic selection; Tropical cattle.

1. INTRODUCTION

Growth and carcass traits are determinants for the productivity and profitability of beef cattle production systems. Genetic improvement programs have historically emphasized body weight (BW), given its direct influence on growth efficiency, commercial value, and economic return (Enns et al., 2008). Among tropically adapted cattle, Caracu is a Brazilian breed acknowledged for its resistance to harsh environmental conditions, productivity, and adaptability (Abduch et al. 2022; Pires et al. 2021, 2022; Lima et al. 2020). Descendant of continental European breeds, Caracu animals combine robust musculature, similar to taurine cattle, but a limited capacity for fat deposition. This lean phenotype is likely due to their adaptation to tropical climates and continental origin (ABCC, 2025; Zhou et al., 2022; Cooke et al., 2020; Huuskonen and Pesonen, 2017; Gesualdi Júnior et al., 2006).

Over the decades, selection led to a well-established genetic base for BW in Caracu (Pereira et al., 2008). However, targeted selection for this trait alone may have detrimental effects on other economically correlated traits, such as fat deposition and muscle development, leading to unbalanced genetic progress (Ligori et al., 2025). Understanding the genetic basis of muscle and fat deposition traits is important for designing balanced breeding strategies. Carcass composition traits, such as ribeye area (REA), height-to-width ratio of the *Longissimus dorsi* muscle (HWR), backfat thickness (BFT), and rump fat thickness (RFT), correspond to the balance between muscle and adipose tissue development, being major drivers of carcass quality and yield (Marcelo et al., 2013; Greiner et al., 2003; Hopkins and Roberts, 1995).

Over the past two decades, genome-wide association studies (GWAS) have advanced knowledge of the genetic architecture of these traits in taurine and zebuine populations. Candidate genes such as *CAPN1* and *CAST* have been consistently linked to meat tenderness, while genomic regions on BTA6, BTA14, BTA20, and BTA29 were associated with carcass fatness, marbling, and REA (Yao et al., 2024; Zalewska et al., 2021; Węglarz et al., 2020; Lee et al., 2019; Sun et al., 2018; Leal-Gutiérrez et al., 2018; Hay & Roberts, 2018; Mizell et al., 2017; Corva et al., 2007; Takasuga et al., 2007). In

zebuine cattle, studies identified associations with fat thickness and REA, though most loci showed population-specific effects with limited replication across breeds (Reis et al., 2024; Silva-Vignato et al., 2022; Lopes et al., 2021; Doyle et al., 2020; Hay and Roberts, 2018; Tizioto et al., 2013). Despite these advances, causal mutations remain unknown, and the biological pathways orchestrating muscle and fat deposition are still poorly understood. The genetic architecture of growth and carcass traits in Caracu cattle remains unexplored, limiting the development of tailored genomic selection strategies for this breed.

Because BW and carcass traits are polygenic (Arikawa et al., 2024; Sanchez et al., 2023), methods capable of capturing this complex inheritance are required. The Weighted Single-Step Genomic Best Linear Unbiased Prediction (WssGBLUP) has been proposed as an efficient GWAS strategy for dissecting polygenic traits (Barbosa et al., 2023; Mehrban et al., 2021; Lopez et al., 2019; Wang et al., 2012). However, GWAS analyses only generate lists of associated loci, which restricts the understanding of interactions among genes and biological systems. Integrative approaches, such as the Association Weight Matrix (AWM) combined with PCIT (Partial Correlation and Information Theory), represent a promising strategy to overcome these limitations, since these methodologies allow the reconstruction of gene networks and highlight regulatory relationships underlying complex traits (Botelho et al., 2021; Fortes et al., 2011; Reverter and Chan, 2008).

In this study, we performed the first comprehensive analysis of the genomic architecture of growth and carcass traits in Caracu cattle. Combining a GWAS approach with gene network analyses, we investigated genome regions associated with these traits to understand the biological pathways and regulatory interactions that influence their expression. This integration revealed the polygenic control and pleiotropic effects involved, providing new insights into the genetic basis of adaptation and productivity in Caracu breed.

2. MATERIAL AND METHODS

2.1 Animals and data collection

This study utilized data from the Caracu Selection Program of the Beef Cattle Research and Development Center, Institute of Animal Science (IZ), Sertãozinho, SP, Brazil. The dataset comprised records of animals born from 1977 to 2022. Male animals were selected based on the highest expected selection differential for weight at the end of the performance test, relative to their average contemporaries. The test comprised a 56-day adaptation period followed by a 112-day evaluation period, with weights adjusted to 378 days of age (W378). Females were selected based on the highest expected selection differential for weights adjusted to 550 days (W550).

After weaning (at 7 months of age), males were subjected to a weight gain test for 168 days (56 days for adaptation and 112 days for the test). At the end of the test, males were weighed, and BW was adjusted to 378 days of age (W378). At the same time, carcass measurements such as ribeye area (REA), height-to-width ratio of the *Longissimus dorsi* muscle (HWR), backfat thickness (BFT), and rump fat thickness (RFT) were obtained by ultrasound. Female measurements were obtained at 18 months of age (because of the grazing regimen). Similarly, carcass evaluation was performed, and the BW was adjusted to 550 days of age (W550). For the analyses, W378 in males and W550 in females were considered the same trait (Ceacero et al., 2016), defined from now on as body weight (BW) (Table 1).

Table 1. Descriptive statistics of phenotypic information for body weight (BW), ribeye area (REA), height-to-width ratio of the *Longissimus dorsi* muscle (HWR), backfat thickness (BFT), and rump fat thickness (RFT) of Caracu cattle.

Traits	N	Mean	SD	CV (%)	Min	Max	NCG
BW (kg)	3496	319	56.7	17,77	89.9	503	349
REA (cm^2)	1291	49.2	11.4	23,17	19.6	78.7	119
HWR	762	0.42	0.06	14,29	0.25	0.63	70
BFT (mm)	1300	1.14	0.87	76,32	0	6.09	119
RFT (mm)	1312	3.50	2.25	64,29	0	11.3	119

N= number of observations; SD= standard deviation; CV= coefficient of variation; Min and Max= minimum and maximum values; NCG= number of contemporary groups.

Carcass ultrasound was performed using a Pie Medical 401347-Aquila apparatus (Esaote Europe B.V.) equipped with a 3.5-MHz linear probe (18 cm). The transducer was positioned perpendicular to the spine between the 12^{th} and 13^{th} ribs, on the left side of the animal, covering the *Longissimus dorsi* muscle region. A standoff pad was used to obtain images for the measurement of REA, HWR, and BFT. For the RFT measurement, the images were obtained by positioning the transducer at the intersection of the *Gluteus medius* and *Biceps femoris* muscles, located between the ilium and ischium. No standoff pad was used for RFT, and vegetable oil was applied as a coupling agent. The Echo Image Viewer 1.0 program (Pie Medical Equipment B.V., 1996) was used to analyze the images and measurements.

2.2. Genotypic data

The pedigree file contained 4,783 animals, of which 862 were genotyped with the GGP Bovine 100K SNP panel (NEOGEN, Lincoln, NE, U.S.A). Quality control of the genomic data was performed by maintaining only autosomal single-nucleotide polymorphisms (SNPs) with a minor allele frequency > 0.05, Hardy-Weinberg equilibrium > 0.15, an SNP call rate > 90%, and a sample call rate > 90%. After quality control, 829 genotyped animals and 76,607 SNPs were retained for further analysis.

2.3. Genome-wide association analysis

The WssGBLUP methodology was used to estimate the proportion of genetic variance explained by genomic windows. To this end, the association model for BW, REA, HWR, BFT, and RFT included the random animal additive genetic effects as well as the fixed effects of contemporary group (year of birth, month of birth and sex), the linear effect of the animal's age at weighing or carcass evaluation, and the linear and quadratic effects of the dam's age at calving as covariates, considering the following model:

$$\mathbf{y = X\beta + Wa + e},$$

where, **y** is a vector of observations for each trait; **β** is the vector of fixed effects; **a** is the vector of additive effects, assumed as $\mathbf{a} \sim N(0, \mathbf{H}\sigma a^2)$, where **H** is the matrix that combines the relationship matrices, based on the pedigree (**A**), and the genomic information (**G**), and σa^2 is the additive genetic variance; **e** is the vector of residual effects, assumed as $\mathbf{e} \sim N(0, \mathbf{I}\sigma e^2)$, where **I** is an identity matrix, and σe^2 is the residual variance; **X** is the fixed

effects incidence matrix relating **β** and **y**; and **W** is the incidence matrix of random effects relating **a** and **y**.

In the Single-Step Genomic Best Linear Unbiased Prediction (ssGBLUP) procedure, the inverse of the numerator of the A^{-1} relationship matrix is replaced by a combined matrix of the pedigree-genomic relation H^{-1} (Aguilar et al., 2010):

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

where, $\mathbf{H^{-1}}$ is the inverse of the modified relationship matrix; A_{22}^{-1} is the inverse of the additive relationship matrix for genotyped animals; and $\mathbf{G^{-1}}$ is the inverse of the genomic relationship matrix (VanRaden, 2008), which is described as:

$$\mathbf{G} = \frac{\mathbf{zz'}}{2\sum_{i=1}^{m} pi(1\text{-}pi)},$$

where, **Z =** (**M – P**), in which **M** is the SNP incidence matrix, with *m* columns representing the number of markers and *n* lines representing the number of genotyped animals. Each element in **M** was set to 0, 1, or 2, for genotypes AA, AB, and BB, respectively. **P** is the matrix containing the allele frequencies expressed in 2pi, where pi is the frequency of the second allele at locus *i.*

The SNP effects were obtained iteratively based on the genomic values (GEBV) of the genotyped animals in a procedure proposed by Wang et al. (2012), using the POSTGSF90 software (Aguilar et al., 2014). The equation for computing the SNP effect can be described as:

$$\mathbf{\hat{u} = \lambda DZ'G^{*-1}\,\hat{a}_g = DZ'[ZDZ']^{-1}\,\hat{a}_g}$$

where, $\mathbf{\hat{u}}$ is the effect vector of each SNP; **D** is a diagonal matrix containing weights for the effect of SNP; **Z'** is the transposed matrix that relates the genotypes of each locus; $\mathbf{G^{*-1}}$ is the inverse matrix of weighted genomic relationships; $\mathbf{\hat{a}_g}$ is the vector with the predicted genetic values for genotyped animals, which is represented by a function of the effects of SNP ($\mathbf{\hat{a}_g} = \mathbf{Zu}$); λ represents the proportion of genetic variation explained by the SNP.

Based on the WssGBLUP procedure (Wang et al., 2012), each SNP effect on the total genetic variance is calculated using weights iteratively, where the GEBV is computed only once, and the SNP effects are estimated considering two iterations. In the first

iteration, **D** is an identity matrix **(D = I)**, and for the second iteration, **D** is the weight vector for the SNP marker computed in the first step. According to Wang et al. (2014), this procedure allows us to increase the weights of SNPs with larger effects and reduce those with minor effects to explain the genetic variance of the target trait. The proportion of genetic variance explained by windows of 1 Mb was calculated according to Wang et al. (2012), as follows:

$$\frac{\mathrm{Var}(a_i)}{{\sigma_a}^2} \times 100\% = \frac{\mathrm{Var}(\sum_{j=1} \mathbf{Z_j}\, \hat{u}_j)}{{\sigma_a}^2} \times 100\%$$

where a_i is the genetic value of the i^{th} region of 1 Mb; ${\sigma_a}^2$ is the total genetic variance; $\mathbf{Z_j}$ is the vector with the genotype of the j^{th} SNP for all animals; and ûj is the estimated effect for the j^{th} SNP within the i-th region.

Manhattan plots containing the genetic variance explained by 1 Mb windows were constructed to provide a genome-wide visualization of the distribution of variance and to highlight broader chromosomal regions with higher contribution to the genetic variance of carcass and growth traits (Arikawa et al., 2024; Wang et al., 2012), using CMplot v4.3.0 R-package (Yin et al., 2021). The choice of 1 Mb windows reflects a summarization strategy, reducing noise from individual SNPs and allowing the identification of genomic regions with broader effects, rather than serving as the final criterion for mapping SNPs to genes.

Candidate genes in the most significant SNP-window regions were identified using the NCBI BioSystems database for cattle using the map *Bos taurus* ARS-UCD1.2. Subsequently, a functional analysis was performed using the g:Profiler software, employing a list of genes identified in the genomic analysis for each trait.

2.4. The Association Weight Matrix (AWM)

To incorporate biological information in the weighting matrix (i.e., diagonal matrix, D), we have proposed the AWM-WssGBLUP method. The AWM was derived directly from the SNP effects estimated in the WssGWAS, serving as an extension of this analysis. An adaptation of the approach presented by Fortes et al. (2010) was carried out to build the AWM and gene networks (Botelho et al., 2021). To this end, the AWM was constructed by selecting the top 5% SNPs (top SNPs) that explained the highest proportion of the

genetic variance for each trait. BW was considered the key phenotype in the analyses, since the studied herd has been selected over time for BW (Ligori et al., 2025).

Importantly, while 1 Mb windows were used in the GWAS for signal visualization at a broad scale, the construction of the AWM was based directly on individual SNPs. This step required higher resolution, and therefore SNP-to-gene assignment followed distance thresholds derived from linkage disequilibrium (LD) patterns specific to the Caracu breed.

Briefly, SNPs identified as top SNPs for BW and for one of the other traits (REA, HWR, BFT, and RFT) were selected to be used in the AWM. To perform the gene network analysis, we selected the genes closest to each top SNP using the bedtools program v2.31.0 (Quinlan & Hall, 2010). The SNPs were classified as “close” (<10 kb), “far” (≥10 and <300 kb), or “very far” (≥300 kb) as proposed by Reverter and Fortes et al. (2013). These thresholds were adopted to ensure that the mapping of SNPs to candidate genes reflected realistic LD decay in Caracu cattle (Verardo et al., 2021), in contrast to the broader 1 Mb windows used for GWAS visualization. Thus, the two approaches are complementary: windows highlight genomic regions of interest, while LD-based thresholds allow biologically consistent SNP-to-gene assignment.

SNPs classified as “very far” from annotated genes were filtered out (Fortes et al., 2011). When more than one SNP was assigned to the same gene, we selected the SNP based on the following criteria: (a) was top in a higher number of traits, (b) showed the highest variance explained, or (c) was the closest to the gene. If the redundancy between more than one SNP and the same gene persisted, the SNPs located in the gene exon were prioritized (Botelho et al., 2021). After filtering, a final set of SNPs was selected and used to build the AWM with as many rows as the identified genes and as many columns as traits under study (five). Each cell {i, j} in AWM was completed with the normalized (z-score) allelic substitution effect of the i^{th} SNP in trait j. After the AWM analysis, a heatmap of the normalized effects of each SNP for each feature was constructed using the pheatmap v.1.0.12 R-package (Kolde, 2019).

2.5. Partial Correlation and Information Theory (PCIT)

Significant correlations among AWM rows (genes) were identified using the PCIT algorithm proposed by Reverter and Chan (2008). In this study, we present a network built

with an absolute correlation threshold of 0.90, found significant by the PCIT algorithm ($P \leq 0.05$).

Additionally, to reduce the network complexity, we built sub-networks to focus on a specific set of genes with the highest degree of connections (Mudadu et al., 2016; Ramayo-Caldas et al., 2014; Widmann et al., 2015). To identify and prioritize transcription factors (TFs), we retrieved the *Bos taurus* TF list from the AnimalTFDB v4.0 database (Shen et al., 2023). The TF list was used to filter and classify genes as transcription factors. Specifically, we overlapped the AnimalTFDB reference list with the genes identified in both the AWM-PCIT and GWAS analyses, and only those present in both datasets and annotated as TFs were retained. This filtering step allowed us to identify the shared set of TFs for subsequent analyses. Further, the TFs with the highest number of connections were selected, ensuring the sub-network provided a representation of the most influential genes (highest degree) associated with the phenotypes under study. Next, a sub-network using only the overlapping genes between the GWAS and the AWM-PCIT was created. This sub-network was used to investigate the functional connections among the genes associated with each trait, allowing the identification of potentially relevant gene clusters and key regulators specific to each trait. Finally, the network visualization was performed on Cytoscape version 3.10.1 (Shannon et al., 2003).

3. RESULTS

3.1 Genome-wide association analysis

Our approach identified the top 10 regions explaining a large proportion of the genetic variance (Fig.1 and Supplementary Tables 1, 2, 3, 4, and 5). The greatest variance was identified for BFT (31.74%) and BW (27.79%), in regions harboring a total of 230 and 502 candidate genes, respectively (Supplementary Tables 1, 2, 3, 4, and 5).

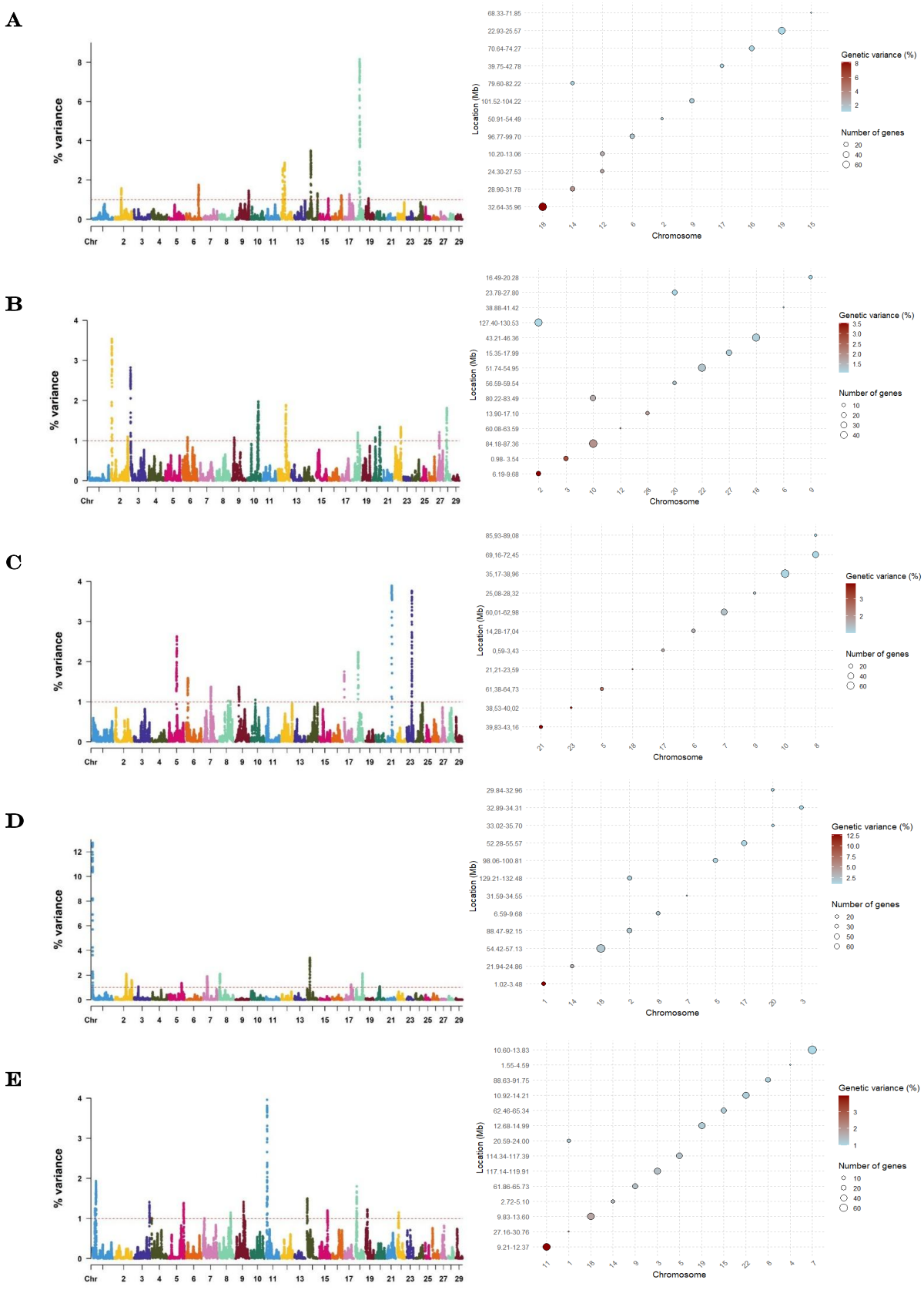
A
B
C
D
E
% variance
Chr
Location (Mb)
Chromosome
Genetic variance (%)
Number of genes

Figure 1. Manhattan plots and balloon plots of the GWAS for the growth and carcass traits analyzed in Caracu cattle. (A) body weight (BW), (B) ribeye area (REA), (C) height-to-width ratio of the *Longissimus dorsi* muscle (HWR), (D) backfat thickness (BFT), and (E) rump fat thickness (RFT). In the Manhattan plots (left panels), the x-axis is the position of each SNP on the bovine chromosomes, and the y-axis is the percentage of explained variance. The black dotted line represents the threshold of 1% variance. In the balloon plots (right panels), each circle corresponds to a candidate genomic window, where the x-axis represents the chromosome, the y-axis the genomic location (Mb), the color scale indicates the percentage of explained genetic variance, and the circle size denotes the number of genes identified within the region.

The SNP-windows on BTA18 (32.64–35.96 Mb) explained 8.16% of the genetic variance for BW (Fig.1A) and harbored several key genes, including *RRAD, PDP2, SLC12A4, SLC9A5, CDH11,* and *CDH5*. The BTA14 window (28.90–31.78 Mb) explained 3.49% of the genetic variance for BW, harboring genes such as *CRH*. Additionally, notable regions included *ATF3* and *BATF3* (BTA16), which together explained 1.21% of the genetic variance; *SMAD9* and *SOHLH2* (BTA12), associated with 2.87%; *TCF24* (BTA14), accounting for 3.49%; and *ZEB2* (BTA2), contributing 1.57%.

For REA (Fig.1B), the SNP-window on BTA2 (6.19–9.68 Mb) explained 3.54% of the genetic variance and included the *COL3A1, COL5A2, CALCRL, TFPI, ITGAV, GULP1,* and *MSTN* genes. Another significant region on BTA3 (0.98–3.54 Mb) explained 2.82% of the variance, harboring genes such as *CREG1, MPZL1, CD247,* and *ALDH9A1*. Additional noteworthy loci included *GRHL3* and *RUNX3* on BTA2, explaining 1.10% of the phenotypic variance; *LTF* on BTA22, associated with 1.34%; and *PROX2* on BTA10, contributing 1.97%.

The top SNP-windows for HWR (Fig.1C) were identified on BTA21 (39.83–43.16 Mb), explaining 3.89% of the genetic variance and harboring genes such as *PRKD1, ARHGAP5, AKAP6, SCFD,* and *HECTD1*. Another significant window on BTA23 (38.53–40.02 Mb) explained 3.76% of the genetic variance, surrounding genes like *KDM1B* and

CAP2. Additionally, the gene *IRX3* on BTA18 was associated with 2.24% of the phenotypic variance.

The SNP-window on BTA1 (1.02–3.48 Mb) explained 12.73% of the genetic variance for BFT (Fig.1D) and included genes such as *KCNE1, KCNE2, ATP5PO, MRPS6, IL10RB, IFNGR2,* and *IFNAR1*. On BTA14 (21.94–24.86 Mb), 3.40% of the genetic variance was explained, including genes such as *RGS20, TCEA1,* and *CYP7A1*.

For RFT (Fig.1E), the SNP-window on BTA11 (9.21–12.37 Mb) explained 3.96% of the genetic variance and included genes such as *FHL2, LOXL3, HK2, MTHFD2, TGFBRAP1,* and *DOK1*. The BTA1 window (27.16–30.76 Mb) explained 1.93% of the genetic variance, including genes such as *GBE1*. Additionally, *LHX1* on BTA19 was associated with 1.22% of the phenotypic variance.

3.2 AWM PCIT analyses

The AWM analysis identified 3,831 significant SNPs ($P < 0.05$). After filtering (see methods), the final SNP list retained 3,524 SNPs, containing the normalized effects for BW, REA, HWR, BFT, and RFT. From the list, a total of 2,078, 1,446, and 307genes were located near (<10 kb), far (≥10 kb and <300 kb), or very far (≥300 kb) to the selected SNPs, respectively. SNPs classified as very far from any annotated gene were filtered out from further analysis. The magnitude and direction of SNP across traits are shown in Figure 2.

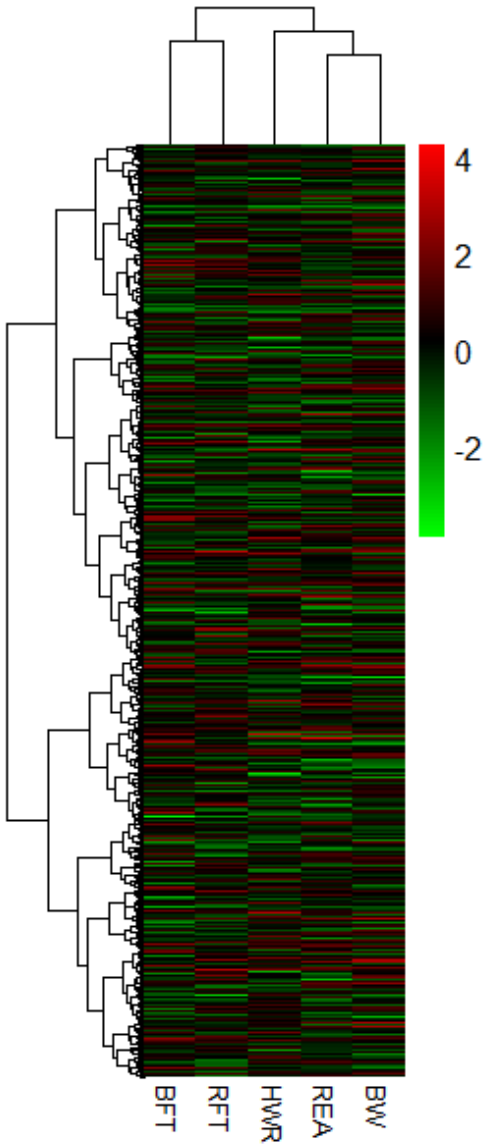

Figure 2. Heatmap of normalized SNP effects selected based on the AWM approach for body weight (BW), ribeye area (REA), height-to-width ratio of the *Longissimus dorsi* muscle (HWR), backfat thickness (BFT), and rump fat thickness (RFT) in Caracu cattle. Each column represents a trait, and each row represents a SNP. Positive and negative SNP effects are color-coded as red or green, respectively.

The gene interaction network, considering the PCIT results consisted of a total of 6,264,030 correlated pairs of genes across all traits. Among them, 340,968 pairs were

retrieved as significant ($|r| \geq 0.90$; $P \leq 0.05$). Next, we focused on transcription factors (TFs) by comparing the TFs identified in both AWM-PCIT and GWAS results, which revealed 15 shared TFs (Supplementary Table 6). To reduce the network dimensionality, the 100 most connected gene pairs from the PCIT results were retained, generating a sub-network with 100 nodes and 2,474 edges (Supplementary Figure 1). Among the top 100 genes, 12 transcription factors overlapped with the GWAS results. A sub-network was then created using these 12 TFs, preserving only their direct connections (Figure 3B).

The correlation matrix highlights different patterns of association between the genes evaluated (Figure 3A). Among them, *ZEB2, LTF*, *IRX3,* and *LHX1* stood out for presenting the highest correlations with genes associated with all analyzed traits. *ZEB2* showed a broader pattern of associations, with seven positive correlations, five with REA and two with HWR, and eight negative correlations, including three with REA, three with HWR, and two with RFT. *LTF* showed five positive correlations, all with BW, and eight negative correlations, including six with BW, one with HWR, and one with RFT. *IRX3* showed nine positive correlations, seven with BW, one with REA, and one with RFT, as well as five negative correlations, three with BW and two with REA. *LHX1* showed a heterogeneous correlation profile, with two positive associations, one with BW and one with HWR, along with five negative correlations, three with BW and two with REA.

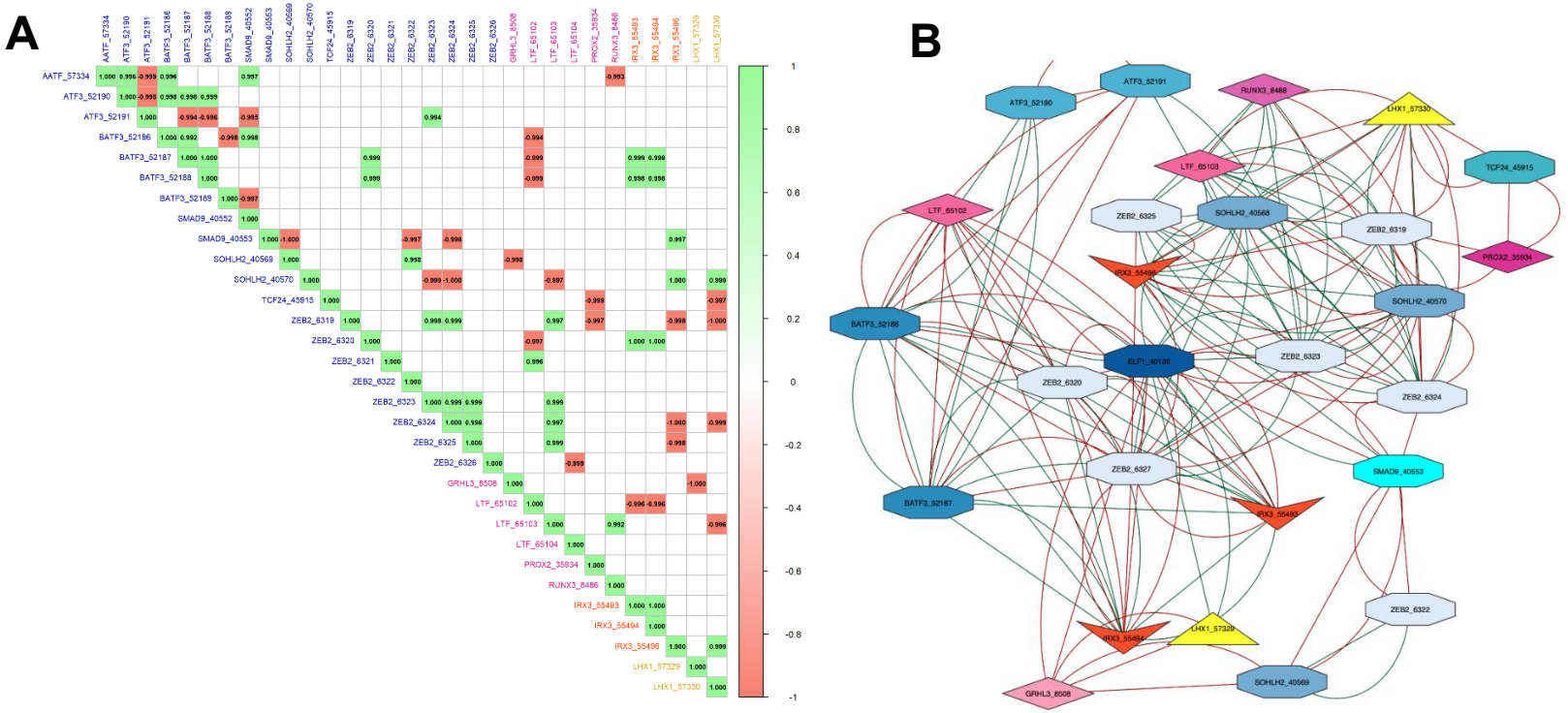

Figure 3. Correlogram and gene interaction networks represent significant SNP effect correlations between growth and carcass traits as estimated by the AWM-PCIT analyses. Only correlations greater than |0.9| are shown. Nodes are genes or key transcription factors with a |r| ≥ 0.9. (A) Correlogram of the gene sub-network showing the correlation coefficients among genes and transcription factors. Positive correlations are shown in green and negative correlations in red. Blank cells without values indicate missing correlations. (B) Gene interaction sub-network comprising genes presenting transcription factors (TFs) shared between the PCIT results and GWAS significant SNPs. The phenotypes are color-coded as blue for BW (body weight), pink for REA (ribeye area), orange for HWR (height × width ratio of the Longissimus dorsi muscle), and yellow for RFT (rump fat thickness).

4. DISCUSSION

We identified and characterized genomic regions, biological pathways, and regulatory networks associated with the polygenic control of growth and carcass traits in Caracu cattle. Furthermore, we examined the complex genetic architecture of these traits and their pleiotropic effects. Based on a multi-tiered approach combining WssGBLUP and AWM-PCIT, we shed light on the polygenic genomic architecture underlying growth and carcass traits in Caracu cattle.

From the GWAS analysis, the distribution of genetic variance across the genome shows that BW, REA, HWR, BFT, and RFT are traits influenced by multiple loci of small effect. These findings suggest that selection for these traits should consider multiple variants simultaneously, since the contribution of each SNP is limited (Visscher et al., 2017). These observations were further supported by the AWM-based analysis, which revealed patterns of pleiotropy between BW and carcass traits. We identified distinct genomic clusters where SNPs associated with BW showed mostly positive effects on muscle traits (REA and HWR), while those related to BFT and RFT showed neutral or adverse effects. Our findings support those of Ligori et al. (2025), who reported positive genetic correlations between BW and muscle traits, and neutral correlations with fat traits, suggesting that selection for BW can indirectly favor muscularity without affecting subcutaneous fat deposition.

The gene network constructed using the PCIT algorithm revealed a complex network of interactions between genes with complementary regulatory functions, reflecting a coordinated architecture that may underlie the pleiotropy observed between productive traits, BW, REA, HWR, and RFT. The identification of associations between genes, both positive and negative, reinforces the idea that gene expression related to growth, metabolism, and tissue differentiation is influenced by interconnected mechanisms that respond to selective and environmental pressures, especially in a herd subjected to BW selection for years (Yan et al., 2024; Zhang et al., 2023; Liu et al., 2020). A sub-network constructed using only the genes simultaneously identified in the GWAS analyses and in the AWM-PCIT network allowed to retrieve 12 key TFs that may be regulating the genes within the windows of variance selected.

The identification of *ZEB2*, *LTF*, *IRX3*, and *LHX1* as hub genes confirms their relevance in the pleiotropic regulation of growth and carcass traits. The observed positive correlations indicate co-expression in pathways that favor body growth and muscle hypertrophy, while the negative correlations indicate regulatory antagonisms, in which one pathway is favored over another. This pattern is expected for genes that occupy a central position in complex networks and modulate both muscle development and fat deposition.

The *ZEB2* (Zinc Finger E-Box Binding Homeobox 2) gene plays a fundamental role in regulating epithelial-mesenchymal transition, an essential process for cell differentiation and tissue development. Its activity is intrinsically linked to the TGF-β signaling pathway, which controls tissue growth and remodeling (Xu et al., 2009). This functional profile explains the gene's influence on muscle and adipose development. The positive correlations of *ZEB2* with REA and HWR indicate its contribution to myoblast differentiation and, consequently, to muscle hypertrophy and skeletal growth. In contrast, the negative correlations with RFT and the additional negative correlations with REA reflect the pleiotropic effect of its regulation, whereby directing resources toward muscle formation reduces fat deposition, establishing a natural antagonism between the traits.

The LTF (Lactoferrin) gene is recognized for its roles in the immune system and in the metabolism of iron, a vital element for energy production, especially in muscle tissue (Kruzel et al., 2017; Rosa et al., 2017; Siqueiros-Cendón et al., 2014). This ability to influence energy metabolism and the inflammatory response confers LTF a pleiotropic role in body composition. Importantly, the activation of inflammatory pathways plays an essential role in skeletal muscle hypertrophy, where macrophages modulate tissue repair and regeneration by regulating inflammation, growth factors, stem cells, extracellular matrix, and cytokines (Silva et al., 2020). Through this mechanism, LTF may participate in balancing catabolic and anabolic signaling, directly impacting muscle development. The complexity of the gene is reflected in its mixed associations with BW. Positive correlations with BW suggest that specific gene variants may enhance metabolic efficiency, resulting in greater weight gain. Conversely, negative correlations with BW, HWR, and RFT indicate an antagonistic effect, in which resource allocation to immune responses or environmental adaptation may override productive growth (Niu et al., 2022; Van Der Most et al., 2011).

The *IRX3* (Iroquois Homeobox 3) gene encodes a transcription factor that acts in embryonic development and in the regulation of energy metabolism, directly influencing the balance between muscle and adipose tissue (Zou et al., 2017). Its positive correlations with BW, REA, and HWR suggest that gene variants favor body growth and the expansion of lean mass. However, the pleiotropic nature of *IRX3* is evidenced by its positive correlations with RFT and negative correlations with BW and REA, indicating that the gene may also favor adipogenesis, which creates an antagonism with muscle growth. Finally, the *LHX1* (LIM Homeobox 1) gene codes for a central transcription factor in embryonic development. Its role in gastrulation gives it a significant, albeit indirect, influence on cell differentiation and tissue formation (Tian et al., 2022). This functional profile explains the gene's heterogeneous associations. *LHX1*'s positive correlations with BW and HWR indicate its contribution to skeletal growth and improved overall animal conformation. Conversely, the negative correlation with REA and additional negative correlations with BW demonstrate a pleiotropic effect, suggesting that different variants may direct growth through distinct pathways, resulting in a natural antagonism between total weight and muscle quality.

The association patterns observed in these genes reflect an interaction between artificial and natural selection. Body weight selection over decades may have favored variants that promote growth and lean mass expansion. Simultaneously, the continental origin and adaptation of the Caracu breed to the tropical climate appear to have preserved the metabolic plasticity conferred by genes such as *IRX3* and *LTF*, where the ability to switch between muscle and fat accumulation, or to direct resources towards survival rather than production, was advantageous in an environment with thermoregulatory challenges and nutritional variability.

Our work fills an important gap by going beyond GWAS and using different approaches to understand the relationship between genes and complex traits in Caracu cattle. We identified genomic regions and candidate genes that suggest shared biological pathways among these traits. However, it is still necessary to investigate how these genes are expressed in different tissues and developmental stages, in addition to functionally validating their effects. Future studies integrating transcriptomic and/or metabolomic data

may deepen this understanding and provide opportunities to translate this knowledge into genetic improvement programs.

5. CONCLUSION

We characterized the polygenic architecture underlying growth (BW, REA, HWR) and carcass (BFT and RFT) traits in Caracu cattle. These traits are controlled by multiple small-effect loci distributed across specific chromosomal regions, involving key genes associated with energy metabolism, muscle development, and adipogenesis. Our integrative analyses revealed pleiotropic patterns, with positive correlations between BW and muscle traits and antagonistic relationships with fat deposition, while regulatory interactions highlighted shared cell signaling and tissue differentiation pathways. Notably, four hub genes, *ZEB2*, *LTF*, *IRX3*, and *LHX1*, were shown to be central regulators connecting growth and carcass phenotypes, suggesting that they play a key role in coordinating muscle accretion, fat deposition, and adaptive responses. Together, these results provide a molecular framework to support balanced genomic selection strategies in Caracu, demonstrating that simultaneously improving growth and carcass quality requires approaches that take into account the individual effects of SNPs and their coordinated regulatory networks.

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Supplementary Table 1. Chromosome (Chr), location, gene symbol, and proportion of additive genetic variance (σ^2_a) explained by the top 10 windows for body weight (BW) in Caracu cattle.

Chr	Location (Mb)	Genes	σ^2_a (%)
18	32.64-35.96	*CDH11, CDH5, BEAN1, TK2, CKLF, CMTM2, CMTM3, CMTM4, DYNC1LI2, TERB1, NAE1, CA7, PDP2, CDH16, RRAD, FAM96B, CES2, CES3, CES4A, CBFB, C18H16ORF70, B3GNT9, TRADD, FBXL8, HSF4, NOL3, KIAA0895L, EXOC3L1, E2F4, ELMO3, TMEM208, FHOD1, SLC9A5, PLEKHG4, KCTD19, LRRC36, TPPP3, ZDHHC1, HSD11B2, ATP6V0D1, AGRP, RIPOR1, CTCF, CARMIL2, ACD, PARD6A, ENKD1, C18H16orf86, GFOD2, RANBP10, TSNAXIP1, CENPT, THAP11, NUTF2, EDC4, NRN1L, PSKH1, PSMB10, LCAT, SLC12A4, DPEP3, DPEP2, DDX28, DUS2, NFATC3, ESRP2, PLA2G15, SLC7A6, SLC7A6OS, PRMT7, SMPD3, ZFP90, CDH3*	8.16
14	28.90-31.78	*BHLHE22, CYP7B1, ARMC1, MTFR1, PDE7A, SNORA72, DNAJC5B, TRIM55, CRH, RRS1, ADHFE1, C14H8ORF46, MYBL1, VCPIP1, SGK3, MCMDC2, SNORD87, TCF24, PPP1R42, 5S_rRNA, COPS5, CSPP1, ARFGEF1, CPA6*	3.49
12	24.30-27.53	*SUPT20H, EXOSC8, ALG5, SMAD9, RFXAP, SERTM1, CCNA1, SPART, SOHLH2, NBEA, MAB21L1, RFC3, STARD13*	2.87
12	10.20-13.06	*OLFM4, PCDH8, CNMD, SUGT1, ELF1, SNORA70, WBP4, KBTBD6, KBTBD7, MTRF1, NAA16, RGCC, VWA8, DGKH, AKAP11, TNFSF11, FAM216B, EPSTI1*	2.59
6	96.77-99.70	*HNRNPD, HNRNPDL, ENOPH1, TMEM150C, SCD5, SEC31A, THAP9, LIN54, COPS4, SNORA70, PLAC8B, PLAC8A, COQ2, HPSE, HELQ, MRPS18C, ABRAXAS1, GPAT3, NKX6-1, CDS1, WDFY3*	1.75
2	50.91-54.49	*ZEB2, GTDC1, ARHGAP15, KYNU*	1.57
9	101.52-104.22	*RPS6KA2, RNASET2, FGFR1OP, CCR6, GPR31, TTLL2, UNC93A, AFDN, KIF25, FRMD1, DACT2, SMOC2, THBS2, WDR27, C6orf120, PHF10, TCTE3, ERMARD, DLL1, FAM120B, PSMB1, PDCD2*	1.45
14	79.60-82.22	*SNX16, CHMP4C, ZFAND1, SLC10A5, IMPA1, ENPP2, TAF2, DSCC1, DEPTOR, COL14A1, MRPL13, MTBP, SNTB1*	1.32

17	39.75-42.78	*RAPGEF2, C17H4ORF45, FNIP2, PPID, ETFDH, C17H4orf46, RXFP1, TMEM144, FAM198B, GRIA2, GLRB, PDGFC*	1.27
16	70.64-74.27	*FLVCR1, NSL1, TATDN3, BATF3, ATF3, NENF, TMEM206, PPP2R5A, DTL, INTS7, LPGAT1, NEK2, SLC30A1, RD3, TRAF5, RCOR3, KCNH1, HHAT, SERTAD4, SYT14, UTP25, IRF6, C16H1orf74, TRAF3IP3, HSD11B1, LAMB3, CAMK1G*	1.21
19	22.93-25.57	*RPA1, RTN4RL1, DPH1, OVCA2, HIC1, SMG6, SRR, TSR1, SGSM2, MNT, METTL16, PAFAH1B1, CLUH, CCDC92B, RAP1GAP2, OR1D3B, OR1D3, OR1G4, OR1A1, OR1A1D, OR1A1C, OR1P1, OR3A1D, OR3A4, OR3A10, OR1R1, OR1E1F, OR1E1H, OR1E2B, OR1E2, SPATA22, ASPA, TRPV3, TRPV1, SHPK, CTNS, TAX1BP3, EMC6, P2RX5, HASPIN, NCBP3, CAMKK1, P2RX1, ATP2A3, ZZEF1, CYB5D2, ANKFY1, UBE2G1, SPNS3, SPNS2, MYBBP1A, TEKT1, SMTNL2, FBXO39, XAF1, SLC13A5, C17orf100, TXNL5, KIAA0753, PITPNM3, PIMREG, AIPL1*	1.06
15	68.33-71.85	*LRRC4C*	1.05

Supplementary Table 2. Chromosome (Chr), location, gene symbol, and proportion of additive genetic variance (σ^2_a) explained by the top 10 windows for ribeye area (REA) in Caracu cattle.

Chr	Location (Mb)	Genes	σ^2_a (%)
2	6.19-9.68	*MSTN, PMS1, ORMDL1, OSGEPL1, ANKAR, ASNSD1, SLC40A1, WDR75, COL5A2, COL3A1, GULP1, TFPI, CALCRL, ZSWIM2, FAM171B, ITGAV*	3.54
3	0.98- 3.54	*MPZL1, RCSD1, CREG1, CD247, POU2F1, DUSP27, GPA33, MAEL, ILDR2, TADA1, POGK, FAM78B, UCK2, TMCO1, ALDH9A1, MGST3, LRRC52*	2.82
10	84.18-87.36	*DPF3, ZFYVE1, RBM25, PSEN1, PAPLN, NUMB, HEATR4, RIOX1, ACOT2, ACOT4, ACOT6, DNAL1, PNMA1, ELMSAN1, ZADH1, ZNF410, FAM161B, COQ6, ENTPD5, BBOF1, ALDH6A1, LIN52, VSX2, ABCD4, VRTN, SYNDIG1L, NPC2, ISCA2, LTBP2, AREL1, FCF1, YLPM1, PROX2, DLST, RPS6KL1, PGF, EIF2B2, MLH3, ACYP1, ZC2HC1C, NEK9, TMED10, FOS, JDP2, BATF, FLVCR2, TTLL5, TGFB3, IFT43*	1.97
12	60.08-63.59	*SLITRK6, HTATSF1, SLITRK5*	1.88
28	13.90-17.10	*BICC1, PHYHIPL, FAM13C, SLC16A9, MRLN, CCDC6, ANK3, CDK1, RHOBTB1*	1.82
10	80.22-83.49	*RAD51B, ZFP36L1, ACTN1, DCAF5, EXD2, GALNT16, ERH, SLC39A9, PLEKHD1, CCDC177, SUSD6, SRSF5, SLC10A1, SMOC1, SLC8A3, SYNJ2BP, COX16, MED6, TTC9, MAP3K9, PCNX1, SIPA1L1, RGS6*	1.63
20	56.59-59.54	*RETREG1, ZNF622, MARCH11, FBXL7, ANKH, OTULIN, FAM105A, TRIO, DNAH5*	1.34
22	51.74-54.95	*MAP4, DHX30, SMARCC1, CSPG5, ELP6, SCAP, PTPN23, NGP, KLHL18, KIF9, SETD2, NRADD, CCDC12, PTH1R, MYL3, PRSS42, TMIE, ALS2CL, FAM240A, TDGF1, LRRC2, RTP3, LTF, CCRL2, CCR5, CCR2, CCR3, CCR1, XCR1, FYCO1, CXCR6, CCR9, LZTFL1, SLC6A20, SACM1L, LIMD1, LARS2, TMEM158, CDCP1, CLEC3B, EXOSC7, ZDHHC3, TMEM42, GHRL, SEC13, ATP2B2, SLC6A11*	1.34
27	15.35-17.99	*ACSL1, HELT, SLC25A4, CFAP97, SNX25, LRP2BP, ANKRD37, UFSP2, C27H4ORF47, CCDC110, PDLIM3, SORBS2, TLR3, FAM149A, CYP4V2, KLKB1, F11, MTNR1A, FAT1, ZFP42, TRIML2, TRIML1*	1.21
18	43.21-46.36	*TDRD12, SLC7A9, CEP89, FAAP24, RHPN2, GPATCH1, WDR88, LRP3, SLC7A10, CEBPA, CEBPG, PEPD, CHST8, KCTD15, LSM14A, KIAA0355, GPI, PDCD2L,*	1.20

		UBA2, WTIP, ZNF599, ZNF181, ZNF792, GRAMD1A, SCN1B, HPN, MAT-8, LGI4, FXYD1, FXYD7, FXYD5, FAM187B, LSR, USF2, HAMP, MAG, CD22, GPR41, FFAR2, KRTDAP, DMKN, SBSN, GAPDHS, TMEM147, ATP4A, PNKD, HAUS5, RBM42	
2	127.40-130.53	*MAN1C1, SYF2, LDLRAP1, TMEM57, TMEM50A, RUNX3, CLIC4, SRRM1, NCMAP, RCAN3, NIPAL3, STPG1, GRHL3, IFNLR1, IL22RA1, MYOM3, SRSF10, PNRC2, CNR2, FUCA1, HMGCL, GALE, LYPLA2, PITHD1, ELOA, RPL11, ID3, E2F2, ASAP3, TCEA3, ZNF436, HNRNPR, HTR1D, LUZP1, KDM1A, TEX46, LACTBL1, EPHB2, C1QB, C1QA, EPHA8, ZBTB40*	1.10
6	38.88-41.42	*SLIT2, PACRGL, KCNIP4*	1.08
20	23.78-27.80	*SKIV2L2, DHX29, CCNO, MCIDAS, CDC20B, GPX8, GZMA, gzmA, GZMK, ESM1, CSPG4B, SNX18, HSPB3, ARFRP2, NDUFS4, FST, MOCS2, ITGA2, ITGA1, ISL1*	1.08
9	16.49-20.28	*HTR1B, MEI4, IRAK1BP1, PHIP, HMGN3, LCA5, SH3BGRL2, ELOVL4, TTK, BCKDHB*	1.07

Supplementary Table 3. Chromosome (Chr), location, gene symbol, and proportion of additive genetic variance (σ^2_a) explained by the top 10 windows for height-to-width ratio of the *Longissimus dorsi* muscle (HWR) in Caracu cattle.

Chr	Location (Mb)	Genes	σ^2_a (%)
21	39.83-43.16	*PRKD1, G2E3, SCFD1, COCH, STRN3, AP4S1, HECTD1, HEATR5A, SNORA62, GPR33, NUBPL, ARHGAP5, AKAP6, Vault*	3.89
23	38.53-40.02	*RNF144B, DEK, KDM1B, TPMT, NHLRC1, KIF13A, NUP153, FAM8A1, CAP2*	3.76
5	61.38-64.73	*TMPO, SLC25A3, SNORA53, IKBIP, APAF1, ANKS1B, UHRF1BP1L, ACTR6, SCYL2, SLC17A8, NR1H4, GAS2L3, ANO4*	2.62
18	21.21-23.59	*CHD9NB, CHD9, RBL2, AKTIP, RPGRIP1L, FTO, IRX3, IRX5*	2.24
17	0.59-3.43	*CPE, TLL1, MAP9, NPY2R, RBM46, LRAT, FGG, FGA, FGB, PLRG1, DCHS2*	1.75
6	14.28-17.04	*PITX2, ENPEP, SNORA70, ELOVL6, EGF, LRIT3, RRH, GAR1, CFI, MCUB, CASP6, SEC24B, COL25A1, SNORA70, ETNPPL, OSTC, RPL34*	1.59
7	60.01-62.98	*HTR4, ADRB2, SH3TC2, ABLIM3, AFAP1L1, GRPEL2, PCYOX1L, IL17B, CSNK1A1, ARHGEF37, PPARGC1B, MIR378A, PDE6A, SLC26A2, HMGXB3, CSF1R, PDGFRB, CDX1, SLC6A7, CAMK2A, ARSI, TCOF1, CD74, NDST1, SYNPO, MYOZ3, RBM22, DCTN4, SMIM3, ZNF300, GPX3, TNIP1, ANXA6, CCDC69, GM2A, SLC36A3, SLC36A2, SLC36A1, FAT2, SPARC, ATOX1, G3BP1*	1.37
9	25.08-28.32	*TRMT11, HINT3, NCOA7, HEY2, HDDC2, TPD52L1, RNF217, NKAIN2, TRDN, CLVS2*	1.37
10	35.17-38.96	*THBS1, FSIP1, GPR176, EIF2AK4, SRP14, BMF, BUB1B, PAK6, ANKRD63, PLCB2, INAFM2, CCDC9B, PHGR1, DISP2, KNSTRN, IVD, BAHD1, CHST14, CCDC32, RPUSD2, KNL1, RAD51, RMDN3, DNAJC17, C10H15orf62, ZFYVE19, PPP1R14D, SPINT1, RHOV, VPS18, DLL4, CHAC1, INO80, EXD1, CHP1, OIP5, NUSAP1, NDUFAF1, RTF1, ITPKA, RPAP1, TYRO3, MGA, MAPKBP1, JMJD7, PLA2G4B, SPTBN5, EHD4, PLA2G4E, PLA2G4D, PLA2G4F, VPS39, TMEM87A, GANC, CAPN3, ZNF106, SNAP23, LRRC57, HAUS2, STARD9, CDAN1, TTBK2, UBR1, TMEM62, CCNDBP1, EPB42*	1.05

8	69.16-72.45	*DOK2, XPO7, NPM2, FGF17, DMTN, FAM160B2, NUDT18, HR, HRURF, REEP4, LGI3, SFTPC, BMP1, PHYHIP, POLR3D, PIWIL2, SLC39A14, PPP3CC, SORBS3, PDLIM2, C8H8orf58, CCAR2, BIN3, EGR3, PEBP4, RHOBTB2, CHMP7, R3HCC1, LOXL2, ENTPD4, SLC25A37, NKX3-1, NKX2-6, STC1, ADAM7, NEFM, NEFL, DOCK5*	1.02
8	85.93-89.08	*ROR2, NFIL3, SYK, DIRAS2, 5S_rRNA, GADD45G, SEMA4D, SECISBP2, CKS2, SHC3*	1.01

Supplementary Table 4. Chromosome (Chr), location, gene symbol, and proportion of additive genetic variance (σ^2_a) explained by the top 10 windows for backfat thickness (BFT) in Caracu cattle.

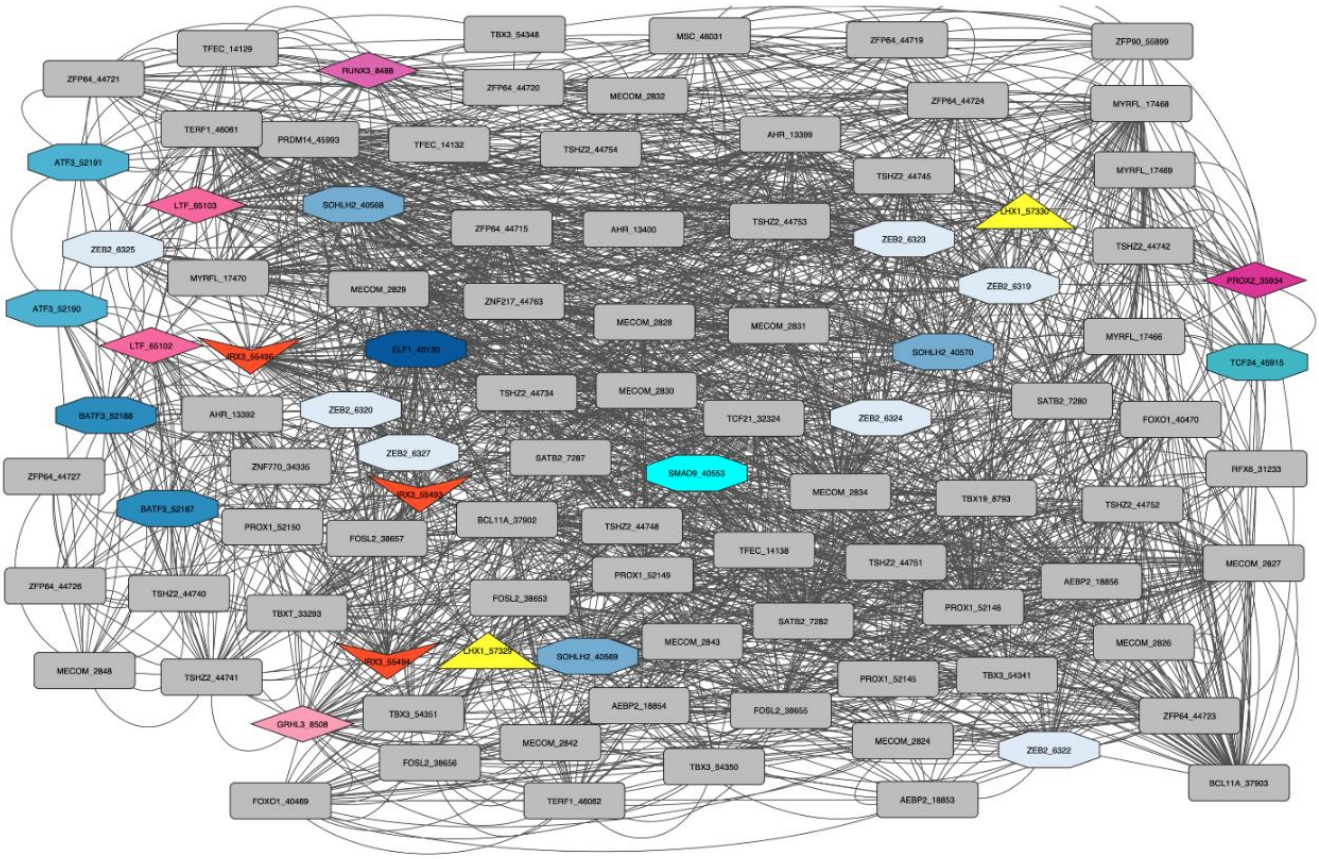
Chr	Location (Mb)	Genes	σ^2_a (%)
1	1.02-3.48	*KCNE1, SMIM34, FAM243A, C1H21ORF51, FAM165B, SMIM11A, KCNE2, MRPS6, ATP5PO, ITSN1, CRYZL1, DONSON, SON, GART, DNAJC28, TMEM50B, IFNGR2, IFNAR1, IL10RB, IFNAR2, OLIG1, OLIG2, C1H21ORF62, PAXBP1, SYNJ1, C1H21orf59, EVA1C, URB1, MRAP, MIS18A*	12.73
14	21.94-24.86	*RGS20, TCEA1, MRPL15, SOX17, RP1, XKR4, TMEM68, TGS1, LYN, RPS20, MOS, PLAG1, CHCHD7, SDR16C5, RDHE2, PENK, IMPAD1, FAM110B, RPL39, UBXN2B, CYP7A1, SDCBP, NSMAF*	3.40
18	54.42-57.13	*SLC8A2, KPTN, NAPA, ZNF541, BICRA, EHD2, NOP53, SNORD23, CRX, ELSPBP1, CABP5, LIG1, ZSWIM9, ZNF114, CCDC114, EMP3, TMEM143, SYNGR4, KDELR1, GRIN2D, GRWD1, KCNJ14, CYTH2, LMTK3, SULT2B1, FAM83E, SPACA4, RPL18, SPHK2, DBP, CA11, NTN5, Se, sec1, MAMSTR, RASIP1, IZUMO1, FUT1, FGF21, BCAT2, HSD17B14, PLEKHA4, PPP1R15A, TULP2, NUCB1, DHDH, BAX, GYS1, RUVBL2, LHB, SAXO3, NTF4, KCNA7, SNRP70, LIN7B, PPFIA3, HRC, TRPM4, SLC6A16, CD37, TEAD2, DKKL1, CCDC155, PTH2, GFY, SLC17A7, PIH1D1, ALDH16A1, FLT3LG, RPL13A, SNORD33, SNORD33, SNORD34, SNORD35A, RPS11, SNORD35B, FCGRT, RCN3, NOSIP, PRRG2, PRR12, RRAS, SCAF1, IRF3, BCL2L12, PRMT1, CPT1C, TSKS, AP2A1, FUZ, MED25, PTOV1, PNKP, AKT1S1, TBC1D17, IL4I1, NUP62, ATF5, VRK3, IZUMO2, MYH14, KCNC3, NAPSA, NR1H2, POLD1, B42b-like, MYBPC2, FAM71E1, EMC10, JOSD2, LRRC4B, SYT3, C18H19orf81, SHANK1, CLEC11A, SMIM47, ACP4, C18H19orf48, SNORD88C, KLK1, KLK15, KLK4, KLK5, KLK6, KLK7, KLK8, KLK9, KLK10, KLK11, KLK12, KLK13, KLK14, ATPBD3*	2.12
2	88.47-92.15	*C2H2orf69, TYW5, MAIP1, H3C13, SPATS2L, KCTD18, SGO2, AOX1, AOX4, AOX2, BZW1, CLK1, PPIL3, NIF3L1, ORC2, FAM126B, NDUFB3, CFLAR, CASP8, FLACC1, TRAK2, STRADB, C2CD6, TMEM237, MPP4, ALS2, CDK15, FZD7, KIAA2012, NOP58, SNORD70, SNORD70B, SNORD11B, SNORD11, BMPR2,*	2.10

		FAM117B, ICA1L, WDR12, CARF, NBEAL1, CYP20A1, ABI2, RAPH1, CD28, CTLA4, ICOS	
8	6.59-9.68	*FBXO8, CEP44, HPGD, GLRA3, ADAM29, DEFB134, DEFB136, CTSB, FDFT1, NEIL2, GATA4, BLK, FAM167A, TDH, MTMR9, XKR6, Metazoa_SRP, PINX1, SOX7, C8H8orf74, RP1L1, PRSS55, PRSS51, MSRA, KIF13B, HMBOX1*	2.09
7	31.59-34.55	*ZNF475, LOX, SRFBP1, FTMT, PRR16, FAM170A, HSD17B4, TNFAIP8*	1.90
2	129.21-132.48	*ID3, E2F2, ASAP3, TCEA3, ZNF436, HNRNPR, HTR1D, LUZP1, KDM1A, TEX46, LACTBL1, EPHB2, C1QB, C1QA, EPHA8, ZBTB40, WNT4, CDC42, ELA3B, HSPG2,* *USP48, RAP1GAP, ALPL, ECE1, EIF4G3, HP1BP3, SH2D5, DDOST, PINK1, CDA, FAM43B, MUL1, CAMK2N1, VWA5B1, UBXN10, PLA2G2C*	1.60
5	98.06-100.81	*ETV6, T2R67, SMIM10L1, T2R46, TAS2R43, T2R65A, T2R12, BOTA-T2R10B, BOTA-T2R10A, T2R10C, TAS2R8, TAS2R7, YBX3, STYK1, MAGOHB, KLRJ, Ly49, KLRC1, KLRC, NKG2-D, GABARAPL1, TMEM52B, OLR1, CLEC7A, CLEC1A, CLEC9A, CLEC1B, CLEC12B, CLEC12A, CLEC2A, KLRF2, KLRF1, CD69, CLECL1, KLRB1, OVOS*	1.36
17	52.28-55.57	*SBNO1, CDK2AP1, C17H12ORF65, MPHOSPH9, PITPNM2, ARL6IP4, OGFOD2, ABCB9, VPS37B, HIP1R, CCDC62, SNORA70, KNTC1, RSRC2, ZCCHC8, CLIP1, VPS33A, DIABLO, B3GNT4, LRRC43, MLXIP, BCL7A, WDR66, PSMD9, HPD, SETD1B, RHOF, TMEM120B, MORN3, ORAI1, KDM2B, RNF34, ANAPC5, CAMKK2, P2RX4, P2RX7, IFT81, ATP2A2, ANAPC7, ARPC3, GPN3, FAM216A, VPS29, RAD9B, PPTC7, TCTN1, HVCN1, PPP1CC, CCDC63, MYL2, CUX2, PHETA1, SH2B3, ATXN2, BRAP, ACAD10, CIT*	1.23
20	33.02-35.70	*PLCXD3, C6, MROH2B, C7, CARD6, SNORD72, PRKAA1, TTC33, PTGER4, DAB2, C9, FYB1, RICTOR, OSMR*	1.09
3	32.89-34.31	*KCNA10, CYM, PROK1, LAMTOR5, SLC16A4, RBM15, KCNC4, SLC6A17, UBL4B, ALX3, STRIP1, AHCYL1, CSF1, EPS8L3, GSTM3, GSTM5, AMPD2, GNAT2, MIR197, GPR61, AMIGO1, CYB561D1, ATXN7L2, SYPL2, PSMA5, SORT1, MYBPHL, PSRC1, CELSR2*	1.07
20	29.84-32.96	*MRPS30, FGF10, NNT, PAIP1, C20H5orf34, TMEM267, CCL28, HMGCS1, NIM1K, ZNF131, SELENOP, CCDC152, GHR, FBXO4, C20H5ORF51, OXCT1*	1.05

Supplementary Table 5. Chromosome (Chr), location, gene symbol, and proportion of additive genetic variance (σ^2_a) explained by the top 10 windows for rump fat thickness (RFT) in Caracu cattle.

Chr	Location (Mb)	Genes	σ^2_a (%)
11	9.21-12.37	*MRPS9, TGFBRAP1, C11H2orf49, FHL2, TACR1, POLE4, HK2, SEMA4F, M1AP, DOK1, LOXL3, HTRA2, AUP1, DQX1, TLX2, PCGF1, LBX2, CCDC142, MRPL53, MOGS, WBP1, INO80B, RTKN, WDR54, C11H2orf81, DCTN1, SLC4A5, MTHFD2, MOB1A, BOLA3, TET3, DGUOK, ACTG2, STAMBP, C11H2orf78, DUSP11, TPRKB, ALMS1, EGR4, FBXO41, CCT7, PRADC1, SMYD5, NOTO, RAB11FIP5, SFXN5, EMX1, SPR, EXOC6B*	3.96
1	27.16-30.76	*GBE1*	1.93
18	9.83-13.60	*CDH13, HSBP1, MLYCD, OSGIN1, NECAB2, SLC38A8, MBTPS1, 5S_rRNA, HSDL1, DNAAF1, TAF1C, ADAD2, KCNG4, WFDC1, ATP2C2, TLDC1, COTL1, KLHL36, USP10, CRISPLD2, ZDHHC7, KIAA0513, FAM92B, GSE1, GINS2, EMC8, COX4I1, IRF8, FOXF1, MTHFSD, FOXC2, FOXL1, FBXO31, MAP1LC3B, ZCCHC14, JPH3, KLHDC4, SLC7A5, SLC7A5, CA5A, BANP, ZNF469*	1.80
14	2.72-5.10	*DENND3, PTK2, MIR151A, CHRAC1, TRAPPC9, KCNK9, COL22A1, FAM135B*	1.50
9	61.86-65.73	*SPACA1, AKIRIN2, ORC3, RARS2, SLC35A1, CFAP206, C9H6orf163, SMIM8, GJB7, ZNF292, CGA, HTR1E, SNORD22, SNORD50B, SYNCRIP, SNX14, NT5E, TBX18, CEP162, MRAP2, CYB5R4, RIPPLY2, THEMIS*	1.42
3	117.14-119.91	*LRRFIP1, RBM44, RAMP1, SCLY, ESPNL, KLHL30, ERFE, ILKAP, HES6, PER2, TRAF3IP1, ASB1, TWIST2, HDAC4, NDUFA10, OR6B2, OR6B3, OR9S41, OR9S3, OR9S29, OR9S33, OR9S43B, OR9S32, OR9S39, OR9S44P, OR9S36B, CSF2RA, IL3RA, P2RY8, AKAP17A, OR9S36, OR9S40, OR9S15, COPS9, OTOS, GPC1, ANKMY1*	1.41

5	114.34-117.39	*EFCAB6, SULT4A1, PNPLA5, SAMM50, PARVB, PARVG, KIAA1644, RTL6, PRR5, ARHGAP8, PHF21B, NUP50, KIAA0930, UPK3A, FAM118A, SMC1B, RIBC2, FBLN1, ATXN10, WNT7B, PPARA, CDPF1, TTC38, GTSE1, TRMU, CELSR1, GRAMD4, CERK, TBC1D22A*	1.38
1	20.59-24.00	*USP25, NRIP1, SAMSN1, HSPA13, ABCC13, RBM11, LIPI, ROBO2, ROBO1*	1.25
19	12.68-14.99	*USP32, CA4, ZNHIT3, MYO19, PIGW, GGNBP2, DHRS11, MRM1, LHX1, AATF, ACACA, C19H17orf78, TADA2A, DUSP14, SYNRG, DDX52, HNF1B, HEATR6, CCL4, CCL14, CCL16, RANTES, HEATR9, TAF15, MMP28, C19H17orf50, GAS2L2, RASL10B, AP2B1, PEX12, SNORD7, SLFN14, SLFN11, UNC45B, NLE1, FNDC8, RAD51D*	1.22
15	62.46-65.34	*ELP4, PAX6, RCN1, WT1, EIF3M, PRRG4, QSER1, DEPDC7, TCP11L1, CSTF3, HIPK3, KIAA1549L, C15H11orf91, CD59, FBXO3, LMO2, CAPRIN1, NAT10, ABTB2, CAT, ELF5, EHF*	1.20
22	10.92-14.21	*ITGA9, CTDSPL, VILL, PLCD1, DLEC1, ACAA1, MYD88, OXSR1, SLC22A14, XYLB, ACVR2B, EXOG, SCN5A, SCN10A, SCN11A, WDR48, GORASP1, TTC21A, CSRNP1, CCR8, XIRP1, CX3CR1, SLC25A38, RPSA, SNORA62, SNORA62, MOBP, MYRIP, EIF1B, ENTPD3, RPL14, ZNF619, HSP60, CTNNB1, ULK4*	1.15
8	88.63-91.75	*SEMA4D, SECISBP2, CKS2, SHC3, S1PR3, Vault, NXNL2, SPIN1, CDK20, MSANTD3, TMEFF1, CAVIN4, PLPPR1, MRPL50, ZNF189, ALDOB, RNF20, GRIN3A*	1.14
4	1.55-4.59	*COBL*	1.00
7	10.60-13.83	*ZNF333, ADGRE3, NDUFB7, TECR, DNAJB1, GIPC1, PTGER1, PKN1, DDX39A, ADGRE5, ADGRL1, ASF1B, PRKACA, C7H19orf67, C19orf67, MISP3, PALM3, IL27RA, RLN3, RFX1, DCAF15, PODNL1, CC2D1A, C7H19ORF57, NANOS3, ZSWIM4, MRI1, CCDC130, CACNA1A, IER2, STX10, NACC1, TRMT1, LYL1, NFIX, GADD45GIP1, RAD23A, CALR, FARSA, SYCE2, GCDH, KLF1, DNASE2, MAST1, RTBDN, RNASEH2A, PRDX2, JUNB, HOOK2, BEST2, GET3, TRIR, TNPO2, SNORD41, FBXW9, GNG14, DHPS, WDR83, WDR83OS, MAN2B1, OR1M1, OR7G7, OR7G44, OR7G8, OR7G50, OR7H5P*	1.00



Supplemental Figure 1. Gene interaction network representing significant SNP effect correlations between growth and carcass traits as estimated by the AWM-PCIT analyses. Only correlations greater than |0.9| are shown. Nodes are genes or key transcription factors with a $|r| \geq 0.9$. Sub-network representing the top 100 most connected genes. The phenotypes are color-coded as blue for BW (body weight), pink for REA (ribeye area), orange for HWR (height × width ratio of the *Longissimus dorsi* muscle), and yellow for RFT (rump fat thickness).

Supplementary Table 6. Genes identified as common between GWAS and the AWM-PCIT analyzes.

Gene	SNP	BW	REA	HWR	BFT	RFT
ATF3	52190 and 52191	×				
BATF3	52186, 52187, 52188 and 52189	×				
ELF1	40130 and 40131	×				
SMAD9	40552 and 40553	×				
SOHLH2	40567, 40568, 40569 and 40570	×				
TCF24	45915	×				
ZEB2	6327, 6328, 6317, 6318, 6319, 6320, 6321, 6322, 6323, 6324, 6325 and 6326	×				
GRHL3	8506, 8507 and 8508		×			
LTF	65102, 65103 and 65104		×			
PROX2	35934		×			
RUNX3	8488, 8486 and 8489		×			
IRX3	55495, 55493, 55494 and 55496			×		
PLAG1	45662, 45663, 45664, 45665, 45666, 45667 and 45668				×	
SOX17	45629, 45625, 45626, 45627, 45628 and 45630				×	
LHX1	57330, 57328 and 57329					×

BW body weight, REA ribeye area, HWR height-to-width ratio of Longissimus dorsi muscle, BFT backfat thickness, RFT rump fat thickness.