

Running title: Meat quality relation to feed efficiency in Wagyu

Title: Phenotypic relationships between meat quality parameters and Residual Feed Intake in Japanese black Wagyu cattle.

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Lay summary

The Japanese black cattle, or Wagyu is known because of its precious meat quality and its high degree of marbling, however, to achieve this condition, animals are fed with high amount of concentrate and during long periods of time. In order to decrease both environmental impact and economic profitability of Wagyu producers, feed efficiency may be improved. Therefore, the present work evaluates the phenotypic relationship between meat quality variables of Japanese black cattle and their efficiency of feed utilization. Results showed how efficient individuals present higher degree of marbling than non-efficient, which may represent the footprint of a new genetic selection program which encompasses both meat quality criteria and feed efficiency values. These results have to be confirmed by genetic studies to verify heritability of these treatments.

Teaser text

Residual feed intake, one of the most popular efficiency index used for genetic selection in cattle, was related with meat quality parameters in Japanese black cattle. This study reveals that selection by efficient RFI individuals may also improve meat quality parameters such as marbling in Wagyu cattle.

Abstract

Japanese black Wagyu cattle are renowned for producing some of the world's most highly valued and recognized beef with exceptional marbling. Therefore, the primary focus of genetic selection for Wagyu cattle has historically been on meat quality, particularly achieving high marbling levels. However, even when the price of the final product is high, production costs also remain high, especially considering that most of the feed have to be imported. The objective of this study was to evaluate phenotypic relationships between feed efficiency, specifically Residual Feed Intake (RFI), and various meat quality parameters in Japanese black

cattle in order to determine if a common genetic selection could be feasible. For this, a total of 39 Wagyu cattle were evaluated for feed efficiency over their entire fattening period (900 days), with a focus on RFI as a key indicator. Animals were fed high-starch diets with vitamin A deprivation to achieve the desired marbling. Results revealed positive correlations between feed efficiency and meat quality in Wagyu cattle. Specifically, animals with higher efficiency exhibited superior meat quality traits, including firmness, marbling, and overall meat rating. When comparing the 50% most and least efficient ones according to RFI, we observed that efficient RFI individuals showed increased marbling levels (+13.2%, $P=0.05$) and ranking quality (+12%, $P=0.06$) of the meat. In conclusion, this research contributes to understanding the interplay between feed efficiency and meat quality in Japanese black Wagyu cattle. Phenotypic correlations observed suggest the possibility of incorporating RFI criteria into genetic selection programs without compromising the prized meat quality traits of Wagyu beef. This study provides valuable insights for Wagyu producers, breeders, and researchers working towards optimizing both feed efficiency and meat quality in this highly esteemed breed.

Key words: Japanese black cattle, meat quality, phenotypic relationships, residual feed intake, wagyu.

List of abbreviations: ADG; average daily gain, DMI; dry matter intake, FCE; feed conversion efficiency, BW; body weight, RFI; residual feed intake.

Introduction

Wagyu cattle is known because of providing one of the most valued and recognized beef meat in the world. This meat is famous for presenting the highest degree of marbling among all other beef breeds with also higher degree of marbling, such as Angus or Hereford (Lunt et al., 1993). Thus, the main objective in genetic selection of Japanese black cattle “Wagyu” since 1966 has been meat quality, and especially the high marbling (Motoyama et al., 2016). Achieving a

higher level of marbling is important for Wagyu producers to maintain the status of “gourmet food” and to achieve better results in the evaluation of the carcass. In fact, the scores obtained by the Japanese beef evaluation method are one of the most important criteria that influence the selling price of the carcass, which in the domestic market could range from 6550 JPY/kg (~44 USD/kg), for lower scores, up to 13290 JPY/kg (~90 USD/kg), for higher scores (Agriculture and Livestock Industries Corporation, 2023). Besides the genetics, to achieve the highest degree of marbling, these animals are fed with high-starch diets for long periods [900 days (d)] and are vitamin A deprived (Zhao et al., 2023). Consequently, considering the high price of calf’s purchase and the high price of the feed, which is almost totally imported to Japan, production costs are very high. In 2017, the mean price of calves (9.1 months of age on average) at market was 653,827 yen (around 6 226 USD), while the mean price of carcasses in the beef market was 1 313 694 yen (around 12 511 USD). However, the average total cost of production per carcass was 1,054,763 yen (around 10 045 USD) for a 29.2 months’ age and 756kg body weight (BW) (Gotoh et al., 2018). Therefore, even when there exists a global need to increase feed efficiency in beef cattle to both decrease environmental impact and feeding costs, the need to improve the latter is especially important in Wagyu cattle (Smith et al., 2018).

Japanese black cattle have been never genetically selected by feed efficiency, and consequently, their performance in this sense is low compared to other breeds (Hoque et al., 2005). Nowadays, feed efficiency is measured, evaluated and selected through feed efficiency indices, where the most used in cattle is Residual Feed Intake (RFI) because of its moderate-high heritability and its influence on dry matter intake (DMI) and feeding costs. Hoque et al., (2006a) already demonstrated how genetic and phenotypic correlations for RFI were significantly high (>0.95), showing the possibility of selecting Japanese Wagyu cattle by this index. In addition, Hoque et al (2006b) provided evidence of selecting efficient RFI individuals, which could improve carcass traits and marbling of animals. This could differ from other works which evaluated meat

parameters of cattle selected by RFI founding a decreased (McDonagh et al., 2001) or without differences (Baker et al., 2006) in meat quality and marbling between efficient and non-efficient individuals. Japanese Wagyu cattle present physiological differences in skeletal-muscle tissue [such as collagen cross-links (Liu et al., 2021a), genes such as fatty acid synthase (FASN) or acetyl-CoA carboxylase alpha (ACACA) (Wang et al., 2023) or both adipogenesis and fibrogenesis (Liu et al., 2021b)] with other cattle breeds, which may influence different relationships with feed efficiency. There is a need to determine to what extent genetic selection by feed efficiency (selecting efficient RFI animals) could indirectly improve or decrease meat quality of Japanese Wagyu cattle. Therefore, the objective of the present work is to evaluate phenotypic relationships between meat quality parameters and feed efficiency (RFI) of Wagyu cattle raised in Japanese conditions in order to better guide genetic selection towards an improved efficiency and meat quality.

Material and Methods

Ethical approval for animal trials

Animal Care and Use Committee approval was not obtained for this study because data were collected from beef cattle shipped to a meat processing plant in Hyogo, Japan. This study was carried out in strict compliance with the regulation of animal experiments at Kyoto University in the Guide for the Care and Use of Laboratory Animals. The regulation was approved by the Kyoto University Animal Experimentation Committee. The study did not involve endangered or protected species. All efforts were made to minimize animal suffering.

Animals, diets and experimental design

A total of 39 Japanese black Wagyu cattle were evaluated for feed efficiency during their whole fattening period (900d). These animals were encompassed in several studies from 2015 to 2017. Animals arrived after the weaning (130 ± 20.5 d and 205 ± 18.9 kg BW) at Hyogo Prefectural

118 Agriculture, Forestry and Fisheries Technology Center, and after a quarantine (21d) they were
119 randomly allotted by BW into 5 fattening pens. Animals were fed a classical fattening Japanese
120 diet composed of a concentrate [crude protein (CP)=12.0 % , total digestible nutrients
121 (TDN)=73.8%] accompanied by oaten (CP=2.55 % , Starch=46%, TDN=44.4%) ad-libitum.
122 Fattening facilities were in Asago-city in Hyogo-Prefecture, their fattening capacity is about
123 120 heads, each pen has door feeder and the ground is covered with sawdust which is cleaned
124 monthly. After completing the whole fattening, animals were driven to the Kakogawa city
125 abattoir to be slaughtered.

126 Measures of animal performance and estimation of feed efficiency

127 Parameters to calculate efficiency were evaluated on average (the whole fattening period) and
128 by each of three periods [first (130 to 400 days age), middle 400 to 616 days age) and final
129 (from 616 days age until reaching the slaughter body weight)]. Body weight was measured
130 through a calibrated electronic weight scale (Model XXXX) each 56 d. Individual daily intake
131 was calculated by removing the refusals from the total offered, both manually weighted every
132 day at the same time (5pm). Samples of feeds, offers and refusals were conducted daily and
133 stocked at environmental temperature until sending them to the XXXXX external laboratory
134 for a chemical analysis. Thus, dry matter intake (DMI) was calculated by multiplying individual
135 intake by the percentage of dry matter of the feed. Height was measured by body measurement
136 scale and tape measure (Model XXXX). Feed efficiency was measured through feed efficiency
137 indices; Feed Conversion Efficiency (FCE) and Residual Feed Intake (RFI). The FCE was
138 calculated by dividing the average daily gain (ADG) by the intake (DMI). The RFI was
139 calculated through a residuals model as described in Koch (1963), and fully detailed on the
140 statistical analysis (calculation of RFI).

Slaughter, determination of carcass composition and meat quality parameters

Kakogawa city abattoir conducted the slaughter, carcass and meat quality evaluations of each individual through the Japan Carcass Grading Association method. Each individual slaughter was conducted following XXXX and animals were stunned through XXXX. Each carcass was graded at the 6th- to 7th-rib interface by official Japanese graders in accordance with the Japanese Grading Standards (JMGA, 1989). Analyzed traits consisted in: CW (kg), rib eye area (REA, cm²), rib thickness (RT, cm), subcutaneous fat thickness (SFT, cm), carcass yield estimate (YE), beef marbling standard [BMS, ranging from 1 (poor) to 12 (very abundant)], beef color standard [ranging from 1 (light) to 7 (dark)], luster [ranging from 1 (debased) to 5 (excellent)], firmness [ranging from 1 (debased) to 5 (excellent)], and texture [ranging from 1 (debased) to 5 (excellent)]. Carcass yield estimate was calculated using CW, REA, RT, and SFT as the estimated percentage of salable meat [$YE (\%) = 69.419 + 0.130REA + 0.667RT - 0.025CW - 0.896SFT$].

Statistical analysis

Statistical and mathematical analyses and algorithm applications were performed in R (RStudio Core Team, version 1.1.463, 2018). All data were tested for normality with the Lillie test and for homoscedasticity with the Levene test (Nortest package in R). Differences between treatments (Multiphase vs commercial diets) were tested via parametric (variables with normal distribution) or non-parametric (variables with non-normal distribution; Kruskal-Wallis test) analysis and declared significant when $P \leq 0.05$.

Descriptive analysis

Descriptive analysis of main variables here evaluated, both animal performance (DMI, BW, Height, Chest perimeter, ADG, carcass yield and weight, FCE and RFI) and meat quality parameters (meat color, tenderness, firmness, ranking quality and quantity, marbling, rib-eye

area, thickness of subcutaneous fat and rib beef), was performed by using means, standard deviation (SD) and the coefficient of variation in percentage (CV%), which represents the SD divided by the mean. In the case of RFI, CV% represents the SD of RFI divided by the mean of DMI.

Calculation of Residual Feed Intake

Residual feed intake was calculated using individual average DMI, ADG and mid-metabolic BW (mid-test $BW^{0.75}$) of the whole fattening period or by each phase. The ADG of each animal was calculated by regressing its BW over the time on test. Mid-test BW was predicted from the BW over time regression equations, and expressed at the power of 0.75. The RFI model considered the effect of the experiments' year, the diet within the year, and the effect of the pen. Animals within the same trial (year), consuming the same diet and in the same pen, are in the same contemporary group (CG). RFI was calculated as the difference between observed DMI and the DMI expected for a given mid-test $BW^{0.75}$ and ADG adjusted by contemporary group (CG) effect as follows:

$$Y = \beta_0 + CG + \beta_1 (\text{mid-test } BW^{0.75}) + \beta_2 (ADG) + e$$

where Y is the observed individual DMI, β_0 is the intercept, CG is the contemporary group effect, β_1 is the regression coefficient for mid-test $BW^{0.75}$, β_2 is the regression coefficient for ADG, and e is the residual of the model or RFI. In addition, we identified the 50% of more extreme individuals (n=20) in terms of efficiency [extremely efficient (n=10) and non-efficient (n=10)], in order to evaluate differences in main meat quality parameters between the two extreme groups.

Repeatability of feed efficiency

Repeatability between RFI values across the different phases of the fattening was determined through Pearson's correlation (function COR in R). We also conducted a correlation matrix

(Pearson's correlation) to evaluate relationships within contemporary group between key variables analyzed in this study (function COR in R).

Relationships between variables

Relationships between feed efficiency and meat quality variables were conducted through Pearson's correlations and a Principal Components Analysis (PCA) in R. The PCA was carried out using the main standardized variables (packages "FactoMineR" and "Factoextra").

Anova analysis to compare between efficient and non-efficient RFI individuals

Differences in terms of animal performance and meat quality parameters between extreme efficient and non-efficient Japanese black cattle were conducted through an analysis of variance (Anova). For this, a general linear model (GLM) was run that included the year, the effect of diet, the pen, and their interactions as fixed effects (Year, Diet, pen, Year × Diet, Year × pen and Diet × pen);

$$Y_{ijkl} = \mu + Y_k + D_i + P_l + D_i \times Y_k + P_l \times Y_k + D_i \times P_l + \epsilon_{ijkl}$$

where Y_{ijkl} is the dependent variable for animal j , receiving diet i , in year k and belonging to pen l , μ is the overall mean, Y_k is the fixed effect of the year ($k = 1, 2$), D_i is the fixed effect of the type of diet used ($i = 1, 2$), P_l is the fixed effect of pen as efficient or non-efficient ($l = 1, 2$), $D_i \times Y_k$ is the interaction between the effect of the diet and year, $P_l \times Y_k$ is the interaction between the effect of the pen and year, $D_i \times P_l$ is the interaction between the effect of the diet and the pen and ϵ_{ijkl} is the residual term. Mean values are reported as least square means with pooled standard error of the mean (SEM) values. Effects were declared significant when $P \leq 0.05$, and a trend was considered when $0.05 < P < 0.10$.

Ethical approval for animal trials

This study was carried out in strict compliance with the regulation of animal experiments at Kyoto University in the Guide for the Care and Use of Laboratory Animals. The regulation was

approved by the Kyoto University Animal Experimentation Committee. The study did not involve endangered or protected species. All efforts were made to minimize animal suffering.

Results

All variables followed a non-normal distribution, except DMI. Also, DMI did not fulfill homoscedasticity ($P < 0.05$).

Animal performance during the whole fattening period

As it could be seen in Table 1, the first fattening period, which represents the shortest period (130d), shows the highest rates of gain (see ADG) followed by their highest feed efficiency in terms of FCE. In addition, these high rates are also associated to a high between-animal variation, showing CVs of 19% and 18% respectively. In the middle period, animals showed higher ingestion (DMI) (+28%) and weight (+48%) than in the first period. In contrast, both ADG and feed efficiency (see FCE) were lower (-59% and -70%, respectively). Also, it is remarkable to underline that, even when the middle fattening period is the longest period, the variance of main animal performance remained low (<10%CV). Finally, in the last period, animals increased their weight (+33%), gain (ADG) (+31%) and ingestion (DMI) (+22%) while maintaining similar feed efficiency (see FCE) than in the middle period. Also, variation in ADG, DMI and feed efficiency, both FCE and RFI, were higher (>14%CV) in this final period.

Repeatability of feed efficiency

Repeatability of the two main feed efficiency indices, FCE and RFI, was measured across the three periods of the fattening. The first period was the shortest and presented the highest rates of gain and efficiency (see ADG and FCE, respectively) while in the middle and final periods, those rates tended to decrease. Figure 1 shows how FCE and RFI evolve across the time, comparing the first period with the middle period (blue) and the middle period with the final

period (red). The FCE index remains repeatable across the whole fattening, however, its repeatability is higher in the middle-final period ($r=0.76$, $P<0.001$) than in the initial-middle period ($r=0.29$, $P=0.07$). Regarding RFI it was not repeatable during the first and middle period ($r=0.14$, $P=0.37$) but it presented a high repeatability between the middle and final period ($r=0.81$, $P<0.001$).

Relationships between feed efficiency indices and meat quality parameters

Relationships between the two feed efficiency indices here evaluated were performed with individual meat quality parameters measured in the slaughterhouse. Individual values of efficiency belonged to efficiency values determined in the middle-final period, which were similar between them and closer to the slaughter moment. First, we conducted a principal component analysis (PCA) to visually observe the distribution and relationships between all these variables (Figure 2).

As it can be seen in figure 2, meat quality parameters, such as texture, firmness, marbling and the rating quality, are related between them. Body composition parameters related to meat quality such as carcass yield, thickness of the rib, rib-eye-area and thickness of subcutaneous fat were related to the rate of gain (see ADG). Finally, as expected by model's construction, RFI was positively related to the intake (DMI) and negatively with FCE. This PCA explained a 61% of the total variance, pointing out the RFI as the first component and the firmness of the meat the second component of the PCA.

Table 2 just shows correlations between meat quality parameters and feed efficiency indices. The FCE was positively related to the rating quality (0.34 , $P<0.01$) and tended to present negative relations with the carcass yield ($r= -0.28$, $P=0.07$). Regarding RFI, the main efficiency index currently being used in genetic selection of cattle, it can be observed how it presents

negative relationships with rating quality ($r = -0.37$, $P = 0.06$), marbling ($r = -0.30$, $P = 0.07$) and firmness of meat ($r = -0.27$, $P = 0.08$).

Animal performance and meat quality of efficient vs non-efficient RFI individuals

As RFI represents the residual of DMI of animals within the same contemporary group, animals with negative RFI represent animals with a minor level of intake for the same rate of gain and body weight, which can be translated as “efficient” individuals. We evaluated the 10 most and 10 least efficient RFI individuals to compare if animal performance and meat quality variables were different between them. Table 3 shows main animal performance and meat quality of efficient and non-efficient RFI individuals.

Efficient RFI individuals showed lower ingestion (DMI) (-15% , $P = 0.001$) with similar rates of gain (ADG) ($P = 0.76$) than non-efficient individuals, which also influenced a higher feed efficiency (FCE) ($+18\%$, $P = 0.002$). The rest of parameters, BW, carcass yield and height remained non-different between extreme RFI individuals. Regarding meat quality, it was observed how marbling was higher ($+13.2\%$, $P = 0.05$) and ranking quality of meat tended to be higher ($+12\%$, $P = 0.06$) in efficient RFI individuals without great differences in the rest of meat quality parameters.

Discussion

Genetic selection of main occidental breeds such as Charolais, Limousin, Angus and Hereford to improve their feed efficiencies has been conducted since the last decades (Kenny et al., 2018). Feed efficiency has been determined as a moderate heritable character in occidental beef cattle breeds (0.33 ± 0.01 , Berry and Crowley, 2013), which means that it could be used for genetic selection. Therefore, the aims of the present study were to, 1) evaluate feed efficiency of the oriental breed Japanese black cattle and 2) evaluate the interaction of feed efficiency with meat quality parameters. Thus, the main objective of this work is to build the footprint of the genetic

selection for feed efficiency in Wagyu cattle and to discuss to what extent the feed efficiency could be compatible with the main desired character of this breed, meat quality and marbling.

Feed efficiency of Japanese black cattle during the fattening period

Before addressing feed efficiency, it is important to consider that the fattening of Japanese black cattle is one of the longest in terms of duration among all cattle breeds accounting for 716 d to reach a commercial slaughter BW. As in occidental feedlots, Japanese fattening diets present high levels of net energy to increase both the gain and the fat deposition, therefore, the longer duration of the fattening period is more related to animal requirements of Wagyu cattle. Animal requirements and especially body composition of Wagyu cattle significantly differ from European cattle breeds; longissimus muscle of Wagyu cattle at 24 months of age presented 23.3% of intramuscular fat whereas other occidental breeds just presented values ranged from 0.6% to 4.7% (Gotoh et al., 2009). This difference in body composition may impact energy balance and resources allocation of Japanese black cattle, likely using proportionally higher energy for maintenance than for gain in comparison with other breeds. This may be associated to their low rates of gain, which averaged 0.7 kg/d in Liu et al., (1993) or 0.82 kg/d in this work (average of the whole period), and consequently to the long period of fattening of these animals to reach a commercial BW (650kg). In addition, the breed itself determines a difference related to time; the peak of the adipocyte enzymes activity reaches its maximum at 14 months in Angus cattle whereas it reaches its maximum at 16 months in Japanese cattle (Lunt et al., 2005). Therefore, a slower fattening is also convenient to profit this peak of adipocytes activity, which is also associated to the slower maturity of this Japanese cattle (Takeda et al., 2018). The fattening is usually divided in three periods, the first starts just after the weaning (110 d), when animals present the higher rates of gain and efficiency. The weaning is conducted early, first to allow dams to get pregnant again by maximizing resources (all animals in Japan are stabled and

feed with concentrate), and second, because early weaning in Wagyu cattle promotes higher rates of growth and meat quality (Khounsaknalath et al., 2021). This first period of the fattening keeps animals until 240-d's age, which explains the highest (1.51kg/d, Table 1) rates of gain and efficiency due to the state of growth of the cattle. After this first period, the gain remains moderate-low (0.76kg/d on average), which is similar to the average rate of gain observed (0.70kg/d) by other works feeding Japanese Wagyu cattle in north America (Lunt et al., 1993).

Previous physiological explanations of Wagyu cattle serve to justify the higher rates of gain and efficiency observed in animals during the first period and in comparison with the following fattening periods. This is relevant to explain the low (FCE) or inexistent (RFI) correlation of feed efficiency indices between the first period of growth and the rest of the fattening (Figure 1). Feed efficiency is mainly related to the gain and ingestion (Koch et al., 1963), and even when ingestion remained repeatable during the whole fattening ($r = 0.67$, $P = 0.001$), the gain was significantly higher in this first period (Table 1), which impacted the repeatability of the feed efficiency indices. However, once the first step of growth was reached, gain rates and the rest of performance remained more stable and repeatable, impacting higher repeatability values for both FCE and RFI (Figure 1). The importance of the repeatability of feed efficiency indices relies on the usability of these indices for genetic selection. Repeatability rates of feed efficiency indices here evaluated demonstrate that they can be used for genetic selection. In addition, Hoque et al., (2006a) evaluated genetic heritability of feed efficiency indices used in this work founding moderate-heritability for RFI (ranging from 0.24 to 0.49) and low for FCE (0.15). This agrees with other works showing higher genetic heritability and repeatability of RFI (0.31 to 0.42) than FCE (0.25) conducted in continental breeds (Lahart et al., 2020).

Repeatability values of this work supported by scientific bibliography allow to use feed efficiency as a criterion of genetic selection in Japanese black cattle. Genetic selection by feed

efficiency and especially RFI could improve resources utilization to make beef cattle production more economically profitable and environmentally sustainable (Guarnido-Lopez et al., 2021).

Meat quality of efficient RFI Japanese black cattle

Still when demonstrating that feed efficiency is a repeatable character in Japanese black cattle and it may be used for genetic selection, culturally, the main target of genetic selection in Wagyu cattle is meat quality (Shojo et al., 2006). Therefore, genetic selection by feed efficiency indices has to be compatible with high meat quality standards demanded by Wagyu consumers.

Phenotypic relationships established between feed efficiency and meat quality parameters determined a positive correlation between quality and efficiency. Both in our PCA figure (Figure 2) and in the table of correlations (Table 2), meat quality parameters such as firmness, marbling or meat rating were higher in efficient individuals according to FCE and RFI. It's important to notice that Hoque et al., (2006a) demonstrated a high relation (>0.95) between phenotypic and genetic correlation in Japanese black cattle. Therefore, this phenotypic relation between feed efficiency and meat quality may underline a genetic relationship which may allow Japanese cattle geneticist to use efficiency criteria without decreasing meat quality. However, this relation contrasts with other works which observed negative effects of efficient RFI individuals on meat quality (McDonaugh et al., 2001) or non-different effects (Guarnido-Lopez et al., 2023). In addition, McGee et al., (2013) did not find differences in body fat accretion between efficient and non-efficient Japanese black cattle. In contrast with the present work, these previous mentioned studies did not directly measure meat quality parameters, and they accessed meat quality indirectly through enzymes analysis or ultrasound measurements. In studies where meat quality was directly measured at the slaughter moment in the abattoir, such as the present study or Hoque et al., (2006b), efficient RFI Japanese black cattle present higher marbling rates. Theoretically, it is logical to think that animals with lower ingestion (efficient

RFI) will present lower marbling rates, as it can be observed for subcutaneous or visceral body fat (Basarab et al., 2003) in European cattle. Different amounts of body fat, subcutaneous, visceral and inter/intramuscular, will likely impact requirements of energy for maintenance, energy for gain (Garret et al., 1959), and energetic efficiency (Reid and Robb, 1971). Consequently, differences on fat composition and energetic efficiency could explain differences on feed efficiency between animals. In the present study, we only observed differences between efficient and non-efficient RFI animals in intramuscular fat (Table 3), not in the subcutaneous portion. This could be relevant considering that intra-muscular and subcutaneous fat are metabolically different in cattle (Hudson et al., 2020). Aldai et al., (2007) demonstrated how intramuscular fat presented a higher proportion of polyunsaturated fatty acids (PUFA) than subcutaneous fat, with also a higher ratio PUFA/saturated fatty acids (SFA). In the case of Japanese black cattle, animals have the ability to store enormous amount of intramuscular fat, both monounsaturated (MUFA) and PUFA, which make the Wagyu a good animal to evaluate adipogenesis and lipid metabolism (Gotoh et al., 2009; Liu et al., 2021). In addition, cattle with greater marbling propensity, such as Japanese black cattle, appear to genetically upregulate adipogenesis at a younger chronological and physiological maturity state (Jaborek et al., 2023). This higher marbling impacts on the better ranking quality and palatability of the meat (McBee et al., 1967) in this case observed in efficient RFI individuals.

Previous studies and the present work may coincide in indicating a positive phenotypic (and genetic) correlation between feed efficiency, with a special mention to RFI, and meat quality in Japanese black cattle. While extreme RFI individuals from European breeds seem to present non-significantly differences in fat composition, Japanese black cattle allocate more intramuscular fat in efficient animals. This difference may be explained by energy and fat metabolism differences associated to the breed. European cattle breeds may increase intramuscular fat as a storage of energy while Japanese black cattle may present the ability to

deposit intramuscular fat as a part of 1) the natural growing of Wagyu's tissues and 2) their energy resources allocation and energy metabolism, which may be more associated to a lipolytic vs glycolytic pathways to release energy for muscles or other tissues. These are hypothetical theories which should be evaluated by analyzing intramuscular fat (i.e. through serial biopsies) of efficient vs non-efficient RFI individuals across their whole growing and fattening periods. In addition, our study was conducted by comparing the 10 most and 10 least efficient individuals from a total of 39 young bulls which were raised to evaluate their fertility performance. Therefore, even when results of this study and other evaluating genetics may coincide in pointing out that efficiency could be associated to higher marbling in Japanese black cattle, more in-vivo studies should be done to confirm this hypothesis.

In conclusion, this work could initiate the footprint of a new genetic selection in Japanese black cattle which considers not only meat quality variables but also feed efficiency parameters in order to maintain the famous meat standards of Wagyu meat while being more economically profitable and environmentally sustainable.

Disclosure of potential conflict of interest

None

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Tables

Table 1: Descriptive analysis of animal performance during the three main periods of the fattening.

	Mean	SD	CV (%)
<u>First period</u>			
Duration (d)	130	20,5	16
Weight (kg)	206	18,9	9,0
Height (cm)	110	2,15	2,0
Chest perimeter (cm)	146	4,51	3,0
ADG (kg/d)	1,51	0,29	19
DMI (kg/d)	4,49	0,11	2,0
FCE (g/g)	0,33	0,06	18
RFI (kg/d)	0,00	0,06	1,0
<u>Middle period</u>			
Duration (d)	272	20,7	8,0
Weight (kg)	398	26,7	7,0
Height (cm)	120	2,01	2,0
Chest perimeter (cm)	178	4,71	3,0
ADG (kg/d)	0,62	0,06	10
DMI (kg/d)	6,21	0,62	10
FCE (g/g)	0,10	0,01	10
RFI (kg/d)	0,00	0,52	8,0
<u>Final period</u>			
Duration (d)	214	22,2	10
Weight (kg)	590	41,2	7,0
Height (cm)	131	2,31	2,0
Chest perimeter (cm)	210	6,63	3,0
ADG (kg/d)	0,90	0,13	14
DMI (kg/d)	7,96	1,55	19
FCE (g/g)	0,11	0,02	18
RFI (kg/d)	0,00	1,27	16

Abbreviations: ADG; average daily gain, DMI; dry matter intake,

FCE; feed conversion efficiency, BW; body weight, RFI; residual feed intake.

Table 2: Pearson's correlations between feed efficiency indices and meat quality variables

	DMI	BW	Height	Rating quality	Marbling	ADG	Text	Firm	Meat color	Thick SubFat	Thick Subbeef	Rib-eye area	Carcass yield	Carcass weight
RFI	0,74	-0,07	-0,13	-0,37 ^t	-0,30 ^t	0,07	-0,18	-0,27 ^t	0,15	0,18	0,08	-0,06	0,32 ^{**}	0,11
FCE	-0,67	0,19	0,28 ^t	0,34 ^{**}	0,13	0,09	0,15	0,24	-0,17	-0,13	-0,01	0,18	-0,28 ^t	0,02

Statistical values are represented by ** ($P < 0.01$) and t ($P > 0.05$, $P < 0.10$).

Abbreviations: ADG; average daily gain, DMI; dry matter intake, FCE; feed conversion efficiency, BW; body weight, RFI; residual feed intake, text; texture of the meat, Firm; firmness of the meat, Thick Subfat; thickness of subcutaneous fat, Thick Subbeef; thickness of subcutaneous muscle.

Table 3: Animal performance and meat quality variables of efficient vs non-efficient RFI individuals

RFI in the final period					
RFI class	Efficient		Non-Efficient		Anova
kg/d	-1,64		1,49		
<u>Animal performance</u>	Mean	SD	Mean	SD	<i>P</i> -value
Average BW (kg)	402	26,1	402	33,2	0,96
Average height (cm)	121	2,29	120	1,71	0,51
Average chest perimeter (cm)	179	3,66	180	5,46	0,71
ADG (kg/d)	0,63	0,06	0,64	0,06	0,76
DMI (kg/d)	5,75	0,75	6,79	0,36	0,001
FCE (g/g)	0,11	0,011	0,09	0,007	0,002
Carcass weight (kg)	371	29,1	381	36,8	0,51
Carcass yield (%)	0,62	0,019	0,63	0,018	0,16
<u>Meat quality</u>					
Rib-eye area (cm ²)	50,1	7,39	50,2	8,08	0,91
Rib thickness (cm)	6,78	0,58	7,04	0,63	0,35
Subcutaneous fat thickness (cm)	2,35	0,83	2,54	0,79	0,61
Marbling	6,8	1,13	5,9	1,52	0,05
Ranking quantity	2,9	0,31	2,8	0,42	0,56
Ranking quality	4,2	0,42	3,7	0,67	0,06
Meat color	3,7	0,48	3,9	0,56	0,32
Meat firmness	4,2	0,42	3,9	0,87	0,35
Texture	4,5	0,53	4,2	0,78	0,23

Abbreviations: ADG; average daily gain, DMI; dry matter intake, FCE; feed conversion efficiency, BW; body weight, RFI; residual feed intake.

Figures

Figure 1: Repeatability of feed efficiency (FCE on the left and RFI on the right) between the three main fattening periods.

Figure 2: Principal component analysis (PCA) of meat quality variables and feed efficiency.