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REVIEWS

Compilations and updates on residual feed intake in sheep

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Abstract

The increasing global demand for food and the strong effect of climate change have forced animal science to advance regarding new methods of selection in search of more efficient animals in production systems. Feed consumption represents more than 70% of the costs of sheep farms, and more efficient animals can increase the farmers' profitability. One of the main measures of feed efficiency is estimated residual feed intake (RFI), created in 1963 by Robert Koch for estimation in cattle and later adapted for sheep. Animals with negative RFI values (RFI-) are more efficient than animals with positive values (RFI+), with influence on the variables of performance, carcass quality and production of enteric gases. The RFI is the most common and accepted metric of the feed efficiency trait for genetic selection, since it is independent of growth traits, unlike the feed conversion ratio. The purpose of this review article was to present updated literature information on the relationship of RFI estimates with performance measures, molecular markers, greenhouse gas production and feed efficiency, the technical aspects and physiological basis of metabolic in sheep.

Keywords Animal efficiency · Genetic improvement · Meat production · Phenotypic selection · Ruminants

Introduction

The current trend of precision livestock farming increases the sustainability of animal production, bringing greater longevity to production systems and promoting more efficient use of environmental resources. This is of fundamental importance in meat sheep breeding systems, especially in arid and semiarid regions of the world, with production of about 79.2 thousand tons a year, worth US$ 70.41 million (Lôbo 2019; Silveira et al. 2021; Farrell et al. 2022).

Although sheep production has promising potential for expansion among the various meat production chains, structural problems still exist at the level of organizational management, along with practical problems linked to nutrition/feeding, environment and/or genetic improvement, which reduce the efficiency of farms. In this respect, most developing countries have not succeeded in developing programs for genetic improvement of livestock (FAO 2007). Most sheep genetic improvement programs emphasize selection based on traits such as birth weight (Shiotsuki et al. 2016), weaning weight, number of weaned lambs (McManus et al. 2011), age, reproductive and maternal traits (Lôbo et al. 2009).

Significant advances in sheep feed efficiency have been achieved in recent decades, meaning greater competitiveness of farms by producing more meat in less time and space, as well as reducing environmental impacts. The pioneer study by Koch et al. (1963) described an alternative measure of feed efficiency, first applied to cattle, called residual feed intake (RFI). This estimate is defined as the difference between an animal's actual feed intake and its expected feed intake based on its size and growth. It is independent of the level of production, and the lower the value the more

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efficient the animal is. Although not directly implemented in breeding programs, because it does not show correlation with body weight and weight gain rates, it can provide guidance to select individuals with merits within a population.

During the more than 50 years since RFI's introduction, many animal species have been investigated for variation of RFI, but only in the last 20 years have RFI estimates been performed for sheep (Cummins et al. 1997; François et al. 2007; Knott et al. 2008; McDonnell et al. 2016; Muir et al. 2020; Freitas et al. 2021; Ellison et al. 2022; Amarilho-Silveira et al. 2022; Arce-Recinos et al. 2022b), generating promising information for animal production. However, studies evaluating this measure are still limited in number and poorly referenced. Furthermore, today RFI is now the most common and accepted way to characterize the feed efficiency trait for genetic selection, since it is independent of growth traits, unlike the feed conversion ratio (Pryce et al. 2015). Another important factor is that RFI shows negative phenotypic and genetic correlations with dry matter intake (DMI) and greenhouse gases production such as methane (CH_4) (Paganoni et al. 2017; Johnson et al. 2022; Arce-Recinos et al. 2022a). Finally, RFI has moderate heritability in sheep (Tortereau et al. 2020; Amarilho-Silveira et al. 2022; Johnson et al. 2022), which suggests genetic gains in individual or flock feed efficiency if used as a selection and improvement tool.

Therefore, the purpose of this review article was to present updated literature information on the relationship of RFI estimates with performance measures, molecular markers, greenhouse gas production and feed efficiency, the technical aspects and physiological basis of metabolic in sheep.

RFI measurement in sheep

The increasing global demand for food and the strong effect of climate change has forced animal science to advance in the determination of new methods of animal selection in search of more efficient animals. The increase in productivity has become dependent on issues linked to feed efficiency, where the data on animal feed consumption serve as criteria for selection of efficient animals, with consequent increase in meat production (Bezerra et al. 2013). The amount of feed and/or water, the length of time to feed, frequency of trough visits, and feeding behavior are basic elements in phenotypic feed efficiency studies (Muir et al. 2018; Freitas et al. 2021; Amarilho-Silveira et al. 2022; Sartori et al. 2024).

Countries like Australia and New Zealand have breeding programs focused on productive and reproductive characteristics and meat and carcass quality traits of a particular breed or genetic group. However, most sheep breeding programs fail to develop or do not support these traits (Fogarty et al. 2007; Morris & Kenyon 2014). Some variables, such as the feed conversion ratio (weight gain/dry matter intake quotient), feed efficiency ratio (dry matter intake/weight gain), animal weight at different ages, daily gain, age to reach a certain weight (François et al. 2007; Silva et al. 2015), disease resistance (Toscano et al. 2019), carcass characteristics, reproductive performance (Tortereau et al. 2020) and thermotolerance (Leite et al. 2018), are not commonly applied to support efforts to improve flock efficiency and thus meat production systems.

According to Richardson et al. (2002) and Fogarty et al. (2006), the RFI denotes the difference between the actual and predicted intake to meet the nutritional requirements of the animal, along with weight and weight gain of a given individual. Thus, animal efficiency can be determined based on these data. Animals with negative RFI values are more efficient than those with positive values, and this efficiency or inefficiency is observed in the variable's performance, carcass, and production of enteric gases (Koch et al. 1963). Table 1 identifies some scientific articles that have estimated this variable in sheep in various regions of the world. We only discuss the influence of different RFI values on performance and carcass merits in lambs (Freitas et al. 2021; Ramos et al. 2021; Arce-Recinos et al. 2022a), feeding behavior (Muir et al. 2018), diet (food and water) (Ellison et al. 2022; Freitas et al. 2021), sex and maternal malnutrition (Tillquist et al. 2021). Although Hendriks et al. (2013) stated that stress is determined by a group of variables that together account for 37% of the variations in RFI, aspects concerning the relationship of adaptability indicators and thermal stress, such as rectal temperature, respiratory rate and sweating, have still been little studied to illustrate the influence of these variables on feed efficiency of sheep (Fontes et al. 2023; Matos et al. 2024; Sartori et al. 2024).

The influence of RFI measurements on performance and carcass characteristics indicates the possibility of implementing this variable in genetic improvement programs, in addition to identifying the best use of inputs in sheep diets (Asher et al. 2018). Ramos et al. (2021) reported that animals with low RFI showed higher body weight (BW) and better average daily weight gain (ADG), generating lower feed costs. Ellison et al. (2022) reported that concentrate-based diets provide lower variations in RFI in comparison with forage-based diets, explained by the greater variations in forage feed intake. In addition to BW and ADG, the authors also evaluated carcass characteristics.

The water use efficiency and the relationship with RFI estimates were measured by Freitas et al. (2021), who reported the presence of correlations between water intake, performance, and carcass characteristics of Santa Inês breed sheep, in addition to associating the use of measures with RFI values and indicating the efficient use of water for

Table 1 Scientific papers involving estimated residual feed intake (RFI, kg), methods to calculate RFI, breed, sex, age, country, and feed condition of sheep

Paper	RFI	Method to calculate RFI	Breed	Sex	Age/category	Country	Diet description
Muir et al. (2020)	0.0 ± 0.201	Not cited	Maternal composite	F	Post weaning	Australia	Pasture hay, straw-based pellets and barley grain
	0.005 ± 0.211		Maternal composite	F	Hogget—536 days	Australia	Pasture hay, straw-based pellets and barley grain
	0.0 ± 0.280		Maternal composite	F	Hogget—533 days	Australia	Pasture hay, straw-based pellets and barley grain
	0.002 ± 0.38		Maternal composite	F	Adult	Australia	Pasture hay, straw-based pellets and barley grain
Ellison et al. (2022)	0.01	Koch et al. (1963)	Hampshire, Rambouillet and Suffolk	M	Lambs	USA	Forage (pelleted alfalfa)
	−0.01		Hampshire, Rambouillet and Suffolk	M	Lambs	USA	Concentrate (pelleted corn)
Freitas et al. (2021)	0.0 ± 0.05	Koch et al. (1963); Gomes et al. (2012)	Santa Ines and Dorper × Santa Ines	M and F	3 months	Brazil	Hay (*Cynodon* cv. Tifton 85), bran, commercial concentrate, water, and mineral salt *ad libitum*
Johnson et al. (2022)	−0.00094 ± 1.33	Koch et al. (1963)	–	F	9 months	New Zealand	Alfalfa pellets
Tillquist et al. (2021)	−0.17	Not cited	Dorset	M	Lambs—252 days	USA	Complete pelleted feed and water *ad libitum*
	0.23		Dorset	F	Lambs—252 days	USA	Complete pelleted feed and water *ad libitum*
Ramos et al. (2021)	−0.115	Koch et al. (1963); Cockrum et al. (2013)	Dorper	M	Lambs—Low RFI	Brazil	Elephant grass (*Pennisetum purpureum*), ground corn, soybean meal, mineral mixture and water *ad libitum*
	−0.092		Dorper	M	Lambs – High RFI	Brazil	Elephant grass (*Pennisetum purpureum*), ground corn, soybean meal, mineral mixture and water *ad libitum*
Zhang et al. (2017)	−0.10	Koch et al. (1963)	Hu		Lambs—90 days—Low RFI	China	Complete pelleted feed and water *ad libitum*
	0.11		Hu		Lambs—90 days—High RFI	China	Complete pelleted feed and water *ad libitum*

sheep selection. The efficient use of natural resources such as water, for example, is fundamental for the sustainability of ruminant production systems (Araújo et al. 2019). Therefore, farmers should establish sustainable water use measures in animal production systems, particularly animal consumption.

The difference between males and females is a common effect when evaluating RFI estimates. Tillquist et al. (2021) reported that male lambs are more efficient compared to females (−0.17 kg vs. 0.23 kg of feed eaten for the same weight gain, respectively), and stressed there is no effect of poor maternal nutrition on the RFI of lambs. In practical conditions, the comparison between sexes, ages and different breeds is not recommended due to the difference in the maintenance rate for each category and the fact that RFI results can only be compared within the tested group.

Studies of the metabolism of sheep with different RFI estimates are still scare, with most information referring to other species. Ramos et al. (2021), evaluating the effect of RFI level on lambs, did not identify changes in serum biochemistry and hematology, but did identify a change in protozoa population in the digestive tract without changes in use of nutrients, such as maize starch. Zhang et al. (2017) reported lower plasma concentrations of the hormones thyroxin (T_4) and adrenocorticotrophic (ACTH) in lambs with low RFI, indicating those hormones are important physiological biomarkers of RFI.

Knowledge of RFI differences in sheep can be used to direct breeding programmers and generate offspring that are likely more efficient. Tortereau et al. (2020), analyzing adult males of the Romane breed, and Zhang et al. (2017), studying lambs of the Hu breed, in both cases with high negative (more efficient) and high positive values (less efficient) values, found that the use of RFI measures in selection schemes was able to improve feed efficiency in meat sheep without influencing other production traits. Therefore, including RFI among animal breeding metrics will help breeders reduce feed costs during the fattening period, leading to a significant decrease in the amount of concentrate required for their progeny without compromising growth traits.

In addition to feed costs, low RFI values are associated with reductions in CH_4 emissions, as reported by Paganoni et al. (2017) and Johnson et al. (2022), since there is a positive correlation between RFI and CH_4 production. In this respect, production of less manure is associated with a lower passage rate, and consequently lower DMI and nutrient digestibility in the total digestive tract (Montelli et al. 2019). Another interesting result was described by Tillquist et al. (2021), evaluating the effect of unbalanced diets of ewes on performance and RFI values in lambs. The results indicated the absence of influence of poor maternal nutrition on lamb feed efficiency.

Physiological aspects and modifications according to RFI

The main physiological processes that contribute to variation in RFI are feeding patterns, body composition, protein turnover, tissue metabolism, stress, heat increment of fermentation, digestibility, and physical activity (Herd and Arthur 2008; Hendriks et al. 2013).

According to Zeng et al. (2023), less energy is used in the physiological processes for maintenance requirements for low-RFI animals (lower dry matter intake, higher nutrient digestibility, nitrogen retention, ruminal propionate production and serum glucose utilization). For Montelli et al. (2019) and Ramos et al. (2021) the RFI in sheep does not modify digestibility aspects in the total digestive tract. Gurgeira et al. (2022) reported that RFI + sheep consumed 33% more dry matter in relation to body weight than the RFI- animals, despite having the same weight gain. Efficient animals (RFI-) have less whole-body chemical-fat and more whole-body chemical-protein; thus, there is a positive correlation between RFI and fat gain.

Some studies that evaluated physical activity in sheep according to behavioral aspects has showed variations in animals with different RFI estimate. Montelli et al. (2019) showed that efficient lambs spent less time ruminating and more time feeding (3% more time eating than RFI + lambs). Sartori et al. (2024) reported lower hourly feeding rate per day for efficient animals. The high amount of time spent carrying out activities such as eating, drinking, and chewing results in wasted energy for others functions in organism, therefore, it is believed that efficient animals make better use of this time.

Although studies linked to physiological parameters of thermoregulation in sheep are very common, and these variables represent more than 30% of RFI variations (Herd and Arthur 2008), there are still few that evaluate this effect. In recent studies, respiratory rate, heart rate and rectal temperature are one of the most studied physiological variables in association with RFI. These variables can indicate a body thermal imbalance link a body heat production originating from physical process of rumination and chemical of the digestion (fermentation) (Ferreira et al. 2019). In recent studies, the respiratory rate has been considered the biomarker with the greatest discrepancy between the physiological parameters of sheep with different RFI classifications (Fontes et al. 2023; Matos et al. 2024). Sheep with low-RFI presented lower respiratory rate, however, for rectal temperature, the studies showed no differences between RFI ratings.

For sheep, there are few studies on implications of the RFI in metabolism, and hematological and biochemical parameters of the blood. The associations between RFI and blood parameters are still divergent between studies. According to Ramos et al. (2021) and Matos et al. (2024), the RFI in sheep no changes directly the blood parameters of this species, however, Trapina et al. (2023) verified that the biochemical parameters (IGF-1, insulin, and glucose) were found to be in correlation with feed efficiency indicators.

Genetic and genomic aspects

Some studies have sought to identify genetic markers or key biological pathways associated with RFI, including analyses of gene expression (Freitas et al. 2021; Ellison et al. 2022). Other researchers suggest the importance of more careful observation of general effects, including analyses of gene expression and sensory characteristics, for implementation in breeding programs to promote feed efficiency of sheep (Juan Giraldéz et al. 2021). Because of the rapid development of genomic technologies, the main candidate genes for quantitative traits that affect feed efficiency can be identified and used for sheep genetic improvement. Understanding the molecular mechanisms of RFI in sheep will help to select animals with more sustainable and economically viable traits from the standpoint of efficiency. Currently, there are few studies identifying and directly associating genes with RFI estimates. However, research is increasing aimed at finding candidate genes for feed efficiency and carcass traits to guide sheep selection and genetic improvement programs. Figure 1 shows some genes identified in *ovis aires* that are associated with RFI values.

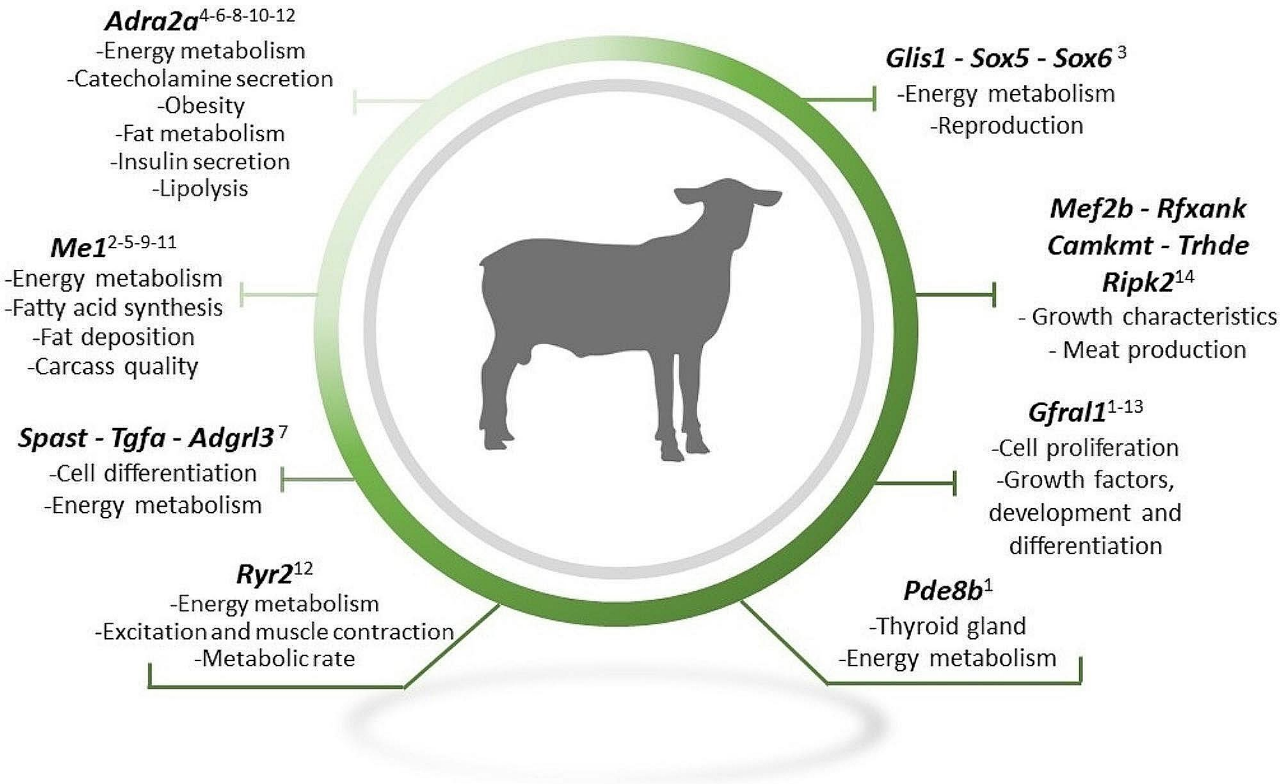

Fig. 1 Genes and biological functions associated directly or indirectly with sheep RFI estimates. References: [1]Alvarenga et al. (2016); [2]Carvalho et al. (2019); [3]Cockrum et al. (2012); [4]Fagerholm et al. (2004); [5]Guay et al. (2007); [6]Kaabi et al. (2016); [7]Ladeira et al. (2022); [8]Lima et al. (2007); [9]Ramírez et al. (2014); [10]Rosmond et al. (2010); [11]Zhou et al. (2011); [12]Zhang et al. (2019); [13]Zhang et al. (2017); [14]Zhang et al. (2013)

Two studies using liver tissues from Chinese Hu lambs (Zhang et al. 2019; Zhang et al. 2021) identified three genes associated with RFI estimates. The first was the malic enzyme or *Me1*, which is a multifunctional protein-coding gene that plays a key role in energy metabolism and fatty acid synthesis (Zhou et al. 2011) and catalyzes the oxidative decarboxylation of malate and pyruvate, producing NADPH. According to Guay et al. (2007), this is necessary for fatty acid synthesis and other metabolic process. Feed efficiency is affected by fat deposition and energy metabolism. Findings in pigs and cattle have shown an influence of fat deposition and carcass quality characteristics (Ramírez et al. 2014; Carvalho et al. 2019). The second and third genes identified by Zhang et al. (2019) were *Adra2a* and *Ryr2*, also associated with feed efficiency. Both participate in the adrenaline pathway and can regulate energy metabolism through adrenaline secretion, thus affecting feed efficiency. *Adra2a* is part of the family of G protein-coupled receptors involved in cell signaling and neural regulation (Fagerholm et al. 2004), known to regulate catecholamine secretion, thus playing a key role in obesity (Lima et al. 2007), fat metabolism (Rosmond et al. 2010), insulin secretion and lipolysis (Kaabi et al. 2016), as studied in cattle (Kaewpila et al. 2018). The *Ryr2* regulatory mechanism deserves further studies in sheep, since it plays a role in regulating the excitation and contraction of skeletal muscle and cardiac muscle cells, in addition to affecting the metabolic rate (Zhang et al. 2019).

Genomic-wide association studies (GWAS) are essential to identify candidate genes for aspects of sheep performance. Genes such as *Glis1* (Glis Family Zinc Finger 1), *Sox5* and *Sox6* (SRY-related box -5 and -6 transcription factors) were identified as associated with RFI in Rambouillet ewes by Cockrum et al. (2012), where their presence was associated with the signaling and energy conservation and metabolic efficiency of the organism. Zhang et al. (2013), studying Sunit and German Mutton sheep through GWAS, identified several genes correlated with growth and meat production characteristics, specifically post-weaning gain: *Mef2b* (myocyte enhancing factor 2B), *Rfxank* (regulatory Factor X Associated Ankyrin Containing Protein), *Camkmt* (calmodulin-Lysine N-Methyltransferase), *Trhde* (triadine) and *Ripk2* (Interacting Serine/Threonine Kinase 2 receptor).

Some genes are considered potential candidates in issues related to feed efficiency, hunting traits, as well as variation in RFI estimates. The gene *Gfral1* (alpha 1 receptor of the GDNF family) has a proven effect on the tyrosine kinase receptor, which in turn influences cell proliferation and growth, development, and proliferation factors. Furthermore, *Pde8b* (phosphodiesterase) is related to the thyroid gland, where it is essential for metabolism through the secretion of hormones such as triiodothyronine (T_3) and T_4 (Zhang et al. 2017). Both were identified in GWAS studies in Santa Inês sheep in Brazil (Alvarenga et al. 2016). Ladeira et al. (2022) identified a relationship between productive efficiency traits and the presence of candidate genes with important biological functions, such as cell differentiation and energy metabolism via insulin signaling of the genes *Spast*, *Tgfa* and *Adgrl3* in Santa Inês sheep.

Souza et al. (2022), studying the genome of Santa Inês sheep, identified 31 genes that can be considered candidates for primary carcass cuts due to their biological functions, showing the possibility of using pedigree and genomic information in selection schemes to improve efficiency. Since there are still few studies that have related RFI with carcass yield in sheep, the search for candidate genes for this trait is a promising field for future investigations. Genomic identifications have been increasing steadily, so at some point they will be related more precisely with RFI estimates.

RFI and its relationship with CH_4 emission

According to Kozloski (2011), the CH_4 production by ruminants is an anaerobic process carried out by the rumen microbial population, more specifically the methanogenic archaea, which remove the hydrogen ions produced in the rumen and convert cellulolytic carbohydrates of dietary origin into short-chain fatty acids, mainly acetic, propionic and butyric acids. According to Rasmussen and Harrison (2011), about 11% of the global emission of CH_4 comes from livestock (enteric fermentation), more than from biomass incineration (6%), recovery sites (6%), coal mines (5%), animal waste (4%) and oceans and lakes (1%). Therefore, livestock breeding has a considerable share in the production of greenhouse gases, mainly enteric CH_4 from digestion in ruminants, which causes severe damage to the ozone layer and consequently promotes an increase in global temperature.

In addition, the production of greenhouse gases by ruminants also contributes to economic losses from the activity, because it is related to inefficient use of inputs and activities related to production systems. The energy losses are estimated at 2–15%, measured as the amount of gross energy of feed lost due to production of enteric CH_4 (Goel & Makkar 2012). The most important factor affecting methane production is the feed provided to ruminants. Diets rich in grains favor higher production of propionic acid, while diets rich in roughage favor production of acetic acid. Thus, during the production of acetic acid, there is greater production of H_2. In turn, H_2 is eliminated by binding to carbon dioxide (CO_2) molecules, forming CH_4.

The production of CH_4 is a physiological mechanism linked to feed intake (Paganoni et al. 2017; Johnson et al. 2022) and indirectly to RFI in sheep. (Nkrumah et al. 2006; Hegarty et al. 2007; Hendriks et al. 2013; Goldansaz et al., 2020). Therefore, since increased efficiency means less gas production, research should focus more on this process. Although RFI estimates are demonstrably linked to food consumption (Hendriks et al. 2013), this factor is not necessarily linked to lower methanogenic potential, but to lower DMI (McDonnell et al. 2016; Escobar-Bahamondes et al. 2017). Muir et al. (2020) and Robinson et al. (2020), for example, used this relationship to support the practice of selection of sheep by feed intake (low intake at a given live weight) to reduce CH_4 more effectively than selection by RFI.

Arce-Recinos et al. (2022b) evaluated Pulibuey lambs, which were classified as efficient according to RFI estimates, and found a 17% decrease in CH_4 emission, indicating improvements in meat sheep breeding from the economic and environmental points of view. The contrast between recent research that supports or contradicts the associations between RFI estimates and CH_4 emissions reinforces the need for more studies focusing on parameters such as age, sex, physiological status, breed, genetic group, and nutrition, in order to identify the direction of this relationship in sheep.

This contrasts with the results presented by Muir et al. (2020), who did not identify a significant relationship between CH_4 and RFI in maternal composite ewes but reported significant correlations between CH_4 and DMI in recently weaned ewes ($r = 0.2007$; $P < 0.01$), which in turn produced less enteric CH_4.

Practical implication for RFI test implementation

The main barrier to the adoption of RFI is cost and second barrier the technical difficulty of experimental testing. The cost of determining the individual feed consumption of animals is much higher than the cost of collecting data on other traits. Recommendations for carrying out RFI tests have been the subject of research, to seek the shortest evaluation period and reduce costs for carrying out food efficiency estimates. The recommendation from RFI test period in sheep is based in studies with cattle (around 70-day) and studies with sheep demonstrated that it is possible to estimate RFI with reduced evaluation periods. In Australia, we can mention the studies by Macleay et al. (2016) evaluating Merino sheep, using periods shorter than 35 days, as well as, in Uruguay, the study by Amarilho-Silveira et al. (2022) evaluating the same breed, however, with periods shorter than 42 days. In addition to these, Cockrum et al. (2013) evaluated the reduction of data collection of pure Rambouillet sheep and the Rambouillet × Targhee cross in the USA, reducing it to 2-week measurement periods.

Final considerations

The use of the RFI estimates is effective for the selection of feed-efficient sheep with a view to the sustainability (excellent relationship between productive, socioeconomic and environmental aspects) of production systems. The limited implementation of RFI estimates in genetic improvement programs are fully related to the practical issues of cost and technical limitations for sheep industry, in addition, information about the RFI is not yet completely disseminated on farms and this makes it difficult to implement the estimate as an active variable for the genetic improvement of the herd. Significant advances have been achieved in terms of proving this parameter is an effective means of improving animals at the phenotypic and genetic levels, through positive associations with better performance, and lower CH_4 emissions. Further investigation of RFI can contribute to more sustainable sheep breeding, highlighting the assessments of the genetic mechanisms underlying RFI or even the assessment of long-term environmental impacts due to selection for feed efficiency based on RFI.

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