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Research Article

Frequency of Favorable Alleles for Meat Quality, Litter Size, Adaptation, and Growth Traits in Closed Nucleus Population of Philippine Native Swine (*Sus philippensis var. markaduke*)

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Abstract The Philippine native swine (PNS) represent valuable heritage genetic resources with significance for food security and geo-cultural traditions. Among these, the Markaduke breed is recognized for producing the "best lechón" and comminuted pork products, while also exhibiting moderate litter size (≥8) and adaptability to local conditions. To support the development of a breeding program suited for an optimal production system, its genetic properties were assessed. A total of 67 animals (17 males and 50 females) from 4.37 ± 0.12 generations, with an inbreeding coefficient of 0.1493 ± 0.0167, were genotyped using molecular markers. Seven gene markers for meat quality, three for litter size, two for adaptation, and one for growth were analyzed, with results tested under Hardy–Weinberg equilibrium and chi-square statistics. For meat quality, *rendement napole* (*RN*), *Cathepsin D* (*CTSD*), and *leptin receptor* (*LEPR*) exhibited genotype frequencies exceeding 50% in both sexes, with the *rn* allele fully expressed (100% rnrn, $p_{0.0001}<\alpha_{0.05}$). Regarding litter size, *prolactin receptor* (*PRLR*) was the major allele, with nearly equal frequencies of 0.77 in both sexes ($p_{0.05}=\alpha_{0.05}$). The N allele of the halothane gene, associated with stress tolerance, was observed at a frequency of 0.97 ($p_{0.80}>\alpha_{0.05}$). The favorable allele for growth (*MYOG*) appeared only in heterozygotes at low frequencies (0.08 in males, 0.14 in females, and 0.13 combined). These findings demonstrate that the closed nucleus population of Markaduke carries favorable alleles essential for genetic improvement, underscoring its potential for sustainable breeding strategies and conservation of native swine genetic resources.

Keywords: Allele, biomarker, genotype, homozygosity, Markaduke, meat quality

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1. Introduction

The Philippine native swine (PNS) represent heritage domestic animal genetic resources that provide substantial economic utility as food sources while holding significant geo-cultural value. Although the precise progenitors of PNS remain uncertain, they are presumed to be products of interbreeding among wild pig species such as *Sus philippensis*, *Sus ahoenobarbus*, *Sus cebifrons*, *Sus oliveri*, and the subspecies *Sus philippensis mindanensis*, along with the introduced *Sus scrofa* [1-6]. Observations of neonates with striped, orange-brown coat coloration reveal phenotypes associated with wild pig ancestry, traits absent in commercial swine breeds. This distinctive characteristic offers a promising avenue for research into genetic lineages and interbreeding patterns between wild and introduced pig species. Several PNS breeds exhibit distinguishing physical traits that have evolved through community-based selection processes, reflecting both cultural practices and adaptive responses to local environments [5, 7]. These traits highlight the dynamic interaction between traditional husbandry and genetic adaptation, underscoring the importance of indigenous knowledge in shaping breed characteristics. Such processes have contributed to the resilience and uniqueness of PNS, positioning them as valuable resources for both food security and cultural heritage preservation.

Among PNS, the Markaduke breed developed by Marinduque State University (13°19′57.8″N, 122°05′59.0″E) is officially listed in the Domestic Animal Diversity Information System (DAD-IS) of the Food and Agriculture Organization (FAO, https://www.fao.org/dad-is/browse-by-country-and-species/en/). It is highly sought after

for *lechón* (roast whole pork) and comminuted meat products such as *tocino*, *longganisa*, *sisig*, and smoked pork (*tapa*), owing to its distinct flavor, juiciness, and tenderness [8–9]. The breed has demonstrated resilience and productivity even during the *COVID-19* pandemic and outbreaks of African swine fever (ASF) [10]. Its reproductive performance is notable, particularly at the third and fourth parity, achieving a number born alive (NBA) of 10 or more piglets, with post-weaning growth averaging 92 g/day and carcass yield of 47.54% [11–12]. These attributes highlight the Markaduke's economic potential as a genetic resource for food security and income generation.

Molecular studies on swine genetics have largely prioritized commercial breeds with intensive selection histories [13–14]. In contrast, indigenous breeds such as the Markaduke are presumed to carry favorable alleles for meat quality, reproductive efficiency, environmental adaptation, and growth traits. These genetic resources remain underexplored, despite their potential to contribute to sustainable swine production systems. Research into the genetic architecture of PNS, particularly through molecular markers, can provide insights into their adaptability and productivity, ensuring that their unique traits are harnessed for long-term breeding strategies.

The application of marker-assisted selection and genomic analyses offers a promising approach to uncover the genetic potential of the Markaduke and other PNS breeds. Such strategies can guide breeding programs toward the enhancement of desirable traits while ensuring the preservation of genetic identity [7]. Incorporating genomic selection frameworks that balance productivity, adaptability, and cultural heritage will be critical for sustaining PNS populations. Ultimately, the conservation and strategic utilization of PNS genetic resources represent a pathway toward resilient, culturally grounded, and economically viable swine production in the Philippines.

2. Materials and Methods

2.1. Management of population

The closed nucleus population of Markaduke was established in 2012 and has been continuously maintained at the Research Center of Marinduque State University, Torrijos Campus, Marinduque, Philippines (13°19'57.8"N, 122°05'59.0"E). All individuals within the nucleus population were properly identified through ear-notching with coded numbers for data collection, recording, and performance evaluation. Breeding stock selection follows a phenotypic protocol, emphasizing qualitative traits such as pure black coat color, a signature of native swine, and quantitative traits including litter size and average daily gain (ADG). Selected individuals are raised to maturity and bred beginning at eight (8) months of age through a line-mating system designed to preserve desirable parental performance, particularly large litter sizes (>8 piglets born alive). Breeding stocks (sows and boars) are housed individually, while piglets and replacement stock are managed in groups of up to 50 heads in range systems with sheds. Feeding practices combine plant-based resources with commercially mixed feeds at ratios tailored to physiological requirements (e.g., 90:10 for boars, 70:30 for sows). Neonates receive iron dextran supplementation within the first week to prevent iron deficiency anemia. Overall, management practices adhere to prescribed husbandry standards under Republic Act No. 8485 and Republic Act No. 10631.

2.2. Sampling and laboratory analyses

The study sample consisted of 67 individuals, comprising 17 males (junior boars) and 50 females (replacement gilts). Pedigree analysis revealed an average of 4.35 ± 0.27 generations for males, with an inbreeding coefficient of 0.1480 ± 0.0302. Females showed a comparable pedigree of 4.38 ± 0.14 generations and an inbreeding coefficient of 0.1497 ± 0.0200. When combined, the pedigree data across sexes averaged 4.37 ± 0.12 generations back, with an overall inbreeding coefficient of 0.1493 ± 0.0167.

Biological samples including blood, hair follicles, and ear fragments were collected from each individual in strict adherence to standardized protocols to ensure sample integrity and ethical compliance. Blood was drawn via sterile venipuncture of the external jugular vein, hair follicles were plucked with intact roots, and ear fragments were obtained using approved punch techniques. All samples were systematically labeled and preserved under appropriate storage conditions (e.g., blood in vacutainers, hair follicles and ear fragments in sterile zip-lock pouches), and were handled in compliance with biosafety regulations and animal welfare guidelines to safeguard reproducibility and reliability of subsequent analyses. During transport, samples were maintained under cold-chain conditions and subsequently stored in a bio-freezer at the Animal Breeding and Genomics Section, Department of Agriculture–Philippine Carabao Center (DA-PCC), National Headquarters, Science City of Muñoz, Nueva Ecija, Philippines (15°43′58″N, 120°55′52″E).

DNA Extraction. Genomic *DNA* was extracted from tissue samples (ear fragments and hair follicles) using the Qiagen DNeasy Blood and Tissue Kit with minor protocol modifications, wherein approximately 25 mg of ear tissue or 5–10 hair follicles were processed in 1.5 ml microcentrifuge tubes with Buffer *ATL* and proteinase *K*, incubated at 56 °C until complete lysis, followed by the addition of Buffer AL and ethanol, and subsequent purification on *DNeasy* mini spin columns with washes in Buffers AW1 and AW2 before final elution in Buffer AE and storage at 2–8 °C. Blood-derived genomic *DNA* was isolated using the Promega Wizard Genomic *DNA* Purification Kit with minor modifications, in which 500 µl of homogenized blood was treated with ammonium chloride to recover white blood cells, subjected to cell and nuclear lysis with protein precipitation, and processed by centrifugation; the supernatant was mixed with isopropanol, stored overnight, and centrifuged again to pellet *DNA*, which was washed with 70% ethanol, air-dried under laminar flow, rehydrated in 50 µl of *DNA* rehydration solution, gently mixed, and stored at 2–8 °C for downstream genotyping.

Mutagenically Separated Polymerase Chain Reaction and Gel Documentation. Seven meat quality markers of *rendement napole* (*RN*), *cathepsin D* (*CTSD*), *leptin receptor* (*LEPR*), *lipoprotein lipase* (*LPL*), *calpastatin* (*CAST*), *insulin-like growth factor binding protein intron 3* (*IGFBP3*), and *insulin-like growth factor binding protein intron 7* (*IGFBP7*) *genes* were analyzed using modified protocols of mutagenically separated polymerase chain reaction (MS-PCR). Similar procedures were applied to litter size (*PRLR, ESR, LIF*), adaptation (*HAL* and *FUT1*), and growth markers (*MYOG*). These targeted loci represent critical genetic determinants of productivity, resilience, and carcass quality in the closed nucleus population of Markaduke (Table A1, 15-24).

Amplification of specific genes (e.g., *ESR*, *FUT1*, *HAL*) was performed using MS-PCR under optimized laboratory conditions. PCR products were verified through 3.5% agarose gel electrophoresis (prepared with Pronadisa Agarose D1 Low EEO and Gel Red Biotium Solution) using the Mupid-exU submarine electrophoresis system. Gel documentation was conducted with the Enduro™ GDS system, and genotype scoring was performed through standard and manual computation. Sequencing provided further validation of gel products and enabled comparison with commercial swine breeds, ensuring accuracy and reproducibility of results (Table A1, 15–24).

2.3. Statistical analysis

The genotype and allele frequencies were tested in Hardy-Weinberg Equilibrium (HWE) and chi-square using an online HWE calculator (https://calculator.now/hardy-weinberg-equilibrium-calculator/). The p-value <0.05 indicates deviation from the HWE; otherwise, it conforms to the null hypothesis of stability in genotype and allele frequencies from one generation to the next.

3. Results

3.1. Meat quality markers

Seven gene markers associated with meat quality traits, namely: *rendement napole* (*RN*), *cathepsin D* (*CTSD*), *leptin receptor* (*LEPR*), *lipoprotein lipase* (*LPL*), *calpastatin* (*CAST*), *insulin-like growth factor binding protein 3* (*IGFBP3*), and *insulin-like growth factor binding protein 7* (*IGFBP7*) were identified in the closed nucleus population of Markaduke (Fig. 1 and Table A2). These loci represent critical genetic markers influencing muscle metabolism, fat deposition, tenderness, and overall carcass quality. The presence of favorable alleles across these biomarkers highlights the genetic potential of the population for producing high-quality pork.

Three biomarkers (*RN*, *CTSD*, and *LEPR*) exhibited genotypic frequencies exceeding 50% in both sexes. Remarkably, the sampled population (n = 67) expressed a homozygous recessive genotype (100% *rnrn*, 0.0001< 0.05) for rendement napole indicating near fixation of this allele within the population. This suggests strong selection for meat quality traits associated with RN, despite its known trade-offs with growth efficiency. In contrast, *CTSD* and *LEPR* conformed to Hardy–Weinberg equilibrium, indicating balanced allele distributions in the absence of active selection. Notably, *CTSD* showed higher favorable genotype and allele frequencies in females (0.90 > 0.50 and 0.95 > 0.75, respectively), whereas *LEPR* displayed relatively equal expression across sexes. These findings emphasize the need for targeted genotyping in males to increase the frequency of the favorable genotype and allele.

The favorable genotypes ***CC*** and ***DD*** for *LPL* and *CAST* were observed only in females, at frequencies of 0.20 and 0.06, respectively. Males acted solely as carriers of the favorable alleles, with frequencies of 0.25 for *C* and 0.13 for *D*. Both loci conformed to HWE ($p > 0.05$), suggesting stable transmission across generations. However, the relatively low frequencies of favorable genotypes necessitate deliberate breeding interventions. Genotyping to identify carriers and structured assortative mating are essential strategies to increase allele frequencies and achieve fixation within the population.

The favorable alleles, *A* and *C*, for *IGFBP3* and *IGFBP7*, were detected only in heterozygous individuals, with low frequencies of 0.12 and 0.07, respectively, across both sexes. Despite their rarity, both loci conformed to HWE, indicating genetic stability and the likelihood of persistence across generations. These insulin-like growth factor binding proteins are important regulators of muscle growth and fat deposition, traits directly linked to meat quality. Their presence, even at low frequencies, underscores the importance of genotyping and selective breeding to increase their prevalence and secure their contribution to carcass traits.

The combined expression of favorable alleles across *RN, CTSD, LEPR, LPL, CAST, IGFBP3,* and *IGFBP7* provides a strong genetic foundation for meat quality improvement in Markaduke. However, the varying frequencies and equilibrium statuses highlight the need for tailored breeding strategies. While *RN* appears fixed, *CTSD* and *LEPR* require sex-specific genotyping, and *LPL, CAST, IGFBP3*, and *IGFBP7* demand deliberate assortative mating to prevent allele loss. Integrating marker-assisted selection and genomic frameworks will be critical to balance fixation of favorable alleles with preservation of genetic diversity, ensuring sustainable improvement of meat quality traits in the population.

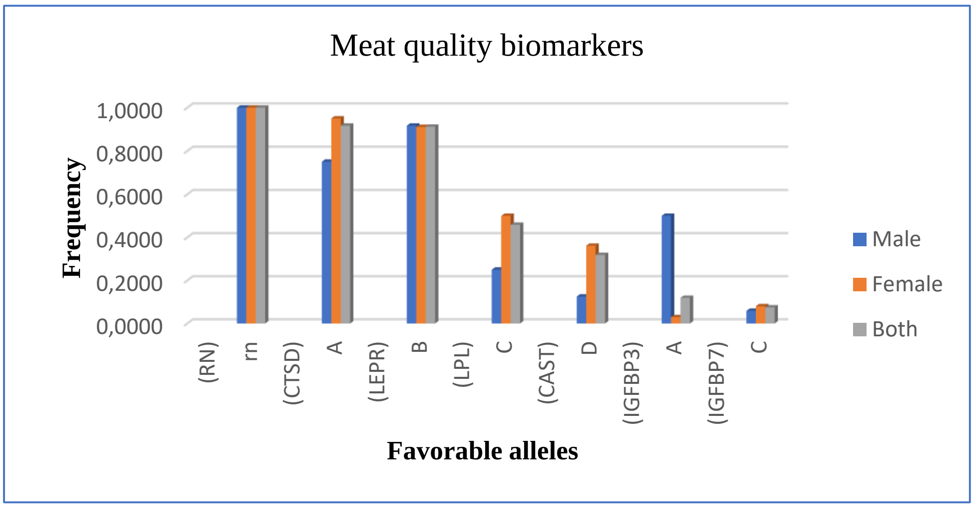

Figure 1. Frequency of favorable alleles of biomarkers (RN, $p<_{0.05}$; CTSD, $p>_{0.05}$; LPL, $p>_{0.05}$; CAST, $p>_{0.05}$; IGFBP3, $p>_{0.05}$; IGFBP7, $p>_{0.05}$) for meat quality traits.

3.2. Litter size markers

Three litter size biomarkers such as *prolactin receptor* (*PRLR*), *estrogen receptor* (*ESR*), and *leukemia inhibitory factor* (*LIF*) revealed the presence of favorable alleles within the closed nucleus population of Markaduke (Fig. 2 and Table A3). The most prominent allele was observed in *PRLR*, with nearly equal frequencies across sexes and a combined value of 0.77. This distribution deviated significantly from HWE ($p < 0.05$), suggesting possible non-random mating or directional selection favoring reproductive efficiency. In contrast, *ESR* exhibited lower allele frequencies (0.36 combined) but conformed to HWE, indicating genetic stability and the likelihood of consistent transmission of genotypes and alleles across generations.

The *LIF* gene was detected only in heterozygous form, with low allele frequencies (0.18), and deviated from HWE, indicating a high probability of allele loss within the population. Given *LIF's* critical role in uterine receptivity and embryo implantation, its potential disappearance poses risks to reproductive performance. The low frequency of favorable alleles suggests that without deliberate intervention, genetic drift or unfavorable selection pressures could accelerate their loss, thereby compromising reproductive success in the long term.

To mitigate these risks, deliberate interventions such as systematic genotyping and structured assortative mating are necessary to preserve favorable alleles. Incorporating genomic selection frameworks that balance *PRLR*, *ESR*, and *LIF* polymorphisms will be essential to sustain prolificacy, maintain genetic diversity, and secure long-term reproductive success in the Markaduke population. These strategies will ensure that favorable alleles are not only maintained but also strategically fixed, thereby enhancing reproductive efficiency while safeguarding the genetic integrity of the breed.

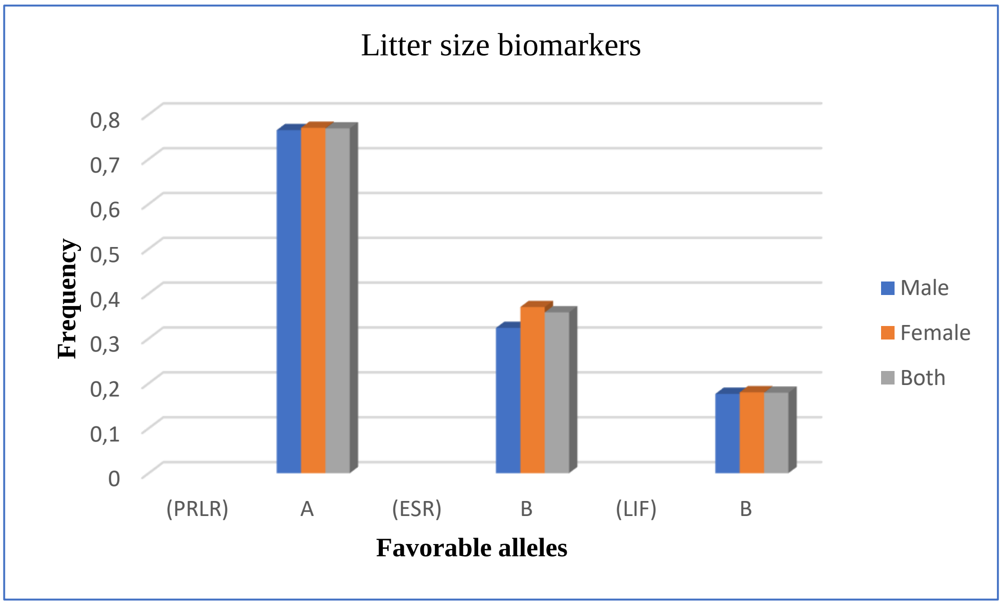

Figure 2. Frequency of favorable alleles of biomarkers (PRLR, p=0.05; ESR, p>0.05; LIF, p=0.05) for litter size traits or number of pigs born traits.

3.3. Adaptation markers

Two biomarkers for adaptation revealed the presence of favorable alleles within the population (Fig. 3 and Table A4). The most prominent was the *N* allele of the halothane (*HAL*) gene, which confers stress tolerance, observed at a frequency of 0.97 in the combined dataset across sexes. This near fixation of the N allele indicates strong resilience against porcine stress syndrome (PSS) and pale, soft, exudative (PSE) meat. However, the persistence of the unfavorable n allele, detected at frequencies of 0.06 in males and 0.02 in females, highlights the need for deliberate breeding efforts to eliminate susceptibility alleles. Given that the population conforms to HWE ($p > 0.05$), the continued presence of the *n* allele suggests that without targeted selection, stress-sensitive genotypes may persist across generations.

Resistance to *Escherichia coli* (*E. coli*) was demonstrated through the favorable allele of the *α(1,2)-fucosyltransferase* (*FUT1*) gene, observed at a frequency of 0.31 in the combined dataset. Notably, males were the primary carriers of the favorable allele, with a frequency of 0.50, deviating significantly from HWE ($p < 0.05$). This deviation suggests potential non-random mating or selective pressures acting on *FUT1*, which may influence allele distribution. Since *FUT1* variants provide defense against enterotoxigenic *E. coli* infections, a major cause of neonatal diarrhea and piglet mortality, maintaining and increasing the frequency of this allele is critical for productivity in smallholder systems. Structured breeding programs, marker-assisted introgression, and continuous monitoring of allele frequencies are essential to conserve disease-resistant traits while ensuring genetic diversity for long-term sustainability.

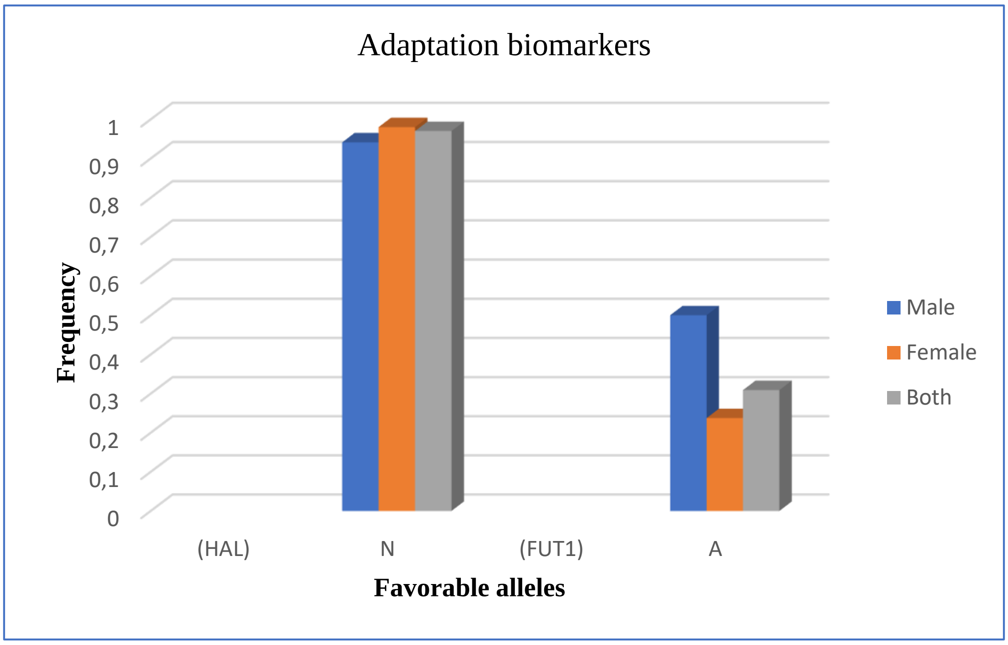

Figure 3. Frequency of favorable alleles of biomarkers (HAL, $p>_{0.05}$ and FUT1, $p=_{0.05}$) for adaptation traits.

3.4. Growth marker

The favorable allele for the *myogenic transcription factor* (*MYOG*) was detected only in heterozygous individuals, with low frequencies of 0.08 in males, 0.14 in females, and 0.13 in the combined dataset (Fig. 4 and Table A4). This limited occurrence suggests that the advantageous allele is not yet widely distributed within the population, potentially reflecting historical breeding practices or genetic drift. Despite its low prevalence, the presence of heterozygotes indicates that the allele remains part of the genetic pool and may contribute to muscle differentiation and growth-related traits when expressed in combination with other loci.

Importantly, both genotype and allele frequencies conform to HWE, suggesting that the *MYOG* allele is likely to persist in the population under current conditions, provided no strong evolutionary forces act upon it. This equilibrium implies genetic stability and the potential for the allele to be maintained across generations. From a breeding perspective, the persistence of heterozygotes highlights opportunities for marker-assisted selection to increase the frequency of favorable alleles, thereby enhancing growth efficiency and carcass quality while preserving genetic diversity.

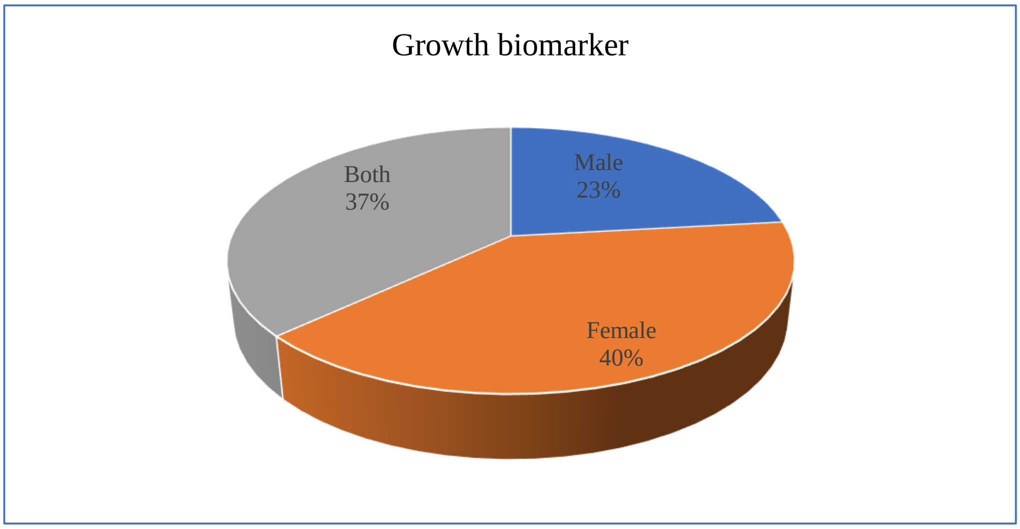

Figure 4. Frequency of favorable alleles of biomarker (MYOG, p>0.05) for growth traits.

4. Discussion

4.1. Favorable alleles for meat quality

The fixation (100%) of the homozygous recessive genotype (*rnrn*) of the *rendement napole* (*RN*) gene within the Markaduke population is unusual, given its relatively low allele frequencies (0.25–0.37) reported in other swine genetic groups (Table A5). The *rnrn* genotype serves as a marker for estimating yield and quality of cured and cooked ham, with the best products scoring highest in color, firmness, marbling, and shear force [27]. In contrast, the dominant *RN* allele is associated with paler meat, reduced water-holding capacity, low ultimate *pH* or "acid meat," and high slicing loss [27–28]. The fixation of *rnrn* in Markaduke supports empirical observations of its exceptional lechón qualities and may reflect historical or ongoing selection pressures favoring superior meat quality. Compared with commercial breeds, where *RN* allele frequencies are moderate (25–37%) and fixation often leads to pale, soft, exudative (PSE) meat [27], the Markaduke's fixation of *rnrn* reflects sustained phenotypic selection for consistent meat quality. This suggests that despite its closed nucleus classification and moderate inbreeding, the population has preserved and enhanced favorable phenotypes through deliberate selection focused on sensory and culinary characteristics.

The elevated frequencies of favorable alleles for *CTSD* and *LEPR* further strengthen the genetic profile underlying Markaduke's exceptional meat qualities. Similar findings have shown that *CTSD* is fixed in certain swine breeds [28]. As a lysosomal protease, *CTSD* contributes to postmortem proteolysis by breaking down myofibrillar proteins, thereby improving tenderness [31]. The higher frequencies observed, particularly among females, might suggest sex-biased selection or differential expression linked to reproductive energy allocation that influences muscle physiology [31]. Moreover, polymorphisms in *LEPR* are recognized as significant modulators of feed intake, energy utilization, and fat storage [32–33]. Their influence on carcass fatness corresponds with the elevated intramuscular fat levels typically found in native swine breeds, enhancing flavor and moisture [34]. Variations in the *LEPR* gene also affect fat distribution and fatty acid profiles, traits that are critical for both health-related qualities and consumer preferences in pork [35]. This study revealed allele frequencies similar to those reported in Landrace (0.88) [39]. The balance of favorable alleles suggests an equilibrium between fat and lean tissue deposition, enabling precise genotyping and targeted selection within the Markaduke population.

Genetic markers such as *LPL* and *CAST* exhibited low but measurable frequencies of favorable alleles, particularly among females, suggesting possible unoptimized sex-specific genetic patterns or selective forces. *LPL* plays a critical role in lipid metabolism, influencing intramuscular fat deposition and fatty acid composition, while *CAST* regulates *calpain* activity, which is essential for post-slaughter muscle tenderness [37–38]. The low frequency of carrier alleles indicates that fixation is unlikely under current conditions, most likely due to limited selection intensity and genotyping efforts. However, the application of marker-assisted selection targeting these loci, combined with systematic genotyping and planned selective mating, could accelerate the fixation of desirable alleles and thereby improve meat texture and flavor [39–41].

Additionally, heterozygosity observed in *insulin-like growth factor binding proteins* (*IGFBP3* and *IGFBP7*) denotes the presence of genetic variation that is essential for regulating muscle growth and development [40]. The *insulin-like growth factor* (*IGF*) pathways play a critical role in muscle hypertrophy, while the relative proportions of different muscle fiber types are key determinants of meat quality and growth efficiency [41]. Retaining heterozygosity at these loci may confer adaptive advantages by maintaining flexibility in morphology and physiology, thereby supporting both genetic resilience and phenotypic diversity within the population.

4.2. Favorable alleles for litter size

The *AA* genotype of the *prolactin receptor* (*PRLR*) *gene* was the most predominant (55.22%) among all samples, consistent with previous findings that associate this genotype with higher litter size. The favorable *A* allele (76.78%) substantially exceeded the *B* allele (23.13%), suggesting either strong selection pressure or a naturally high prevalence of the favorable allele in the studied population. Earlier studies reported that the *PRLR-A* allele was positively correlated with increased total number born (TNB) and number born alive (NBA) in Large White and Landrace pigs [42–45]. Similarly, literature indicates that the *AA* genotype is significantly superior to *AB* and *BB* in terms of TNB, further supporting the findings of this study. These results highlight *PRLR* as a key marker gene for reproductive success, consistent with the observed litter size of eight (8) piglets in the Markaduke population.

The high frequency of favorable *PRLR* alleles, coupled with deviations from HWE, suggests the influence of non-random mating patterns such as assortative mating. Assortative mating, where individuals with similar genotypes are preferentially paired, can amplify the frequency of favorable alleles across generations. In this case, the predominance of *AA* genotypes may reflect deliberate or natural assortative mating that reinforced reproductive efficiency traits. While this mechanism is beneficial for increasing litter size, it may reduce genetic diversity and limit adaptability in the long term [46]. The correlation between *PRLR* allele frequency and the observed reproductive phenotype underscores the importance of balancing allele fixation with genetic variability.

The *estrogen receptor* (*ESR*) gene, long regarded as a major gene influencing reproductive traits, showed notable variation. The *AB* genotype was slightly more frequent among females (46%) compared to *AA* (40%) and *BB* (14%), with the *A* allele (64.18%) still dominating over ***B***. Literature consistently identifies the *ESR-B* allele as favorable for increased ovulation rate and larger litter sizes, especially in European commercial breeds. However, local studies often show inconsistent trends, likely due to differences in linkage disequilibrium or genetic background. For instance, while the *BB* genotype is common in Large White pigs, subsequent studies found the *AB* genotype more productive in terms of piglets weaned [47]. The intermediate genotype findings here may reflect a heterozygote advantage under local environmental or genetic contexts, which assortative mating could either reinforce or diminish depending on breeding strategies.

The moderate frequencies of *ESR* polymorphisms, consistent with equilibrium expectations, indicate genetic stability and polygenic influence on reproductive traits. *ESR* is involved in mediating uterine receptivity and estrogen-related follicular development, both essential for fertility. However, its effects are often indirect, interacting with other loci such as *PRLR* and *LIF* [49]. Assortative mating that favors specific *ESR* genotypes may enhance reproductive efficiency but could also disrupt beneficial heterozygote balances. Careful management of mating strategies is therefore required to avoid narrowing genetic variability while still capitalizing on favorable alleles.

The *leukemia inhibitory factor* (*LIF*) gene exhibited a high frequency of the *AA* genotype (64.18%) and no occurrence of the *BB* genotype, with the *A* allele reaching 82.09%. *LIF* plays a critical role in uterine receptivity and embryo implantation, and its polymorphisms have been significantly associated with litter size traits [18, 49–50]. The low heterozygous frequency and deviations from HWE suggest that assortative mating may be accelerating the loss of genetic variation at this locus. If unmanaged, this reduction in allelic diversity could negatively influence adaptability and compromise reproductive performance. Importantly, the correlation between favorable *PRLR* and *LIF* alleles and the observed litter size of eight (8) piglets, alongside carcass yield of 47.54%, demonstrates the functional link between genotype and phenotype. These findings underscore the importance of systematic genotyping and structured assortative mating to preserve essential reproductive alleles while ensuring that carcass quality traits remain aligned with genetic potential.

4.3. Favorable alleles for adaptation

The *halothane* (*HAL*) *gene* is well known for its role in porcine stress syndrome (PSS), which is associated with malignant hyperthermia, reduced survivability under stress, and poor meat quality such as pale, soft, exudative (PSE) meat. In the present study, the *NN* genotype (non-carrier of the stress allele) was predominant across sexes (94.03%), while the n allele, linked to susceptibility to PSS, was found at only 2.99% of the population. This distribution is highly favorable, indicating a strong presence of stress-resilient genetics in the study group. Indigenous swine populations have frequently demonstrated higher adaptive capacity to harsh conditions, which is advantageous in developing countries facing climatic and disease challenges [7].

The near fixation (97%) of the stress-tolerant *N* allele in the Markaduke population reflects strong selection for resilience against stress-induced disorders. This genetic profile supports stable muscle metabolism under environmental and management stressors, thereby reducing the incidence of PSE meat and sudden death syndrome that are common in susceptible breeds [51]. Populations fixed for the N allele maintain consistent meat quality and survivability, traits that are particularly beneficial in local management systems with limited infrastructure. Such resilience enhances both productivity and animal welfare, reinforcing the importance of *HAL* genotyping in breeding programs.

Immune response-related adaptations were revealed by the presence of the favorable *A* allele for *α(1,2)-fucosyltransferase* (*FUT1*), particularly in males, where allele frequency deviations from equilibrium were observed. *FUT1* variants confer resistance against *enterotoxigenic E. coli* infections, a major cause of neonatal diarrhea and high piglet mortality in smallholder systems [25]. The presence of this allele is critical for productivity, as it reduces reliance on antibiotics and aligns with international antimicrobial stewardship efforts. However, the observed imbalance in allele frequencies suggests potential risks if breeding management does not actively conserve these adaptive traits.

The combined findings on *HAL* and *FUT1* highlight the importance of structured breeding strategies that preserve both stress-resilient and disease-resistant alleles. Marker-assisted selection and controlled assortative mating can help maintain genetic diversity while promoting adaptability. Ongoing monitoring of allele distributions is essential to prevent genetic drift or loss of favorable alleles. Incorporating genomic selection frameworks that integrate stress tolerance (*HAL*) and disease resistance (*FUT1*) loci will provide a robust foundation for sustainable pig production systems, ensuring resilience, productivity, and meat quality in diverse environments.

4.4. Favorable alleles for growth

The *MYOG* gene, which regulates muscle fiber differentiation, was observed with a high frequency of the *AA* genotype (73.53%), followed by heterozygous *AB* (26.47%), and no occurrence of the *BB* genotype. The dominance of the *A* allele (86.76%) is generally associated with enhanced muscle development, higher average daily gain, and improved carcass quality. These results closely resemble allele distributions in Pietrain and Large White pigs [53]. However, the low frequency of favorable heterozygous *MYOG* alleles suggests that historical breeding practices prioritized meat quality and adaptability traits over growth performance. This pattern parallels findings at the *RN* locus, where fixation of *RN* alleles for superior meat quality inadvertently constrained variability in growth-related alleles, underscoring the genetic trade-offs between quality and efficiency [54].

MYOG functions as a myogenic transcription factor essential for muscle differentiation and fiber-type specification. Variants of *MYOG* are linked to differential muscle hypertrophy and intramuscular fat deposition, both of which influence growth efficiency and product quality. Similarly, *RN* alleles at the *PRKAG3* locus affect glycogen metabolism and ultimate *pH*, traits directly tied to meat quality. However, fixation of *RN* alleles has been shown to reduce allelic diversity for growth traits, highlighting the antagonistic pleiotropy between loci that favor meat quality and those that promote growth efficiency [59-60].

Breeding strategies that integrate *MYOG* polymorphisms may enhance growth rates while maintaining high-quality meat and adaptability traits [52-53]. This aligns with studies advocating balanced breeding objectives that preserve native genetic resources while improving production efficiency [7]. Evidence from *RN* allele studies reinforces this need: intense selection for meat quality can reduce allelic diversity for growth traits, thereby limiting the genetic potential for faster growth and leaner carcass yield. Sustainable breeding programs must therefore adopt multi-trait genomic selection frameworks to balance these competing objectives.

The absence of beneficial heterozygous *MYOG* alleles indicates that growth-associated traits require deliberate selective breeding. Muscle fiber composition, growth rate, and intramuscular fat levels are influenced by variations in myogenic regulatory factors such as *MYOG* and *MYH3* (myosin heavy chain), which collectively affect both growth efficiency and meat quality [57-58]. Marker-assisted selection targeting these loci offers potential to improve growth performance while safeguarding adaptability and meat quality. However, caution is warranted as demonstrated in *RN* allele fixation, single-trait selection may lead to unintended consequences such as increased stress sensitivity or compromised meat quality.

A comprehensive genomic selection framework that integrates multiple trait loci and genomic estimated breeding values (GEBVs) provides a robust foundation for achieving balanced improvement [57]. By simultaneously considering *MYOG*, *RN*, and other regulatory loci, breeders can optimize both growth and meat quality traits. This approach mitigates the risk of allelic suppression and ensures that genetic diversity is preserved for long-term adaptability. Ultimately, the integration of *MYOG* polymorphisms with RN allele management exemplifies the importance of multi-trait selection in modern pig breeding, where efficiency, quality, and sustainability must coexist.

5. Conclusion

This study highlights the genetic potential of Markaduke native swine for sustainable breeding programs and food security. The breed exhibits favorable alleles for meat quality, litter size, adaptation, and growth traits. Notably, the complete fixation of the *rnrn* genotype of the *RN* gene and high frequencies of *CTSD* and *LEPR* alleles underscore the breed's exceptional meat quality, making it highly sought after for premium pork products like *lechón*. Additionally, the presence of favorable alleles for *PRLR*, *ESR*, and *LIF* genes contributes to the breed's reproductive efficiency, with litter sizes of eight or more piglets. Adaptation traits, such as the stress-tolerant *N* allele of the *HAL* gene and the disease-resistant *FUT1* allele, further emphasize the breed's resilience to environmental challenges, including stress and disease outbreaks.

Despite these strengths, the study identified areas for improvement, particularly in growth traits associated with the *MYOG* gene, which showed limited favorable allele frequencies. This suggests the need for targeted breeding strategies to enhance growth efficiency while maintaining the breed's unique meat quality and adaptability traits. The findings emphasize the importance of integrating marker-assisted selection and genomic frameworks to balance the fixation of favorable alleles with the preservation of genetic diversity. Future breeding programs will implement structured mating designs to minimize inbreeding, thereby sustaining genetic diversity while simultaneously enhancing performance traits. By addressing these genetic gaps, the Markaduke breed can continue to serve as a valuable resource for food security, cultural heritage preservation, and sustainable swine production in the Philippines.

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