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Review

Feed efficiency indexes in hair sheep: meat quality and associated genes. Review

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Abstract:

Hair sheep are essential for meat production in tropical regions, where feed efficiency has been little evaluated. Feed consumption represents more than 70 % of the costs. Therefore, animals with high feed efficiency could increase the profitability of the production system.

There exist tools that help select individuals with increased feed efficiency without compromising the quality of the product. This review aims to identify these genetic-molecular and statistical tools, such as residual feed intake (RFI) and residual intake and gain (RIG). Previous studies report differences ranging from 9 to 30 % in the dry matter intake (DMI) of efficient and inefficient animals, maintaining a similar daily weight gain (DWG) using the RFI index. Moreover, the DMI is similar using the RIG index. Although, the DWG of efficient animals is higher by up to 50 g d^{-1}, reducing feed conversion by one kg. This difference is attributed to a group of genes associated with feed efficiency (*Adra2a*, *Gfra1*, *Gh*, *Glis1*, *Il1rapl1*, *Lep*, *Lepr*, *Mc4r*, *Oxsm*, *Pde8b*, *Rarb*, *Ryr2*, *Sox5*, *Sox6*, and *Trdn*). These genes could be used to select hair sheep with high feed efficiency, considering the genes associated with meat quality (*Capns1*, *Cast*, *Dgat1*, *Fabp4*, *Igf-i*, *Lep*, *Mstn*, and *Scd*).

Key words: Feed efficiency, Meat quality, Genes, Hair sheep.

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Introduction

The global sheep population in 2017 consisted of 1,202 million heads. Approximately 74 % of this population is distributed between Asia and Africa (42.25 and 31.7 %, respectively). The remaining 26 % is located in the rest of the continents. Although America has the smallest sheep population (6.76 %), its average carcass weight is higher (18.6 kg) than that of the other continents, only surpassed by Oceania (21.6 kg)[(1)].

In Mexico, sheep production is one of the livestock activities with more presence regarding territorial distribution. According to the preliminary figures of 2018, the sheep population reached 8'683,835 heads[(2)]; approximately 11 % of this population in the American continent, distributed in around 53,000 production units. About 53 % is located in the center of the country, 24 % in the south-southeast, and 23 % in the north[(3)]. Pelibuey is one of the most numerous breeds; it is used as breeding stock due to its maternal ability, high prolificacy, rusticity, resistance to parasites, and great adaptation to the various climatic conditions in the country[(4)].

Moreover, feed intake is one of the most important factors in intensive meat production systems, representing more than 70 % of total production costs[(5)]. Therefore, the selection of

animals with high feed efficiency, those that require a lower feed intake to maintain their performance or increase their production with a similar intake, could increase the unit's profitability[6]. Reducing feed costs would help keep profitable prices within a fluctuating agricultural supply market and competitiveness in the global market.

Traditionally, the meat production livestock industry has used feed conversion (FC) to assess feed efficiency[7]. Nonetheless, this measure is questionable because the DMI is highly correlated with body size and production level[8]; this tends to select animals with high DWG. However, animals with high DMI are also selected, which increases production costs[7].

Taking a different approach, other authors have defined feed efficiency as the animal capacity to reach a specific weight with a lower DMI[9]. Ruminants' efficiency is low compared to other species. However, they can transform nonfood resources for humans (forages and non-protein nitrogen) into high-quality food (animal protein)[7].

Consequently, several tools have been sought to help explain, predict, and select individuals with greater efficiency in feed utilization and energy intake. Residual feed intake (RFI) being among the most used ones[9,10]. RFI is defined as the difference between the real and the expected feed intake for a specific weight and production level during an established period[8,11]. This tool identifies the animals with the greatest efficiency of feed utilization, improving the herd's genetics and reducing the production costs of each increased kilogram of live weight[8]. Koch *et al*[9] proposed the Residual Gain (RG) index; this tool estimates the expected gain for a specific production level and identifies the animals with the highest weight gain rates.

A new indicator of feed efficiency was recently proposed, the Residual Intake and Gain (RIG) index. This indicator retains the selection characteristic of RFI and RG, which are independent of body weight. RIG selects the animals with the greatest DWG and the lowest DMI since it correlates negatively with the DMI and positively with the DWG[12].

The meat industry is not only interested in the efficiency of feed utilization but also the quality of the final product. Meat quality includes various traits, such as physicochemical attributes (tenderness, color, fat content, intramuscular, and water holding capacity), palatability factors (flavor, juiciness, and smell), and food safety characteristics[13]. These quality traits influence the decision-making of the consumer and the meat processing industry[14]. On this matter, several studies have used RFI to determine the effect of feed efficiency on meat quality. They have reported that selecting efficient Angus bovines (low RFI) does not hurt meat quality[15,16]. However, recent studies in Nelore cattle have reported conflicting results. Some authors observed that efficiency does not affect meat quality and the calpain system[17,18], yet other studies report the opposite. Therefore, animals with low

RFI tend to have tougher meat[19]. This undesirable characteristic is regulated by protein turnover and specific enzymes (especially those in the calpain system), which carry out the muscle postmortem proteolysis[20].

Furthermore, previous reports mention that proteolysis is related to the maintenance energy requirement (MER); a high protein degradation rate is associated with a higher MER[21]. Additionally, the most efficient animals have a lower maintenance metabolizable energy requirement[17,21]. Thus, in Nelore cattle, the most efficient animals have a low protein degradation rate[22], which is associated with a higher shear force at different maturation times (0 d= 4.50 *vs* 4.00, 7 d= 4.22 *vs* 3.61, 21 d= 3.27 *v.* 2.69 kg/cm^2), low myofibril fragmentation index (37.0 *vs* 42 %), and high content of soluble collagen (17.7 *vs* 14.9 %), resulting in lower meat quality[19].

Moreover, the development of molecular genetics, sequencing, and selective gene amplification techniques has increased the detection of genes that have a marked effect on traits of interest, i.e., feed efficiency and meat quality. This allows the detection of the genomic sequences associated with these genes and the establishment of selection programs based on molecular markers[23].

A genetic marker is a specific DNA sequence with a known location in a chromosome; this sequence either has a specific function or is associated with the phenotypic expression level of a trait[24]. The use of genetic markers helps with problems faced during traditional selection by selecting genetically superior individuals[25]. Furthermore, the markers can predict improvement values for the individuals selected at birth more precisely than the classic pedigree index, reducing the generation interval[23]. Therefore, this study aimed to review the feed efficiency indexes and their relationship with meat quality and the genes associated with these traits in hair sheep.

Feed efficiency indexes

The RFI and RG indicators were proposed by Koch *et al*[9] after observing that feeding affects the maintenance of live weight and daily weight gain. They suggested that feed intake can be adjusted to body weight and weight gain, dividing it into two components: 1) The feed intake expected for a specific performance or production level and 2) A residual portion. The residual portion of feed intake could be used to identify animals that deviate below their expected level of feed intake (negative RFI); this allows comparing animals with different production levels during the measurement period.

The RFI has been used as a selection criterion in beef cattle breeding programs. Heifers with low RFI are more efficient regarding feed utilization than those with a high RFI[26]; additionally, their progeny tend to behave more efficiently[27]. The estimated heritability of this characteristic is moderate (0.27-0.58) and independent from growth and production level[9,28,29,30], and it has no adverse effect on other economically important characteristics, such as meat quality[15].

Furthermore, RFI reduces livestock's environmental impact because animals with low RFI tend to produce lower amounts of methane (CH_4) per unit of consumed dry matter due to their lower DMI and best energy use efficiency[31,32,33]. Therefore, RFI is one of the carbon dioxide (CO_2) and CH_4 mitigation strategies of livestock.

The main advantages of using RFI as a selection criterion are improved feed efficiency[8,34] and increased productivity in the breeding sector, reducing the area used per animal unit[35].

The novel RIG index improves feed efficiency and identifies animals with greater growth rates and lower fat proportion without affecting meat and carcass quality, reducing confinement and slaughter times of animals because they reach their commercial weight at early ages[36].

The studies that involve the RFI and RIG indexes have been mainly carried out in cattle, pigs, and poultry. These indexes have also been evaluated in temperate climate sheep. Although some studies have included Brazilian hair sheep crosses, the Santa Inés and Pantaneira breeds stand out[5,36,37,38]; there is also a study in Dorper sheep[39] (Table 1 and 2). In Mexico, this tool is just starting to be implemented, so there are few studies; there is only one previous study in the Rambouillet breed[40]. Therefore, the behavior of hair sheep is still unknown (Table 1).

Estimating the RFI and RIG indexes

The RFI determines the expected DMI and is estimated through a multiple linear regression equation as a function of mean metabolic weight (MMW) and DWG.
The model used by Koch *et al*[9]:

$$Y_i = \beta_0 + \beta_1 GDP_i + \beta_2 PMM_i + \varepsilon_i$$

Where:
$\mathbf{Y_i}$= Dry matter intake of the i-th animal.
$\boldsymbol{\beta_0}$= Regression intercept.

$\boldsymbol{\beta_1 GDP_i}$= partial regression coefficient of dry matter intake in the i-th DWG of the animal.
$\boldsymbol{\beta_2 PMM_i}$= partial regression coefficient of dry matter intake in the i-th mean metabolic weight of the animal.
$\boldsymbol{\varepsilon_i}$= residual error in the dry matter intake of the i-th animal.

Moreover, RG helps estimate the expected DWG through a multiple linear regression as a function of DMI and MMW.

$$Yi = \beta 0 + \beta 1(CMS_i) + \beta 2(PMM_i) + \varepsilon_i$$

Where:
$\boldsymbol{Y_i}$= Weight gain of the i-th animal.
$\boldsymbol{\beta_0}$= Regression intercept.
$\boldsymbol{\beta_1 CMS_i}$= partial regression coefficient of the DWG of the i-th DMI of the animal.

$\boldsymbol{\beta_2 PMM_i}$= partial regression coefficient of the DWG of the i-th MMW of the animal.
$\boldsymbol{\varepsilon_i}$= residual error in the DWG of the i-th animal.

RIG is calculated with the two previously described models using the following equation: $GIR(CAR * -1) + GR$. The index requires prior standardization (Mean = 0 and Standard Deviation = 1) of the RFI and RG.

After determining the RFI, animals are classified into high (>0.5 SD above the mean, higher feed consumption than expected for maintenance and production; thus, lower efficiency), medium (±0.5 SD from the mean), and low RFI (<0.5 SD below the mean, lower feed consumption; thus, higher efficiency)[41]. The same categorization procedure is used to determine the RIG groups. However, high RIG indicates greater efficiency, and low RIG means lower efficiency.

Intervening physiologic factors

There are numerous and interrelated physiologic mechanisms associated with higher feed utilization efficiency. However, they have not been completely elucidated. Richardson and Herd[42] synthesized the results of a series of experiments in Angus cattle selected divergently for RFI. They estimated the proportion of the variation in RFI that explains the following processes: protein turnover, tissue metabolism and stress (37 %), digestibility (10 %), increase of heat and fermentation (9 %), physical activity (9 %), body composition (5 %), and feeding patterns (2 %). The mechanisms responsible for more than 25 % of the variation in RFI are not yet known. The physiologic processes associated with the variation in feed utilization efficiency have been grouped into five categories: 1) Feed intake capacity, 2) Feed

digestion, 3) Metabolism (anabolism and catabolism), 4) Heat production related to digestion and physical activity, and 5) Thermoregulation[30].

Knowing the biological processes involved and the degree to which they contribute to the feed efficiency of hair sheep is crucial since information is scarce in these breeds. Therefore, it is necessary to carry out studies that help understand how these mechanisms favor this behavior, which would allow the selection of more efficient and productive animals.

Feed intake and productive performance

Voluntary feed intake is regulated by a complex interaction between neuroendocrine control mechanisms and the physicochemical properties of feed; this interaction changes according to the physiologic state of the animal[43]. Moreover, feed intake directly correlates with the energy used for digestion; at higher the intake, the higher the energy expenditure. This results from an increase in digestive organ size and the energy used in the tissues of these organs[30]. This energy expenditure is known as heat increase during fermentation; in ruminants, it represents approximately 9 % of the metabolizable energy intake[44].

Most studies (Table 1) indicate that sheep with low RFI show the same DWG as animals with high RFI[5,6,38-40,45-55]; animals with low RFI have a better energy use efficiency[33]. However, Rocha *et al*[37] reported significant differences in DWG, making energy use efficiency more noticeable. In all the studies, DMI was lower on the most efficient animals, with a difference ranging from 9 to 30 % compared with those less efficient. Therefore, it is expected that the more efficient animals show a better FC (Table 1).

Previous studies in sheep, using the RIG index[5,36,38], have shown that sheep classified with high RIG have a lower DMI, higher DWG, lower FC, and higher feed efficiency (FE) (Table 2). Although the difference in DMI is not as high as that observed with RFI, the DWG differs by up to 50 g d^{-1}. Moreover, FC differs in more than one kg, so the FE is greater in animals with high RIG. Considering that feed is the most significant production cost in animal production systems, lower feed consumption and greater weight gains represent an important reduction in operation costs and increase the profitability of the production units and the efficient use of the supplied energy.

Methane production

The rumen microbial ecosystem is extremely diverse. It includes Eukarya, Archaea, and Bacteria phylotypes that interact between them, the feed, and the host, with densities of 10^{10} bacteria mL^{-1}, 10^6 protozoa mL^{-1}, and 10^3 fungi ml^{-1} of ruminal fluid[56].

The diversity and concentration of the organisms that live in the rumen are influence by several factors, such as diet, breed, age, health status, environment, and geographic location[57]. However, diet is considered the primary determinant of ruminal microbial diversity and the fermentation parameter in cattle and sheep[58]. Thus, animals fed forage have a more diverse microbial ecosystem, with more frequent methanogenic groups, compared to those provided concentrate-based diets[59]. This implies greater use of free H_2 (produced by a more acetic fermentation) to reduce CO_2 into CH_4[60].

The results reported by Henderson *et al*[61] indicate that regardless of the type of diet and geographic location, there is a central microbiome in the rumen comprised of seven groups. These groups represent 67.1% of the bacterial sequences in the global analyzed samples. This major group includes *Prevotella*, *Butyrivibrio, Ruminicoccus*, *Lachnospiraceae*, *Ruminococcaceae, Bacteroidales,* and *Clostridiales*. However, some genera are more abundant with specific diets. For example, *Bacteroidales*, *Clostridiales, Fibrobacter,* and *Ruminococcaceae* are more abundant in animals fed with forage; *Prevotella* and *Succinivibrionaceae* are more abundant with concentrate-based diets. Moreover, in the same study, they reported that the archaea population is constituted mainly by *Methanobrevibacter gottschalkii* and *Methanobrevibacter ruminantium*, representing 74 % of all the archaea inside the rumen. Other found species were *Methanosphaera* sp. and two groups belonging to *Methanomassiliicoccaceae.* These five species constituted 89 % of the total archaea*;* Methanobacterias being one of the main species that utilize free H_2 to reduce CO_2 to CH_4[62]. These species are associated with fibrous diets, where fermentation is more acetic and H_2 release is higher

Recent studies indicate that feed efficiency is related to CH_4 production[31,62,63]. It has been reported that the methanogenic communities in animals with high RFI are more diverse compared to efficient animals, with a high prevalence of *M. stadtmaniae* and *Methanobrevibacter* sp. Thus, animals with high RFI emit more CO_2 and CH_4 due to their higher fiber intake, which increases ruminal CH_4 production. Animals with low RFI tend to modify their bacteria consortia. Therefore, they can use the fibrous components of the ration more efficiently, reducing the passage rate and increasing digestibility. Thus, completely fermenting rations at a ruminal level[62].

Using statistical prediction models, female sheep have shown significant differences in CH_4 emissions. Emissions are lower in animals with low and medium RFI, compared to those with high RFI (0.025^a, 0.028^a, and 0.032^b CH_4 kg^{-1} d^{-1}, respectively). However, no differences were observed in male sheep due to the lack of significant difference in the DMI of efficient and inefficient animals[40].

Furthermore, greater efficiency could be related to bacteria that modify the fermentation pattern towards a more propionic fermentation, which favors meat production[33]. Propionate is the main substrate contributing to the gluconeogenesis process; glucose is required as an energy source in protein synthesis[43]. Previous studies have reported greater propionate concentrations in highly efficient sheep (low RFI) fed concentrate-based diets, compared to those less efficient (41.2 *vs* 30.2 % Molar)[6]. Therefore, animal selection based on feed efficiency indexes could reduce the greenhouse gases (GHG) produced by sheep.

Candidate genes associated with feed

Various studies have reported many single nucleotide polymorphisms (SNP) associated with feed efficiency in bovine species[64-67]. Few studies have focused on sheep. Knowing the genes implicated in the biological processes related to desirable, productive characteristics (feed efficiency and meat quality) of farm animals[20,55,68-86] helps understand the relationship between these parameters and then use these genes as molecular markers for the selection of animals with desired traits (Table 3).

Cockrum *et al*[87] identified markers through genome-wide association studies (GWAS) with a nominal threshold of $P<3.02^{-4}$ in sheep genes associated with RFI. The candidate genes were: Glis Family Zinc Finger 1 (*Glis1*), SRY-related box -5 and -6 transcription factor (*Sox5, Sox6*), and Interleukin 1 Receptor Accessory Protein Like 1 (*Il1rapl1*). Another gene associated with this index is the Leptin receptor (*Lepr*). The association of a SNP in exon 2 of *Lepr* has also been reported in lactating ewes ($P<0.05$); the homozygous CC genotype had the highest RFI (2.579^a), compared to the TC (1.218^b) and TT (1.005^b) genotypes[88].

Recent studies have reported the association of DWG and specific SNPs; these associations can be considered in selecting animals with better productive performance. For example, in sheep, three genes have been associated with DWG. The triadin gene (*Trdn*) is in chromosome 8, and the 3-oxoacyl-ACP synthase (*Oxsm*) and Retinoic acid receptor beta (*Rarb*) genes are located in chromosome 26[89]. Furthermore, the Leptin gene (*Lep*) has been associated with DWG, with significant differences ($P<0.05$) in the DWG (six-month weaning) of heterozygous BC, AB, and AC genotypes than in the homozygous AA and CC

(116, 103, 99, 94, and 94 g d^{-1}, respectively)[90]. In the Salsk breed, significant differences (P<0.001) were observed in the growth hormone (*Gh*) genotypes; AB was superior to AA (128.64 *vs* 81.51 g d^{-1})[91]. The Melanocortin-4 receptor gene (*Mc4r*) has also been associated with DWG. A SNP located in the 3' untranslated region of the gene (NM_001126370.2) causes a G>A nucleotide variation in the 1016 position. The heterozygous GA genotype was superior to the homozygous GG at 120 (210.23 *vs* 192.01 g/d) and 180 d (166.35 *v.* 155.66 g/d) of fattening. Furthermore, SNP 292 G> A was detected with a variation in amino acid 98 Gly> Arg, which affected the eye area of the *Longissmus* muscle[92].

The association of FC with some genes has been reported. In exon 3 of the *Lep* gene in lactating ewes, significant differences (P<0.001) were found in the genotypes of a SNP with amino acid variation (c.314 G>A, Arg>Gln). The GC genotype showed lower FC (2.019 kg) compared to the AG genotype (3.886 kg) in milk production[88]. Additionally, the g.1429 C>A and g.1117 A>C synonym mutations in the Alpha-2A adrenergic receptor (*Adra2a*) and Ryanodine receptor 2 (*Ryr2*) genes had a positive effect with this efficiency indicator. In *Adra2a*, three genotypes were identified (CC, CA, and AA); the homozygous CC genotype had the lowest FC (4.67^{b}, 5.18^{a}, and 5.14^{a} kg, respectively). As for *Ryr2*, similar genotypes were identified. However, the homozygous had the lowest FC, but it was statistically similar to the CC genotype (5.14^{b}, 5.08^{b}, and 5.46^{a} kg, respectively)[55]. Recently, in Santa Inés sheep, the GDNF family receptor alpha 1 (*Gfra1*) and Phosphodiesterase (*Pde8b*) genes have been associated with FE[93].

The genes implicated in feed efficiency can help identify superior individuals using molecular techniques. These techniques have been scarcely used in hair sheep. Their use will help identify and select, at an early age, those individuals with higher feed efficiency, reducing the generation interval.

Meat quality and associated candidate genes

Previous studies in sheep[5,37,39,46-49,51] suggest that carcass characteristics (*Longissimus* area, subcutaneous fat thickness , and *Longissimus* muscle depth) are not negatively affected when using the RFI index. However, regarding carcass yield, there tends to be a significant difference (P<0.1) between efficient and inefficient animals[37,54]. Moreover, genes have been associated with the physicochemical parameters that determine meat quality, such as pH, tenderness, water holding capacity, and color.

pH

In small ruminants, a normal pH ranges from 5.5 to 5.8[94] and is related to desirable characteristics in meat quality, such as color, shear force, and water holding capacity[95]. Some studies have demonstrated the relationship between the pH and the polymorphism of some genes. A previous study reported the association of the *Lep* gene (intron 2, g.103 A>G) in the Suffolk breed and identified the AA and AG genotypes. The homozygous genotype had a lower pH value (5.53) when compared to the heterozygous ($P<0.05$)[96]. Moreover, genotypes of the Fatty acid-binding protein gene (*Fabp4*) were identified in Chinese sheep with an effect on pH ($P<0.1$). The AG heterozygous genotype had a lower pH (6.3); AA and GG had a pH of 6.5[97]. Although the final pH was higher than that reported as desirable in the literature[94].

Tenderness

As rigor mortis begins, sarcomeres shorten, and myofibrils undergo transverse contraction, increasing shear force. Within myofibrils, protein density increases in specific areas when the space between myofilaments decreases. Therefore, it is likely that this space reduction reduces the protease activity in the myofibril proteins, affecting meat tenderness[98]. The decrease in temperature and pH in the carcass, along with the increase in cytoplasmic calcium, activates proteolytic enzymes, such as caspases and calpains[95], improving meat tenderness. Calpains are responsible for up to 90% of the proteolytic tenderizing of meat[99]. Other proteolytic systems in the muscle, such as the lysosomal proteases and the multicatalytic proteasome complex, participate in cytoskeleton proteolysis and meat tenderizing, although to a lesser extent[100].

In sheep, some genes have been associated with shear force. Calpastatin (*Cast*) being the main gene associated with the texture. In Iranian breeds, significant differences have been reported between *Cast* genotypes (B, C, D, I)[101]. Genotype I required a shear force of 8.39 kg; genotype C required 12.69 kg. Sheep with genotype I are more desirable for this parameter. Additionally, a previous study reported a nucleotide variation (197A>T) in exon 6 of *Cast*, changing amino acid 66 from glutamine (Gln) to leucine (Leu). The heterozygous AT genotype had a lower shear force than the homozygous AA (6.68 *vs* 8.71 kg). For this same gene, two genotypes were detected on the Awassi breed. These genotypes showed significantly different ($P<0.05$) shear forces. The MN genotype had a higher force than the MM genotype (4.36 and 3.98 kg, respectively)[102]. In Chinese breeds, previous studies have reported the association between Diacylglycerol O-acyltransferase 1 (*Dgat1*) genotypes and

tenderness. The TT genotype required a lower force than TC and CC (2.30, 2.69, and 2.73 kg)[103]. Also, in Chinese breeds, the association of *Fabp4* genotypes and tenderness has been previously reported. The AA genotype was more tender than the AG and GG genotypes (2.24, 2.78, and 2.88 kg, respectively, $P<0.05$)[97]. *Lep* is another gene associated with this parameter. For example, previous studies have reported the polymorphism of this gene in the Suffolk breed (intron 2, g.103 A>G). The shear force of the AA genotype is lower than that of the AG genotype (3.6 and 4.7 kg, respectively)[96].

Water holding capacity (WHC)

WHC is defined as the ability of meat to retain its total or partial water content[104]; it is closely related to the pH and isoelectric point of muscle proteins (pH 5.1-5, net charge 0). Thus, under these conditions, WHC is minimized[98]. This parameter is evaluated by drip loss and cooking loss tests. The first test measures the water lost because of gravity[105], i.e., the extracellular water. In contrast, the second test measures the water loss derived from cooking the meat[104].

In Awassi sheep, the *Cast* gene is related to cooking loss, with differences ($P<0.05$) between the MM and MN genotypes. The homozygous genotype had the highest percentage of water loss (48.45 and 45.69 %, respectively)[102].

Moreover, genes associated with the drip loss parameter have been previously identified. For example, three genotypes of the *Dgat1*gene were identified; the water loss in the TT genotype was lower than that of TC and CC, which showed similar losses (67.1, 92.6, and 92.4 g kg^{-1})[103]. Furthermore, the *Fabp4* gene is also associated with this parameter. Of the AA, AG, and GG genotypes, AA had the lowest loss percentage (8.86, 9.48, and 9.39 %, respectively), although there were no significant differences ($P<0.1$)[97]. Polymorphisms of the Calpain small subunit 1 (*Capns1*) gene have also been associated with WHC. Five genotypes with different water loss percentages ($P<0.01$) have been identified. The genotype B1B1 had a 4.11 % water loss, while A1A1, A1B1, A1C1, and B1C1 ranged from 2.23 to 3.30 %[14]. Additionally, two genotypes of the Insulin-like growth factor 1 (*Igf-1*) with significant effects on drip water loss have been reported. The homozygous AA genotype lost 2.47 %, while the heterozygous AB lost 3.33 %[106]. Furthermore, the polymorphism of the Myostatin (*Mstn*) gene has also been associated with this parameter. Two genotypes with significant differences ($P<0.05$) in their water loss percentages have been identified. The AA genotype had a water loss of 2.5 %, while AE lost 3.5 % of water[107].

Color

Meat color is largely the main attractive factor for the consumer, who perceives this parameter as a sign of freshness and quality; thus, red color in sheep meat is preferable. The color of meat changes as the myoglobin pigments in the meat surface interacts with oxygen, changing from deoxymyoglobin (purple) to oxymyoglobin (red) to metmyoglobin (brown)[108]. The CIE-L* (black-white), a* (red-green), and b* (blue-yellow) values have been used to determine meat color. A light reflectance ratio of 630/580 nm is used to detect the chemical changes that result from the oxygenation or oxidation of myoglobin[109].

In Merino sheep, significant differences ($P<0.05$) in the L* reflectance coordinates between *Capns1* genotypes (A1A1, B1B1, A1B1, A1C1, and B1C1) have been reported. Genotypes B1B1 and A1C1 showed the lowest and highest luminosity (38.05 and 41.13, respectively)[14]. Like calpains, the antagonist of *Cast* is associated with color. Significant differences ($P<0.05$) in L* have been observed between the MM and MN genotypes in Awassi sheep; the luminosity of the homozygous genotype was higher than that of the heterozygous (37.60 and 32.47, respectively)[102]. In Iranian sheep, two genotypes (A and B) were identified for the Stearoyl-CoA Desaturase (*Scd*) gene. These genotypes showed significant differences in L* and a*; the B genotype had a higher L* (40.96 and 43.16, respectively) than A, while A had a higher a* value than B (16.0 and 15.08, respectively)[110]. In hair sheep, no previous study has evaluated the genes associated with carcass characteristics and meat quality. Therefore, using molecular techniques that evaluate these genes is critical to accelerating the genetic improvement of hair breeds.

Conclusions

RFI and RIG are indexes that allow identifying and selecting animals with high feed utilization efficiency. In sheep, a negative effect on the carcass characteristics has not been detected. The heritability of feed utilization efficiency is moderate and is associated with multiple genes. These genes can be used as molecular markers for genetic improvement. Therefore, the study of these indexes and the use of molecular techniques in the selection and breeding of hair sheep could help predict animal behavior. Furthermore, some of the genes related to carcass characteristics and meat quality can be included in the breeding programs of these breeds. This would promote the development of sheep farming since more efficient animals have lower feed requirements without affecting growth rate (RFI), or greater weight gains with similar feed intake (RIG), reducing production costs and increasing the

profitability of the production units. In addition to producing the quality food demanded by the global market and contributing to reducing the ecological footprint of livestock.

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Table 1: Production parameters in sheep classified by residual feed intake (RFI)

Breeds	Residual feed intake										Author
	Low	Medium	High	Low	Medium	High	Low	Medium	High	DDMI	
	Daily weight gain			Dry matter intake			Feed conversion			%	
½D½SI	0.280	-	0.270	1.24^{b}	-	1.41^{a}	4.43^{b}	-	5.15^{a}	12.06	5
RHS	0.260	-	0.240	2.23^{b}	-	3.22^{a}	-	-	-	30.74	6
¾T¼P	0.321^{a}	0.277^{b}	0.306^{ab}	1.34^{b}	1.35^{b}	1.52^{b}	4.18^{a}	4.90^{b}	5.00^{b}	11.84	37
½D½SI	0.284	0.301	0.286	1.25**	1.37**	1.44**	-	-	-	13.19	38
Dorper	0.266		0.253	2.63^{b}		3.00^{a}	5.94^{b}		6.91^{a}	12.33	39
Rambouillet	0.180	0.170	0.180	1.39^{c}	1.48^{b}	1.67^{a}	-	-	-	16.77	40
Targhee	0.350	0.330	0.360	1.92^{b}	2.02^{b}	2.32^{a}	6.58^{b}	7.71^{a}	7.83^{a}	17.24	45
Ghezel	0.210	-	0.200	1.01^{b}	-	1.12^{a}	4.95^{b}	-	5.53^{a}	9.82	46
Ile de France	0.329	-	0.335	1.42^{b}	-	1.63^{a}	4.35	-	4.93	12.88	47
Targhee	0.297	0.302	0.286	2.15^{b}	2.31^{b}	2.52^{a}	-	-	-	14.68	48
Targhee	0.294	-	0.293	2.21^{b}	-	2.43^{a}	-	-	-	9.05	49
RHS	-	-	-	2.10^{b}	-	2.89^{a}	-	-	-	27.34	50
Kurdi	0.260	-	0.260	1.82^{b}	-	2.11^{a}	-	-	-	13.74	51
Hu	0.280	-	0.250	1.50^{b}	-	1.72^{a}	-	-	-	12.80	52
Ghezel	0.280	-	0.290	1.52^{b}	-	1.72^{a}	5.47	-	5.93	11.63	53
Hu	0.250	0.260	0.260	1.09^{c}	1.25^{b}	1.33^{a}	4.51^{c}	4.84^{b}	5.39^{a}	18.04	54
Hu	0.260	-	0.270	1.05^{b}	-	1.48^{a}	3.92^{b}	-	5.62^{a}	29.05	55

DDMI= Difference in dry matter intake (%), ½D½SI= ½Dorper ½Santa Inés, RHS= Rambouillet, Hampshire, and Suffolk, ¾T¼P= ¾Texel ¼Pantaneira.
**, ^{abc}= Significant differences.

Table 2: Production parameters in sheep classified by residual intake and gain (RIG)

Breed	Residual intake and gain												Author
	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High	
	Dry matter intake			Daily weight gain			Feed conversion			Feed efficiency			
½D½SI	1.39[a]	-	1.31[b]	0.26[b]	-	0.30[a]	5.32[a]	-	4.28[b]	0.19[b]		0.23[a]	5
¾T¼P	1.28	1.27	1.22	0.26[b]	0.29[a]	0.31[a]	4.99[a]	4.28[b]	3.91[c]	0.20[c]	0.24[b]	0.26[a]	36
½D½SI	1.41	1.37	1.31	0.26**	0.29**	0.30**	5.36*	4.61*	4.27*	0.18*	0.21*	0.23*	38

½D½SI= ½Dorper ½Santa Inés, ¾T¼P= ¾Texel ¼Pantaneira, *= Calculated data, **, [abc]= Significant differences.

Table 3: Genes associated with sheep feed efficiency and meat quality

Symbol	Gene	Chrom	Biological process	Param	Author
Glis1	*Glis* Family Zinc Finger 1	1	Significantly promotes human and mouse fibroblast reprogramming into induced pluripotent stem cells during embryonic development. It is highly expressed in the fertilized ovum, moderately expressed in metaphase II oocytes, and weakly expressed in two-cell embryos. Additionally, this gene is associated with the regulation (including the transcription factor *Foxa2*, several genes of the *Wnt* and *Esrrb* families) of genes involved in the mesenchymal-epithelial transition, a crucial process in somatic cell reprogramming.	RFI	68-70, 87
Sox5 and *Sox6*	SRY-related box -5 and -6 transcription factor	15	Its expression is related to an efficient process of chondrogenesis, although the *Sox9* gene is required to activate and maintain chondrocyte-specific genes. The *Sox5* and *Sox6* genes significantly increase the transcriptional activity of *Sox9*, ensuring its binding to DNA.		
Il1rapl1	Interleukin 1 Receptor Accessory Protein Like 1	X	Related to intellectual disability and autism spectrum disorders promoted by the absence of the *Il1rapl1* protein. Mutations in *Il1rapl1* result in the absence of the protein or the production of a dysfunctional protein in humans.		
Lepr	Leptin receptor	1	It produces a protein of the same name that, when combined with Leptin, triggers a series of chemical signals (JAK/STAT signaling pathway) that activate the receptor and transphosphorylate the JAK molecules associated with it. This pathway participates in energy homeostasis.	RFI	71, 88
Trdn	Triadin	8	It regulates the release of Ca^{2+} through the *Ryr2* and *Casq2* calcium release channels in the sarcoplasmic reticulum; this is a crucial step	DWG	72-74, 89

			for the contraction of the skeletal and cardiac muscles. In humans, the lack of triadin results in cardiac arrhythmia with sudden cardiac death.		
Oxsm	Mitochondrial 3-oxoacyl-ACP synthase	26	An enzyme related to the synthetic α-lipoic acid pathway. Its activity is essential for the elongation of the fatty acid chains in the production of α-lipoic acid. α-lipoic acid deficiency represents a risk factor for diabetes.	DWG	
Rarb	Retinoic acid receptor beta	26	Overall, retinoic acid receptors are essential for retinoic acid signaling during embryonic development and organogenesis. Mice lacking two isotypes of *Rara, Rarb, Rarg* show some characteristics of vitamin A deficiency syndromes in fetal and postnatal stages, as well as some congenital malformations.	DWG	
Lep	Leptin	4	Hormone synthesized in the adipose tissue with an important role in the regulation of appetite and energy metabolism. Additionally, leptin has been linked to fat deposition in mammals.	DWG FC pH Tenderness	75, 90 75, 88 75, 96
Gh	Growth hormone	11	Activates anabolic processes that regulate the increase in body size and skeletal growth. It controls and coordinates the flow of metabolic processes, such as stored fat mobilization and fatty acid and glucose catabolism in tissues.	DWG	76, 91
Mc4r	Melanocortin-4 receptor	23	This receptor is predominantly expressed in the hypothalamic appetite regulator nucleus; it regulates food intake and energy homeostasis.	DWG	77, 92
Adra2a	Alpha-2A adrenergic receptor	22	Catecholamine regulator; associated with energy metabolism. This receptor also participates in the adrenaline pathway and can regulate energy metabolism through the secretion of adrenaline, which affects FC.	FC	51, 55, 72, 78

Ryr2	Ryanodine receptor 2	25	Main channel of Ca^{2+} release from the sarcoplasmic reticulum in ventricular myocytes. This receptor is related to heart disease. This receptor also participates in the adrenaline pathway and can regulate energy metabolism through the secretion of adrenaline, which affects FC.	FC	
Pde8b	Phosphodiesterase 8B	7	This gene encodes a cyclic adenosine monophosphate-specific phosphodiesterase that regulates thyroid-stimulating hormone levels. The thyroid synthesizes thyroxine, which binds to the receptors to control biological processes, such as gene expression, growth, development, and metabolism.	FE	79-81, 93
Gfra1	GDNF family receptor alpha 1	22	Associated with the tyrosine kinase receptor, which regulates cell proliferation, growth factors, and neuronal development and differentiation.	FE	
Fabp4	Adipocyte fatty acid-binding protein	9	Known as intracellular lipid chaperons, they bind and transport long chain fatty acids in mammals. In cattle, these proteins are associated with growth, fat deposition, and carcass traits.	pH Tenderness WHC	82, 97
Capns1	Calpain small subunit 1	14	Mainly associated with the postmortem degradation of myofibrillar proteins and the production of free amino acids, resulting in meat tenderization.	WHC Color	20, 14
Cast	Calpastatin	5	This enzyme inhibits calpain activity and is related to the regulation of muscle protein degradation. The inhibition of muscle protein degradation by the calpastatin system increases production efficiency but affects meat tenderness.	Tenderness WHC Color	20, 101,102 20, 102
Dgat1	Diacylglycerol O-acyltransferase 1	9	This enzyme modulates the synthesis of triglycerides and regulates their circulation. Additionally, it is directly related to glucose metabolism, obesity, insulin resistance, and hepatic steatosis.	Tenderness WHC	83, 103

Igf-1	Insulin-like growth factor 1	3	This protein participates in the control of skeletal growth and cell differentiation by activating the cell cycle.	WHC	84, 106
Mstn	Myostatin	2	Myostatin is a potent negative regulator of muscle mass in mammals. The natural mutations in *Mstn* inactivate or suppress the protein, which increases musculature. The skeletal muscles affected by these mutations increase their myofibrils (hyperplasia) and, to a lesser extent, the cross-sectional area of the myofibers (hypertrophy). These mutations have a greater impact on homozygous individuals compared to heterozygous individuals.	WHC	85, 107
Scd	Stearoyl-CoA Desaturase	22	It regulates lipid synthesis and oxidation.	Color	86, 110

Chrom= Chromosome, Param= Parameter, RFI= residual feed intake, DWG= daily weight gain, FC= feed conversion, FE= feed efficiency, WHC= water holding capacity.