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Frequencies of the variants associated with the calpain and calpastatin genes in Brazilian Brahman cattle

Abstract – The objective of this work was to estimate the frequency of favorable genotypes in the gene markers *CAPN1* 316, *CAPN1* 4751, *CAPN3*, and *CAST* c.2832 in Brazilian Brahman cattle. A total of 108 DNA samples from purebred Brahman cattle were analyzed to genotype the animals for each marker through polymerase chain reaction and direct Sanger sequencing. These samples were originated from 54 bulls and 54 cows used as semen and oocyte donors, respectively. The genotype frequencies, known to be associated with meat tenderness, were 48% AA in *CAST* and 14% GG in *CAPN3*. *CAST* has been used in the selection of animals with a meat tenderness phenotype across various cattle breeds, including Brahman cattle from other countries. The CC genotype, which is favorable in *CAPN1* 316 and *CAPN1* 4751, was not identified in the analyzed samples. The highest prevalence of the AA genotype in *CAST* observed in bulls and cows used in purebred breeding programs in Brazil indicates that this marker can be used to guide mating strategies in order to increase the frequency of this genotype and enhance meat tenderness.

Index terms: breeding stock, genetic markers, genotyping, meat tenderness.

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Frequência das variantes associadas aos genes calpaína e calpastatina em bovinos Brahman no Brasil

Resumo – O objetivo deste trabalho foi estimar a frequência de genótipos favoráveis dos marcadores genéticos *CAPN1* 316, *CAPN1* 4751, *CAPN3* e *CAST* c.2832 em bovinos Brahman brasileiros. Um total de 108 amostras de DNA de bovinos puros da raça Brahman foram analisadas para genotipar os animais para cada marcador, por meio de reação em cadeia de polimerase e sequenciamento direto de Sanger. Essas amostras provieram de 54 touros e 54 vacas doadores de sêmen e oócitos, respectivamente. As frequências genotípicas, conhecidas por estarem associadas à maciez da carne, foram de 48% AA em *CAST* e 14% GG em *CAPN3*. O *CAST* tem sido utilizado na seleção de animais com o fenótipo de maciez da carne em várias raças de gado, incluindo o gado Brahman de outros países. O genótipo CC, que é favorável em *CAPN1* 316 e *CAPN1* 4751, não foi identificado nas amostras analisadas. A maior prevalência do genótipo AA em *CAST* observada em touros e vacas usados em programas de reprodução no Brasil indica que este marcador pode ser utilizado para orientar estratégias de acasalamento, para aumentar a frequência desse genótipo e melhorar a maciez da carne.

Termos para indexação: reprodutores, marcadores genéticos, genotipagem, maciez da carne.

Introduction

Although *Bos indicus* cattle are known to have less desirable growth performance and carcass characteristics (Royer et al., 2016), producers and breeders should be aware that meat quality is a complex trait, affected by many factors, such as tender stretch, hormonal growth promoters, marbling, aging, pH, and juiciness (Robinson et al., 2012; Saucedo-Uriarte et al., 2024). Meat tenderness, in particular, is an important component of palatability, and its variation has a significant effect on consumer satisfaction (White et al., 2005). Since phenotypic data concerning meat quality before slaughter is limited and difficult to collect (White et al., 2005), many gene markers or single nucleotide polymorphisms (SNPs) have been recommended to increase meat quality, affecting especially tenderness (Robinson et al., 2012).

Compared with other selection tools, the use of SNPs has increased genetic improvement. SNP panels available commercially can provide molecular value predictions for breeding, and their use should be stimulated among producers and breeders in order to increase meat quality and consumer satisfaction (Robinson et al., 2012; Royer et al., 2016; Enriquez-Valencia et al., 2017; Ardiçli et al., 2019; Saucedo-Uriarte et al., 2024). Among these panels, those associated with calpain and calpastatin genes can be highlighted (White et al., 2005; Barendse et al., 2008; Enriquez-Valencia et al., 2017; Saucedo-Uriarte et al., 2024). The calpain-calpastatin system is composed of calcium-dependent proteases encoded by the calpain gene and its endogenous inhibitor calpastatin, being activated postmortem, enhancing proteolytic activity and contributing to meat tenderization during the aging period (Blecha et al., 2019). According to previous studies, the presence of genotypes CC in *CAPN1* 316, CC in *CAPN1* 4751, GG in *CAPN3*, and AA in *CAST* c.2832 was considered favorable for meat tenderness in Brahman cattle (White et al., 2005; Barendse et al., 2008; Robinson et al., 2012; Nattrass et al., 2014; Bosques et al., 2015; Royer et al., 2016; López Rojas et al., 2017; Ardiçli et al., 2019; Pereira et al., 2022). Therefore, these SNPs are useful in assisting producers in the selection of animals that match the desired meat quality traits (Nattrass et al., 2014; Blecha et al., 2019).

In Brazil, SNPs associated with the calpain and calpastatin genes have been analyzed in zebuine cattle, particularly Nellore cattle, as well as in taurine and crossbred cattle (Curi et al., 2010; Tizioto et al., 2014; Pereira et al., 2015; Carvalho et al., 2017; Enriquez-Valencia et al., 2017; Rosa et al., 2018; Blecha et al., 2019). However, these SNPs have not yet been evaluated in Brazilian Brahman cattle, which are characterized by a high adaptability, with early maturity and excellent muscling, offering hardiness and high-quality beef genetics (Lemos, 2006).

The objective of this work was to estimate the frequency of favorable genotypes in the gene markers *CAPN1* 316, *CAPN1* 4751, *CAPN3*, and *CAST* c.2832 in Brazilian Brahman cattle.

Materials and Methods

All procedures were previously approved by Comissão de Ética no Uso de Animais (CEUA) of Universidade Estadual Paulista (UNESP) under protocol number 0194/2020 CEUA UNESP. The used samples were collected in a manner that ensured the anonymity of the animals and breeding farms.

A total of 108 hair follicle bulb samples of purebred Brahman were collected from the tails of 54 bulls and 54 cows, being used to evaluate the *CAPN1* 316, *CAPN1* 4751, *CAPN3*, and *CAST* c.2832 gene markers. These samples are part of a genetic database belonging to the Laboratory of Molecular Biology of the veterinary clinic of UNESP, which were used in a prior study by Trecenti et al. (2018). All the analyzed animals were registered at Associação Brasileira dos Criadores de Zebu (ABCZ, Uberaba, MG, Brazil). In the study, a total of 40 frozen semen samples from purebred Brahman bulls were also used: 24 from the United States, 14 from Brazil, 1 from Argentina, and 1 from Australia, all obtained from reproduction companies in Brazil. Additionally, 54 donor cows and 14 bulls were randomly sampled by ABCZ technicians during the certification of the animals on 18 farms located in different geopolitical regions of the Brazil: four in the North, Midwest, and South, and ten in the Southeast. These animals were included in the study because the donors were known to be extensively used in in vitro embryo production, and the bulls, as commercial semen producers within purebred breeding programs in the country.

For genomic DNA purification, 20 hair follicle bulbs from each animal were incubated in 90 µL lysis buffer with 0.5 µL of proteinase K at 56ºC for 1 hour. Subsequently, 30 µL of protein precipitation

buffer, containing 5.7% ammonium acetate were added, followed by incubation at 25ºC for 2 min and centrifugation at 1,900 G for 12 min. The resulting 90 µL of supernatant were mixed with an equal volume of 100% isopropanol and subjected to centrifugation. The resulting pellet was washed with 70% ethanol. Afterward, the tube was dried by incubation at 37ºC for 10 min. The DNA was eluted with 30 µL elution buffer (Tris EDTA, pH 8.0) and incubated at 56ºC for 30 min. Subsequently, the DNA samples were stored frozen at -20ºC until the polymerase chain reaction (PCR) was performed.

For the PCR technique, specific primers were designed with the PrimerQuest Tool (Integrated DNA Technologies, Inc., Coralville, IA, USA) in order to amplify the SNP points for each marker. The PCR mixture (total volume of 25 µL) contained 2.5 µL of template DNA, 0.3 µmol L^{-1} (0.75 µL) of forward and reverse primers, 12.5 µL of the PCR Master Mix (Promega, Madison WI, USA), and 8.5 µL of nuclease-free water. A nontemplate control reaction was used to ensure that the PCR was not contaminated. The thermal cycling conditions were as follows: 95ºC for 10 min, 35 cycles of 95ºC for 45 s, 60.1ºC for 60 s, 72ºC for 45 s, and 72ºC for 10 min. Amplicons were analyzed through 1.5% agarose gel electrophoresis, and the products of the correct size were purified using the GenElute PCR Clean-Up Kit (Sigma Aldrich, St. Louis, MO, USA), according to the manufacturer's instructions. The Sanger method was used to sequence the DNA, employing 10 µL of each purified PCR product, 5.0 µL of the forward primers, and the BigDye Terminator Cycle Sequencing Kit (Thermo Fisher Scientific, Waltham, MA, USA). The sequences and electropherograms generated were analyzed in the Geneious software (Dotmatics, Boston, MA, USA), and, then, compared with the following accession numbers deposited in the GenBank (2025): AH009246.3, AH009246.3, NC0373377.1, and NC037334.1, corresponding to *CAPN1* 316, *CAPN1* 4751, *CAPN3*, and *CAST*, respectively.

The genotypic frequencies were estimated for each marker, and the data were analyzed descriptively. Genotypes were tested for Hardy-Weinberg's equilibrium, and assessed whether they were in equilibrium for each gene marker through the chi-square test.

Results and Discussion

According to the sequencing results and electropherogram analysis (Table 1), the samples were classified as: AA, CC, AG, CT, GG, TT, standing for homogenous for adenine, homogenous for cytosine, adenine plus guanine (heterogeneous), cytosine plus thymine (heterogeneous), homogenous for guanine, and homogenous for thymine, respectively. For *CAST*, 48% (52/108), 32% (35/108), and 20% (21/108) of the samples were classified as AA, AG, and GG genotypes, respectively. For *CAPN3*, 14% (15/107) were classified as GG, 49% (52/107) as GT, and 37% (40/107) as TT. Regarding *CAPN1* 316, 97% of the samples (105/108) were classified as GG and 3% (3/108) as CG. For *CAPN1* 4751, 94% (102/108) were classified as TT and 6% (6/108) as CT. All genotypes, except those in *CAST*, were in Hardy-Weinberg's equilibrium.

CAST and *CAPN3* were the most prevalent SNPs for identifying favorable genotypes, i.e., AA and GG, respectively. In the studied samples, 7% (7/107), 50% (53/107), and 43% (47/107) of the samples presented both, one, and none of these genotypes, respectively. Likewise, Nattrass et al. (2014) concluded that *CAST* SNP is the most prevalent marker to identify the favorable AA genotype.

The prevalence of the AA genotype in the present study was higher than that reported in Australia (Barendse et al., 2008; Robinson et al., 2012; Nattrass et al., 2014) and Colombia (López Rojas et al., 2017), where the occurrence of this genotype ranged from 30.8% (Barendse et al., 2008) to 44.21% (Robinson et al., 2012; Nattrass et al., 2014). This finding suggests that *CAST* may be the primary marker for meat tenderness in Brazilian Brahman cattle, probably due to the influence of Australian Brahman genetics, given the high prevalence of AA in studies on these animals (Robinson et al., 2012; Nattrass et al., 2014). In researches on the Nellore breed in Brazil, the AA genotype also prevailed, ranging from 16.85% (Tizioto et al., 2014) to 56.4% (Enriquez-Valencia et al., 2017). These results reinforce the use of the SNP *CAST* marker as a trait selector for meat tenderness, with a medium to high prevalence in Brahman, Nellore, and crossbreeds (Barendse et al., 2008; Robinson et al., 2012; Nattrass et al., 2014; Tizioto et al., 2014; Enriquez-Valencia et al., 2017; López Rojas et al., 2017; Blecha et al., 2019). Barendse et al. (2008) described the SNP *CAPN3* as more prevalent in zebuine and composite

breeds than in taurine breeds, for which the GG is the favorable genotype for meat tenderness. For Brahman cattle, however, this marker was only evaluated in Australia (Barendse et al., 2008; Robinson et al., 2012; Nattrass et al., 2014), where the prevalence of favorable genotypes varied from 27.03% (Barendse et al., 2008) to 37.68% (Robinson et al., 2012; Nattrass et al., 2014), differing from that of the present study, where a lower frequency of the GG genotype was registered. Even though Brazilian Brahman genetics include Australian, American, and African lineages (Lemos, 2006; Trecenti et al., 2018), *CAPN3* is not commonly used as a trait marker in Brazilian animals despite its relatively high prevalence in zebuine cattle (Barendse et al., 2008) and the influence of Australian lineages (Lemos, 2006; Trecenti et al., 2018). Up to the present, there is no known study on *CAPN3* performed in Brazil.

Regarding *CAPN1* 316, the presence of the CC genotype positively influences meat tenderness (White et al., 2005; Curi et al., 2010). The prevalence rates in the present study (Table 1) are aligned with those reported in Australia (Robinson et al., 2012; Nattrass et al., 2014), Bolivia (Pereira et al., 2022), Colombia (López Rojas et al., 2017), the United States (White et al., 2005), Puerto Rico (Bosques et al., 2015), and Turkey (Ardiçli et al., 2019). These similar results are associated with the previously mentioned lineages of Brazilian Brahman cattle, as well as to the high exportation of beef breed semen from Brahman cattle to Latin America and Asia (Lemos, 2006; Trecenti et al., 2018). However, the presence of the CC genotype was not observed in Nellore cattle, a zebuine breed, which composes Brahman genetics (Lemos, 2006; Trecenti et al., 2018), neither by Curi et al. (2010) and Carvalho et al. (2017) in Brazil nor by Pereira et al. (2022) in Colombia. These studies reinforce the idea that GG is fixed in Brahman and zebuine cattle (White et al., 2005; Carvalho et al., 2017), and that *CAPN1* 316 is associated with taurine breeds and crossbreeds (Curi et al., 2010).

The SNP *CAPN1* 4751 was described by White et al. (2005), who found that genotype CC is also favorable for meat tenderness and that *CAPN1* 4751 is the only described marker to influence shear force in the case of heterozygosis in the CT genotype. The findings of the present work (Table 1) differed from those of studies performed in Australia (Robinson et al., 2012; Nattrass et al., 2014), Bolivia (Pereira et al., 2022), and Colombia (López Rojas et al., 2017), where the CC genotype showed a prevalence varying from 6.82% (Robinson et al., 2012; Nattrass et al., 2014) to 28.9% (López Rojas et al., 2017). However, the results obtained here were similar to those reported in Puerto Rico (Bosques et al., 2015) and in the United States (White et al., 2005), where the CC genotype was not observed. In this line, frequencies of 0, 3.15, and 3% were also observed for the CC genotype in the Nellore breed by Blecha et al. (2019), Carvalho et al. (2017), and Rosa et al. (2018), respectively. These results suggest that some Brazilian animals descend from lineages where *CAPN1* 4751 is not a selected marker, explaining the absence of the CC genotype in the present study.

Although *B. indicus* breeds present less desirable growth performance and carcass characteristics (Royer et al., 2016), Brahman cattle are characterized by an efficient beef production, with good results in crossings with zebuine and taurine breeds for meat or dual-purpose systems (Lemos, 2006). The four SNPs (*CAPN1* 316, *CAPN1* 4751, *CAPN3*, and *CAST*) analyzed in the present work are widely recognized

Table 1. Biological gene markers, identified genotypes (Gene), number of detected alleles, genotypic frequency, and Hardy-Weinberg's equilibrium analysis (HWE) for 108 DNA samples of Brazilian purebred Brahman cattle.

Gene marker	Genotype frequency[1]									HWE[2]	
	Favorable homozygous			Heterozygous			Unfavorable homozygous				
	Gene[3]	Alleles (number)	Frequency (%)	Gene	Alleles (number)	Frequency (%)	Gene	Alleles (number)	Frequency (%)	State[4]	p-value
CAPN1 316	CC	n/d	n/a	CG	3	3	GG	105	97	In	0.878963
CAPN1 4751	CC	n/d	n/a	CT	6	6	TT	102	94	In	0.757110
CAPN3	GG	15	14	GT	52	49	TT	40	37	In	0.728309
CAST c.2832	AA	52	48	AG	35	32	GG	21	20	Out	0.002246

[1]n/d, not detected; and n/a, not available. [2]Indicates the state of the population and the p-value of the chi-square test. If $p < 0.05$, the chi-square test is not consistent with Hardy-Weinberg's equilibrium. [3]Identified genotypes. [4]In, population in equilibrium; and Out, population evolving.

for enhancing meat tenderness across breeds, such as Brahman, Nellore, taurine, and crossbreeds (White et al., 2005; Barendse et al., 2008; Curi et al., 2010; Robinson et al., 2012; Nattrass et al., 2014; Tizioto et al., 2014; Bosques et al., 2015; Pereira et al., 2015; Royer et al., 2016; Carvalho et al., 2017; Enriquez-Valencia et al., 2017; López Rojas et al., 2017; Rosa et al., 2018; Ardiçli et al., 2019; Blecha et al., 2019; Pereira et al., 2022; Saucedo-Uriarte et al., 2024). These findings are aligned with those of studies comparing Brahman and Nellore to Angus and Caracu cattle, which are: a lower *CAPN1* 316 and *CAPN1* 4751 frequency in zebuine breeds, the prevalence of *CAPN3* and *CAST* in taurine breeds, and a moderate to high prevalence of *CAPN3* and *CAST* in zebuine breeds (Robinson et al., 2012; Blecha et al., 2019). Robinson et al. (2012) linked SNP *CAPN3* to meat traits, such as marbling and juiciness, concluding that, beyond tenderness, consumer-preferred qualities could also be improved.

Although the findings of the present work are valuable, factors other than genotype may influence the final outcome in terms of meat quality and tenderness. Therefore, the use of the evaluated markers in animal selection should be combined with appropriate management and nutrition practices in order to enhance the final product. The main limitation of this study was the absence of muscle biopsy, and the inability to correlate genotypes with meat tenderness phenotypes. Muscle biopsy samples could not be collected for meat tenderness analyses since the assessed DNA samples come from semen collection centers or farms specialized in oocyte production for in vitro fertilization. However, because these markers have been previously associated with meat tenderness phenotypes across various cattle breeds, including Brahman cattle from other countries (White et al., 2005; Barendse et al., 2008; Robinson et al., 2012; Nattrass et al., 2014; Bosques et al., 2015; Pereira et al., 2015; Royer et al., 2016; López Rojas et al., 2017; Ardiçli et al., 2019; Pereira et al., 2022), this limitation should be appropriately addressed.

Conclusions

1. Increasing the AA genotype in *CAST* c.2832 through mating strategies may improve the production of Brazilian Brahman animals with desirable phenotypes.

2. Markers 316 and 4751 of the *CAPN1* CC genotype are not found in the studied samples.

3. The GG genotype in *CAPN3* has a lower frequency than that observed in other studies with Brahman cattle.

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Data in article: research data are available in the published article.

Declaration of use of AI technologies

No generative artificial intelligence (AI) was used in this study.

Conflict of interest statement

The authors declare no conflicts of interest.

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