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RESIDUAL FEED INTAKE IN CATTLE: PHYSIOLOGICAL BASIS. A Review

El consumo residual en bovinos: base fisiológica. Revisión bibliográfica

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Summary
Residual feed intake (RFI) is an estimate of feed efficiency independent of the level of production. Briefly, RFI is estimated as the difference between the observed and the expected intake for a given live weight gain and metabolic body weight. Therefore, cattle with lower RFI are considered to be more efficient. No single biological mechanism explain the variability in RFI. Research has shown that low RFI cattle generate less methane per unit of live weight gain, but it is not clear if they yield less methane per unit of dry matter intake. Differences in digestion and rumen function have been reported. According to some evidence, low RFI cattle would have lower maintenance requirements, but results are inconclusive. Some evidence suggests that they have a lower protein turnover. Activity and feeding behavior differs in cattle contrasting in RFI and more efficient cattle would be less active and would show lower daily number of feeding events. Gain composition seems also related to RFI but it does not appear to be the main factor. Visceral weight, mitochondrial function and hormones have also been studied, with inconclusive results. Residual feed intake relies on multiple physiological traits and further elucidation of implications will be important for the implementation of selection programs in cattle.

Key words. residual feed intake, efficiency, energy.

Resumen
El consumo residual (residual feed intake, RFI) es una medida de eficiencia alimenticia independiente del nivel de producción. Brevemente, el RFI es estimado como la diferencia entre el consumo observado y el esperado para un aumento de peso vivo y un peso metabólico dados. Por lo tanto, bovinos con un menor RFI son considerados más eficientes. No existe un mecanismo biológico único para explicar la variabilidad en RFI. La investigación ha encontrado que los animales con menor RFI producen menos metano por unidad de aumento de peso, aunque no está claro si a su vez producen menos metano por unidad de materia seca consumida. Se han reportado diferencias en digestión y funcionamiento ruminal. De acuerdo con cierta evidencia, los animales con menor consumo residual tendrían un menor costo de mantenimiento, pero las evidencias no son concluyentes. Hay también evidencia de que podrían tener una menor tasa de recambio de proteínas (protein turnover). El comportamiento alimenticio y el nivel de actividad difieren entre animales que contrastan en RFI. Los animales más eficientes serían los menos activos y muestran menos episodios diarios de asistencia al comedero. La composición de la ganancia también parece estar relacionada con RFI, pero no parece ser el componente fundamental. Los roles del peso visceral, funcionamiento mitocondrial y factores hormonales han sido estudiados, sin alcanzarse conclusiones definitivas. El consumo

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residual depende de múltiples factores fisiológicos cuya elucidación será importante para la implementación de programas de selección en bovinos.

Palabras clave. consumo residual, eficiencia, energía.

1. Introduction

Even though feed costs are the main determining factor of beef industry profitability, genetic selection programs have historically been focused on increasing the individual animal output [i.e., live weight gain] rather than on optimizing the inputs [i.e., feed intake] (Sainz and Paulino, 2004, Herd and Arthur, 2009). Traits such as gain to feed ratio (G:F) are used to summarize efficiency, but the final result may have been misleading. Gain to feed ratio is highly related to live weight gain and, even though it can result in a dilution of the maintenance cost, does not necessarily improves the energy efficiency. Selecting on G:F basis can lead to selection for growth potential, which also leads to selection for higher mature size and higher dry matter (DM) intake (Barlow, 1984, Owens et al, 1995; Arthur et al, 2001). This method of selection might also have led to cattle which are very efficient when allowed *ad libitum* intakes (i.e., feedlot), but perform poorly when DM intake is limited, as usually occurs in grazing situations (Jenkins and Ferrell, 1994).

Residual Feed intake (RFI) is an indicator of feed efficiency, independent of the level of production (Herd and Arthur, 2009). Originally, Koch et al (1963) proposed that feed intake could be adjusted for body weight and weight gain and partitioned into 2 components: 1) intake expected for a given performance or level of production, and 2) individual deviation from the expected value based on the regression line (i.e., residual portion). As a result of this calculation, animals that showed intake lower than the expected for a given live weight gain would have lower (negative) RFI and would be more efficient. The progeny would also show the feature (Arthur et al, 2001, Herd et al, 2004). In practical terms, RFI is calculated as the difference between actual DMI and expected DMI, with data obtained from the individual measurements of daily feed intake and average daily gains (ADG) in long term feeding trials (at least 70 to 84 days, Sainz and Paulino, 2004). Expected DM intake (eDMI) is in turn calculated using a multiple regression model, using metabolic body weight (MBW) and ADG as independent variables, as follows:

$$eDMI_j = \beta_0 + \beta_1 MBW + \beta_2 ADG + e_j$$

Since the variability in RFI was acknowledged, there has been abundant research to assess the physiological mechanism underlying it (Herd et al, 2004, Herd and Arthur, 2009). Evidence shows that no single physiological mechanism is responsible for the observed variability (Herd et al., 2004). At least theoretically, every physiological step that affects the conversion of gross energy contained in feed to animal product (i.e., meat) can be considered potentially responsible for the observed variability in RFI. Therefore, understanding these factors is an important prerequisite before implementing an effective breeding strategy towards more efficient animals (Nkrumah et al, 2006). Research indicates that RFI has a moderate heritability ($h^2 = 0.3 – 0.4$, Herd and Bishop, 2000, Arthur et al, 2001). However, given its complex nature and the underlying multiple biological processes, genetic selection on the base of RFI has not always been successful (Karisa et al., 2014). The present review focuses on the evidence explaining the factors that affect the RFI in cattle.

2. Residual Feed Intake and its Relation wirh Animal Performance

Predictably, RFI is positively correlated with feed intake (r = 0.66; Rolfe et al., 2011); however, numerous reports show that genetic correlation between RFI and ADG or MBW is near zero (Arthur et al., 2001, Richardson et al., 2004, Castro Bulle et al., 2007, Rolfe et al., 2011, Fitzsimons et al., 2013, Perkins et al., 2014). Rolfe et al. (2011) reported a strong and negative genetic correlation between G:F and RFI (r = 0.92). Arthur et al. (2001) found that a selection based on feed conversion ratio (kg DM intake / kg ADG) leads to selection for greater ADG, which in turn leads to larger mature size. On the contrary, a selection plan based on RFI should not lead to an increase in mature size, yielding more efficient cattle, able to perform adequately even when feed resources are scarce.

3. Genetic Basis of RFI

Since Koch et al (1963) first introduced the concept of using residuals to express production efficiency, numerous authors have focused on dissecting the genetic components of RFI. Residual feed intake has been found to be moderately heritable by multiple authors (Arthur et al, 2001, Rolfe et al, 2011, Saatchi et al, 2014) and as a consequence should respond favorably to selection. The availability of high-density genomic information via tens to hundreds of thousands of single nucleotide polymorphisms (SNP) have allowed for the dissection of the heritable fraction of RFI at the genomic level. In example, Saatchi et al. (2014) discovered ten significant 1-Megabase SNP windows located on eight autosomes for RFI with the largest effect 1-Megabase SNP window detected on chromosome 15 in a Simmental x Angus population which explained 2.40% of the additive genetic variance. Large-effect QTL associated with RFI were also detected on chromosomes 6, 10, 14, 18, 19, 20 and 25.

4. Biological Basis for the Variability in RFI

4.1 Methane emission

Methane (CH_4) production is the most important "hydrogen sink" in the process for regenerating oxidized co-factors (NAD^+) in the rumen. Methane production per mole of fermented hexose is higher in high fiber diets than in high grain diets, due to differences in the ruminal metabolic pathways (Fahey and Berger, 1988). Acetate and butyrate production promotes more methane emission, while propionate is considered a competitive pathway for hydrogen uptake in the rumen (Moss et al, 2000). Methane production is an energy loss from the rumen, affecting the overall energy efficiency and represents between 2 to 12% of the total gross energy intake (Nagaraja, 2012). In the last few years, great attention has been paid to the emission of methane from ruminants due to its contribution to global warming (Moss et al, 2000).

Selecting for lower RFI could yield cattle that produce less methane while attaining the same performance, thus reducing the environmental impact of beef and milk production. However, the basis on which these differences rely remains unclear. Fitzsimons et al (2013) reported lower methane production in low RFI cattle, both when expressed in g $CH_4.d^{-1}$ or g CH_4. g MBW^{-1}. However, no differences were detected when methane production was expressed in g CH_4. kg DMI^{-1}. Hegarty et al (2007) also reported a positive correlation between RFI and methane production. They compared steers with high and low RFI and found that the steers with low RFI produced 24% less methane per unit of ADG. However, similar to Fitzsimons et al (2013) findings, no differences in methane yield per kg of DMI intake were found. Similar findings were reported by Waghorn and Hegarty (2011). Together, these results suggest that the mechanism underlying the lower methane production by low RFI cattle would depend on the lower total DM intake rather than on differences in rumen metabolism (Fitzsimons et al, 2013). However, Nkrumah et al (2006) found that cattle selected for lower RFI produced less methane per kg of MBW or per kg of ADG and that these differences persisted even when DM intake was used as a covariate, indicating that mechanisms other than lower DM intakes might be underlying the lower methane production.

Recently, Carberry et al. (2014) reported no differences in the total abundance of methanogens between cattle contrasting in RFI. These results agree partially with those of Zhou et al (2009), who also found no differences in the total population of methanogens, but reported differences in the composition, diversity and proportion of methanogen species between high RFI and low RFI. However, none of the studies attempted to relate the differences in methanogen population with total methane production.

Regardless if differences are due to ruminal microbial composition or simply to a lower DMI, it is clear that low RFI cattle produce less methane per unit of production (i.e., kg of gain). Each 1 $kg.d^{-1}$ increase in RFI is associated with between 14 $g.d^{-1}$ (Hegarty et al, 2007) and 26 $g.d^{-1}$ (Fitzsimons et al, 2013) of additional methane emission. However, most studies have been done with cattle consuming high concentrate diets. The mitigating effect of low RFI on methane production might be dependent on diet quality. For example, Jones et al (2011) found no differences in methane production among heifers selected divergently on RFI when they grazed a low quality pasture (55% digestibility). However, when the same set of animals grazed a high quality pasture (82% digestibility), those selected by lower RFI had 27% lower methane emission. Additionally, the lower methane production was accompanied by a reduced DM intake.

4.2 Digestibility and rumen function

Nkrumah et al (2006) found a tendency for a higher DM and crude protein digestibility in cattle selected for lower RFI. Similar results were reported by Richardson et al (1996), who estimated that differences in digestibility would explain 19% of the total variation in RFI. It has been suggested that differences in DM intake, ruminal retention time and feeding behavior could be the mechanism underlying the higher digestion efficiency in low RFI cattle (Nkrumah et al, 2006). However, several other authors have found no relation between digestibility and RFI (Cruz et al, 2010, Gomes et al, 2013, Fitzsimons et al, 2014). Herd and Arthur (2009) advised caution in allocating digestibility as a major factor determining RFI, mainly because of the difficulties in accurately detecting differences in digestibility.

Evidence of differences in rumen digestion between cattle differing in RFI exists. However, results are contradictory and evidence is far from conclusive (Lawrence et al, 2011, 2013, Fitzsimons et al, 2013, 2014). Fitzsimons et al (2014), using a high concentrate diet (rolled barley 860 g/kg DM) reported no differences in rumen pH, VFA proportions or lactic acid concentration. However, a previous report using a diet comprised purely of grass silage (*in vitro* DM digestibility 766 g/kg DM) from the same group of researchers (Fitzsimons et al, 2013) found that cattle with lower RFI tended to have a higher propionate concentration and a lower acetate:propionate ratio in rumen. This agrees with the results reported by Lawrence et al (2011, 2013), who also used high fiber diets. It seems, therefore, that differences in rumen fermentation profile are evident in high fiber diets but not in high concentrate diets. Lower acetate:propionate ratio in low RFI cattle is consistent with a higher energy efficiency and lower methane production.

4.3 Metabolism, maintenance and heat production

Some research suggests that low RFI cattle could have lower maintenance requirements (Archer et al, 1999, Herd and Bishop, 2000, Castro Bulle et al, 2007, Gomes et al, 2012), although evidence is not totally conclusive. Since an accurate and "true" measure of maintenance requirements implies long term experiments, most of the estimations are obtained indirectly. For example, Herd and Bishop (2000) estimated maintenance as the difference between the total ME intake and the ME used for growth, taking into account the gain composition and using standard efficiencies for fat and protein deposition. Nkrumah et al

(2006) assessed heat production indirectly using oxygen consumption and found that heat production was decreased 21% in low RFI vs high RFI steers. Consistently, the energy retention was higher. The authors concluded that these differences were independent of the level of intake. Basarab et al (2003) calculated heat production from ME intake and gain composition and estimated that low RFI cattle produced less heat. Montanholi et al (2010) used infrared thermography, which measures the body surface temperature, to assess the heat production of cattle. The authors found that low RFI cattle showed lower surface temperature in the eye, cheek and snout regions, and concluded that this was an indicator of lower heat production in more efficient steers. However, these results should be taken carefully, since heat production is affected by DM intake, and estimations would be more accurate if done under similar DM intakes.

Protein turnover is an energy demanding process which accounts for an important portion of the total basal metabolic rate (Richardson et al, 2004) and strongly influences maintenance requirements. Castro Bulle et al (2007) estimated that the maintenance requirements increased by 16.6 kcal. kg MBW. d^{-1} for each percentage increase in protein breakdown. Therefore, several researchers have looked for relations between RFI and protein turnover rate. Richardson et al (2004) reported that less efficient cattle (higher RFI) showed higher levels of total plasma protein, urea and aspartate aminotransferase, all possible indicators of increased protein breakdown. However, the authors did not find differences in urine 3-methyl histidine:creatinine ratio, which is an indicator of rate of protein breakdown. Castro Bulle et al (2007), working with *Bos taurus,* as well as Gomes et al (2013) working with *Bos indicus,* compared high and low RFI steers, finding no differences in 3-methyl histidine:creatinine ratio nor in estimated fractional protein breakdown, synthesis or accretion rate. However, McDonagh et al. (2001) reported higher calpastatin activity (+13%) with no differences in calpain activity in low RFI cattle. Since the calpain-calpastatin system is related to the rate of protein breakdown in the live animal, with calpastatin being an inhibitor of protein breakdown, these results would indicate that low RFI steers could have a lower energy cost due to protein turnover.

Other processes occurring at cell level have been proposed as partially responsible for variations in feed efficiency (Herd and Arthur 2009, Karisa et al, 2014). Great attention has been paid to mitochondrial proton leak and ion pumping associated with Na+/K+ ATPase (Cartens and Kerley, 2009). Mitochondria possess an efficient mechanism that allows capturing the energy generated by the electronic transport, and use it to pump protons against a gradient into the intermembrane space and then take advantage of that gradient by coupling the proton flux with the synthesis of ATP. However, sometimes this highly efficient mechanism can be uncoupled, and the protons leak back into the mitochondrial matrix generating heat rather than ATP, in a process that dissipates energy (Stuart et al, 1999, Harper et al, 2002, Neufer, 2015). This waste of energy is thought to account for at least 20% of the basal metabolism of rats (Nobes et al, 1990, Rolfe and Brand, 1996). Proton leak can occur both by simple diffusion through the lipid bilayer of the inner mitochondrial as well as facilitated by proteins, known as uncoupling proteins, of which many isoforms have been described (Stuart et al, 1999). The importance of mitochondrial proton leak in energy efficiency has been noted by researchers, who aimed to elucidate its importance in livestock. Both in poultry (Ojano-Dirain et al, 2007, Bottje and Cartens, 2009) and pigs (Grubbs et al, 2013, Lonergan, 2015), it has been shown that proton leakage is related to RFI. In cattle, Kolath et al. (2006) compared mitochondrial function in low and high RFI and did not find differences in proton leakage, however more efficient cattle surprisingly had an increased rate of respiration. Simielli-Fonseca et al (2015) analyzed the expression of mitochondrial proteins in Nelore cattle and found that low RFI (more efficient) showed higher expression of certain isoforms of uncoupling proteins in the liver and no difference in uncoupling protein expression was found in the muscle. Similarly, no difference in proton leak kinetics in beef cattle hepatocytes were reported by Lancaster et al (2014). Therefore, evidence of mitochondrial function differences in cattle is far from conclusive. Further research is needed in this area.

4.4 Visceral weight

Given their high metabolic activity per unit of tissue, visceral organs are responsible for a large proportion of oxygen consumption and heat production (Reynolds, 2002). The gastrointestinal tract and liver, representing 7.0 and 2.5% of body weight, respectively, account for more than 40% of the total energy demands of the body (McBride and Kelly, 1990). Therefore, there is a negative correlation between energy efficiency and visceral organ size, which in turn is also affected by total intake (Johnson et al, 1990). The above mentioned explains why there has been an interest in correlating visceral weight and RFI. Basarab et al (2003) reported that high RFI steers had heavier liver, stomach and intestine than low RFI steers. Fitzsimons et al. (2014) found a higher ruminal reticular weight in high RFI bulls compared to low RFI bulls, but did not detect differences in weight for the rest of the splanchnic organs, including liver and intestine. On the other hand, other authors did not find any relationship between total visceral organ mass and RFI (Richardson et al, 2001, Cruz et al, 2010).

4.5 Feeding behavior and activity

In a review, Herd and Arthur (2009) assigned 10% of variability in cattle RFI to physical activity and 2% to feeding patterns. Richardson et al. (1999) reported a positive phenotypic correlation (r=0.32) between RFI and total steps measured by a pedometer, suggesting that activity is a factor influencing RFI. There is also evidence that more efficient cattle spend more time lying down (Gomes et al., 2013). Additionally, feeding behavior traits, like frequency and duration of feeding events, showed significant differences between cattle differing in RFI (Gomes et al., 2013). Robinson and Oddy (2004) recognized three feeding behavior traits associated with RFI. Higher RFI was phenotypically positively correlated with longer daily eating time (min.d^{-1}), more events of bunk attendance and faster rate of eating (g DM.min^{-1}). Coincidently, Nkrumah et al, (2006) recorded the feeding duration (min.d^{-1}) and the number of events of bunk attendance and found that animals selected for lower RFI spent 36% less time eating and had a reduced number of events of bunk attendance. Similar results are reported by Golden et al (2008), Montanholi et al (2010) and Gomes et al (2013). Additionally, data shows that higher RFI cattle have a more variable temporal pattern of feed intake (Golden et al, 2008, Dobos and Herd, 2008). According to the evidence, it seems that feeding behavior and eating patterns, as well as physical activity, differ in cattle divergently selected for RFI. However, according to Golden et al (2008) these correlations, although significant, are not strong enough to allow for an accurate prediction of RFI from feeding behavior assessment alone.

4.6 Body composition and meat quality

Per unit of weight, the deposition of lean tissue is less energetically costly than fat. Gross energy of fat and protein are 9.38 Mcal.kg^{-1} and 5.54 Mcal.kg^{-1}, respectively (Garrett and Hinman, 1969). Additionally, muscle contains a water to protein ratio in average of 4:1, whereas fatty tissue contains very low water concentration (Gerrard and Grant, 2003). Therefore, variations in gain composition affect the nutrient efficiency use (Herd and Arthur, 2009).

Richardson et al (2001) analyzed the progeny of cattle divergently selected for RFI. The authors suggested that carcass chemical composition was correlated to RFI, with progeny of low RFI (more efficient) cattle having less carcass fat and more protein. However, less than 5% of the total variation in RFI was explained by variation in body composition. Basarab et al (2003) found that high RFI cattle had slightly higher empty body fat gain, and that marbling score and backfat thickness were positively correlated to RFI. The authors estimated that 6.8% of the variation in RFI was explained by variation in gain of empty body fat. Similarly, slight differences or weak positive correlations between RFI and subcutaneous fat thickness have been reported by several other authors (Herd and Bishop, 2000, Mc Donagh et al, 2001, Arthur et al, 2001, Schenkel et al, 2004). On the other hand, no ultrasound differences for back and rump fat thickness were detected by Fitzsimons et al (2014) between high and low RFI bulls. Additionally, the authors detected no significant differences in carcass composition except for a moderate correlation with dressing percentage. In fact, numerous studies have found no correlation between RFI and fat proportion and fat:lean ratio (Mader et al, 2009, Cruz et al, 2010, Fitzsimons et al, 2014, Perkins et al, 2014). Similarly, percentage of subcutaneous fat and body cavity fat has not been correlated with RFI (Basarab et al, 2003).

From a selection standpoint, any potential improvement in cattle feed efficiency might be worthless if obtained at the expense of meat quality (Fitzsimons et al, 2014). Some of the evidence reviewed gives reason for two possible concerns derived from ongoing selection, which are potential reduction in marbling score and tenderness. Marbling score, a visual indicator of the intramuscular (IM) fat content, is a factor affecting beef palatability and, in some countries, higher marbling scores result in premium prices. Therefore, establishing the impact of selection based on RFI on marbling and IM fat content has been a concern for many researchers. Nkrumah et al (2007) reported moderate positive genetic correlations between RFI and marbling assessed either by ultrasound (r= 0.32) or measured in the carcass *postmortem* (r=0.28). Similar correlations were reported by Ahola et al (2011). However, other authors have reported no correlation between RFI and IM fat assessed by ultrasound (Schenke et al, 2004, Shaffer et al, 2011) or marbling score assessed postmortem (McDonagh et al, 2001, Perkins et al, 2014).

Evidence indicates that RFI could be linked to calpastatin expression and lower myofibril fragmentation index in low RFI cattle (Mc Donagh et al, 2001). Therefore, potential impacts of selection on beef sensorial quality, mainly tenderness, have been assessed. Ahola et al (2011) found no effect of divergent RFI selection on beef sensory traits assessed by a trained panel (tenderness, juiciness, flavor and presence of off-flavors). They also did not find differences in Warner-Bratzler shear force. Similarly, Mc Donagh et al (2001) reported no differences in Warner-Bratzler shear force or compression values nor in muscle and fat color in steers differing in RFI.

The correlation between body compositions and RFI, although significant in some studies, is low and does not appear to be a determining factor of differences in efficiency. However, to reduce the risk that selection against RFI could lead to leaner cattle, some authors (Schenkel et al, 2004) have suggested to include an adjustment using backfat thickness as an extra coefficient in the regression. Although great effects on meat quality have not been detected, continuous selection may theoretically lead to changes in tenderness. Since most of the reported experiment are a single generation of divergent selection, potential impacts of prolonged selection for RFI may be clearer when multi-generational information is attained.

4.7 Hormones

Associations between hormone concentrations and RFI have been studied. Leptin is a peptidic hormone expressed mainly by white adipose tissue (Ahima and Flier, 2000) which has been considered not only as a sensor of adiposity level but also as a regulator of energy consumption (Houseknecht et al, 1998) and a hastener of oxygen consumption through increased metabolic rate (Scarpace et al,1997, Chilliard et al, 2005). Results are inconclusive with respect to the correlation between leptin levels and RFI. Richardson et al (2004) reported higher leptin concentration in high RFI steers, which the authors associated with a higher fat mass (Frederich et al, 1995, Chilliard et al, 2005). On the other hand, Perkins et al, (2014) found leptin mRNA expression in adipose tissue to be 245% higher in low RFI than in high RFI steers, which the authors found consistent with the lower intakes observed in the low RFI steers.

Perkins et al (2014) also studied gene expression of a series of hypothalamic neuropeptides controlling feed intake in high and low RFI steers. Low RFI showed a higher expression of genes linked to the synthesis of anorexigenic peptides (Pro-opiomelanocortin, precursor of α-MSH) and a lower expression of Neuropeptide-Y and relaxin-3, which stimulate consumption (orexigenic). The authors suggested that this could be the base of the differences in feeding behavior and DMI in cattle differing in RFI. Additionally, RFI showed a relation with the expression of hypothalamic and pituitary hormones linked with the reproductive physiology, but the relation between RFI and reproductive axis remains unclear.

Moore et al (2005) has shown that RFI is positively related with plasma IGF-1 levels, which in turn is correlated positively with subcutaneous and IM fat content. The authors suggested that selecting for lower IGF-1 levels could lead to more efficient and leaner cattle. Several authors have also reported an association between the GH and RFI (Karisa et al, 2013, Kelly et al, 2013), although others have found no correlation (Lancaster et al, 2008).

Research (Richardson et al, 2004, Gomes et al, 2013) has also reported a higher cortisol plasma concentration in high RFI steers, leading them to conclude that high RFI could be more susceptible to stress and this could be part of the explanation for differences in efficiency.

In summary, it seems clear that low RFI show a lower expression of orexigenic neuropeptides and a higher expression of anorexigenic factors. On the other hand, mediators as IGF-1 and GH, which regulate the gain composition and the lean:fat ratio, also seems related to RFI.

5. Conclusions

No single mechanism is responsible for the differences in RFI and nutrient use efficiency. RFI can be considered a restricted selection index, containing multiple components. Future research lines should focus on subcellular mechanisms, in particular variability in mitochondrial function, which appears to affect energy efficiency in monogastrics, while the findings are contradictory in ruminants. Also, from a beef quality standpoint, potential impacts of prolonged selection for RFI (multi-generational) on meat tenderness and IM fat content are interesting to assess, since any improvement in feed efficiency would be worthless if implying beef quality losses.

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