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Invited review: Improving feed efficiency of beef cattle – the current state of the art and future challenges

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Improvements in feed efficiency of beef cattle have the potential to increase producer profitability and simultaneously lower the environmental footprint of beef production. Although there are many different approaches to measuring feed efficiency, residual feed intake (RFI) has increasingly become the measure of choice. Defined as the difference between an animal's actual and predicted feed intake (based on weight and growth), RFI is conceptually independent of growth and body size. In addition, other measurable traits related to energy expenditure such as estimates of body composition can be included in the calculation of RFI to also force independence from these traits. Feed efficiency is a multifactorial and complex trait in beef cattle and inter-animal variation stems from the interaction of many biological processes influenced, in turn, by physiological status and management regimen. Thus, the purpose of this review was to summarise and interpret current published knowledge and provide insight into research areas worthy of further investigation. Indeed, where sufficient suitable reports exist, meta-analyses were conducted in order to mitigate ambiguity between studies in particular. We have identified a paucity of information on the contribution of key biological processes, including appetite regulation, post-ruminal nutrient absorption, and cellular energetics and metabolism to the efficiency of feed utilisation in cattle. In addition, insufficient information exists on the relationship between RFI status and productivity-related traits at pasture, a concept critical to the overall lifecycle of beef production systems. Overall, published data on the effect of RFI status on both terminal and maternal traits, coupled with the moderate repeatability and heritability of the trait, suggest that breeding for improved RFI, as part of a multi-trait selection index, is both possible and cumulative, with benefits evident throughout the production cycle. Although the advent of genomic selection, with associated improved prediction accuracy, will expedite the introgression of elite genetics for feed efficiency within beef cattle populations, there are challenges associated with this approach which may, in the long-term, be overcome by increased international collaborative effort but, in the short term, will not obviate the on-going requirement for accurate measurement of the primary phenotype.

Keywords: beef cattle, digestion, energy utilisation, metabolism, residual feed intake

Implications

Research to date has clearly shown that feed efficiency is a complex multifaceted trait, under the control of many biological processes. Thus, a thorough understanding of the biochemical mechanisms regulating appetite, intestinal absorption, digestion and nutrient partitioning, amongst other key processes, underpinning the trait is warranted to expedite selection for feed efficient cattle, necessary for the continued economic and environmental sustainability of beef production.

Introduction

One of the major economic factors influencing the profitability of beef cattle enterprises is the provision of feed, which represents up to three-quarters of total direct costs (Nielsen *et al.*, 2013). In addition, within the context of climate change and more restrictive environmental legislation, beef production is under increased scrutiny. Consequently, there is considerable interest in improved feed efficiency as a means of augmenting the economic and environmental sustainability of beef production systems.

At the animal level, many alternative definitions of feed efficiency exist, each differing in their application (Berry and Crowley, 2013). Traditionally, feed conversion ratio (i.e. feed: gain) or its mathematical inverse, feed conversion efficiency (i.e. gain:feed), was widely used. More recently, residual feed intake (RFI), defined as the difference between observed feed intake and the expected requirement to support both maintenance of BW and growth, has become the preferred measurement (Savietto *et al.*, 2014). Because the calculation of the RFI index forces it to be mathematically independent

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of the level of animal production, it is considered a particularly useful concept to examine the biological mechanisms associated with inter-animal variation in feed efficiency (Berry and Crowley, 2013).

The contribution of additive genetic variance to deviation in RFI has been highlighted previously (Berry and Crowley, 2013). In their review, Berry and Crowley (2013) indicated that further information on factors such as genotype × environment interactions for feed efficiency and genetic associations between performance traits (both beef and dairy), the environmental impact of beef production and animal health was required. Some of the typical biological mechanisms, previously implicated for young growing beef cattle, include body composition, feeding behaviour and activity (Herd and Arthur, 2009), whereas more recent endeavours have reported variance in less characterised or understood processes such as intestinal cellularity and absorption (Montanholi et al., 2013a), mitochondrial function (Lancaster et al., 2014) and appetite regulation (Perkins et al., 2014). However, many of the preceding studies have employed relatively few animals, therefore limiting the extrapolation of results to other populations of cattle. Expression of feed efficiency cannot be viewed in isolation of the production system within which cattle are raised, as an expression of such traits is further influenced by nutritional and health management as well as the stage of production. Taking cognisance that RFI has been shown to be moderately heritable ($h^2 \approx 0.33$, Berry and Crowley, 2013), the main objective of this review is to understand potential consequences of selection for (or against) the trait. In addition, this review aims to highlight the issues surrounding the measurement of RFI and to quantify and discuss the main biological processes that contribute to inter-animal variation, repeatability and the potential for genotype × environment interactions for the trait. Such information is necessary for the future design of breeding and management programmes to support more sustainable systems of beef production.

Measuring and calculation of residual feed intake

As variation amongst individual animals in feed intake cannot be estimated from knowledge of BW and level of production alone, accurate measurement of feed intake remains a necessary requirement in national cattle evaluation systems (Nielsen et al., 2013). In order to aid the standardisation of the regimen, criteria for measuring, recording and assessing feed efficiency have been established (Beef Improvement Federation, 2010). This includes a period of feed intake measurement of at least 70 days duration, preceded by an acclimatisation period of at least 21 days, with live weight recorded on 2 consecutive days at the beginning and end and periodic intervals throughout. Notwithstanding this, recent studies have attempted to reduce the test duration further (Culbertson et al., 2015; Cassady et al., 2016). Indeed, where BW was recorded for 63 (Wang et al., 2006) and 84 (Manafiazar et al., 2017) days, apparently adequate feed intake test durations as short as 35 to 42 days, respectively have been reported. Although

shortening the duration of the feed intake test period resulted in a loss in accuracy (reduction in Spearman's correlation coefficient) of 5% to 7%, such an approach would reduce the cost of feed intake recording and increase annual animal throughput (Manafiazar et al., 2017). The accuracy of shorter test durations, however, is likely to be dependent on prevailing diet composition and animal growth rate (Goonewardene et al., 2004).

Residual feed intake is the difference between observed and predicted feed intake (dry matter or energy) and is usually calculated as the residuals from a multiple regression model of dry matter intake (DMI) on selected sources of significant energy expenditure or sinks such as maintenance, growth and activity (Savietto et al., 2014). This computation generally forces RFI to be mathematically independent of the traits used to predict DMI at a phenotypic level but does not necessarily ensure genetic independence (Berry and Crowley, 2013). The conventional basic multiple regression model used to predict DMI in many studies includes metabolic live weight and average daily gain (ADG) but other potential sources of variation, such as measures of body composition (see later), can also be included. The coefficient of determination (R^2) of this regression model predominantly quantifies the relative cumulative contribution of various energy-demanding processes, included in the model, to variation in DMI, and, by extension RFI, but also contains measurement error. Despite much research on the topic and assessment of the potential contribution of a variety of traits and physiological processes, very little of the unknown residual component of the model has been explained to-date.

The majority of published studies that have evaluated RFI in growing (finishing) beef cattle pertain to animals offered energy-dense diets. An appraisal of 14 such publications (e.g. Kelly et al., 2010a; Fitzsimons et al., 2014a) indicates a mean R^2 of 0.70 for the 'base' model used to predict DMI. The corresponding value from eight other such studies where growing cattle were offered mainly forage diets (e.g. Shaffer et al., 2011; Lawrence et al., 2012) was 0.61. The lower degree of variation explained for forage-based diets is not surprising considering their poorer intake characteristics and slower rate of passage through the rumen (Forbes, 2005). Compared with concentrate-based diets, feeding high-forage diets may limit voluntary feed intake capacity thus reducing the expression of inherent DMI potential.

Some studies have reported a positive, though weak, phenotypic correlation between RFI and measures of body fat content (see later) and as a result, many studies include an adjustment for body fat in the statistical model for computing RFI. This adjustment can increase the R^2 from less than one (Basarab et al., 2011) to up to five percentage units (Fontoura et al., 2015), although the significance and contribution of body composition per se to the accuracy of the model is not always stated (McGee et al., 2014). In nine studies using pregnant beef females, the mean reported R^2 for the prediction of DMI was only 0.37, even where measures of body composition were included. This poorer

relationship may be partially attributed to the fact that the diets offered were forage-only but also to the relatively low or near zero growth rates (i.e. conceptus-adjusted ADG) of the pregnant females used in those studies (Lawrence *et al.*, 2013). Although variation in tissue accretion and depletion between the conceptus and dam exists during pregnancy, adjusting live weight data for conceptus growth should largely account for the confounding effects of stage of gestation and estimated foetal size. In addition, factors such as maturity (parity, age) and the energy requirements pertaining to stage of gestation and colostrogenesis may influence this.

Few studies have calculated RFI for lactating beef females. Black *et al.* (2013), using ADG, energy-corrected milk yield and change in back fat thickness, reported an R^2 of 0.60 for the prediction of DMI of lactating beef cows, offered a forage-based diet. Of note is that BW was excluded from this prediction model, suggesting that this variable did not account for a statistically significant proportion of the variation in DMI observed. Similarly, it is recognised that measuring RFI in lactating dairy cows is much more complicated than for growing cattle exhibiting a linear growth trajectory (Connor, 2015). Collectively, these studies suggest that the regression models used to predict RFI in fast-growing cattle may not be appropriate for pregnant and lactating beef cows, as the majority of the phenotypic variance in DMI remains unexplained, or alternatively, that the error in estimation of weight and weight gain is too high relative to that of DMI.

Sources of biological variation in phenotypic residual feed intake

There is a substantial inherent inter-animal variation for feed efficiency where cattle are offered feed to appetite. Phenotypic differences in DMI between the most feed efficient and inefficient terciles of up to 15% in young growing cattle (Lawrence *et al.*, 2012; Fitzsimons *et al.*, 2013) and 25% in pregnant beef cows (Lawrence *et al.*, 2013) have been reported. In agreement, significant genetic variance for the trait has been reported (Berry and Crowley, 2013; Savietto *et al.*, 2014). In addition, it must be noted that the inter-animal variance in DMI will be greater than this. Given the existence of such variation, potential biological sources of variation are discussed below.

Appetite, feeding behaviour and activity
Voluntary feed intake of cattle is regulated by a complex interaction between neuro-endocrine control mechanisms and the physicochemical properties of the feed and is modulated by the physiological state of the animal (Allen, 2014). Studies describing the potential contribution of mechanisms regulating appetite to variance in RFI in cattle are scant. In their review, Fitzsimons *et al.* (2017) concluded that further investigation into endocrine function and gene and protein expression within tissues such as the hypothalamus might enhance our understanding of variation in feed efficiency. Activity associated with consumption, particularly within the context of forage diets, is potentially a significant

energy sink within cattle (Fitzsimons *et al.*, 2014b). In an effort to quantify the effect of RFI status on daily feeding duration, we conducted a meta-analysis of nine published studies (Supplementary Table S1) with growing beef cattle offered energy-dense high-concentrate diets. Our results showed that high-RFI cattle spent, on average, 10.3 min longer ($P < 0.001$) eating, out of an average of 93 min within a 24-h period, than their low-RFI contemporaries. In agreement, similar observations have been reported for pregnant beef females offered high-forage diets (Basarab *et al.*, 2007; Hafla *et al.*, 2013; Fitzsimons *et al.*, 2014b). The literature evaluating the association between RFI status and daily feeding events is equivocal. This may be partly due to the diversity of diet types offered and the inconsistent definition of a 'feeding event' across studies and for the latter reason we were unable to conduct a similar meta-analysis for this trait. The occurrence of non-feeding events, where cattle are at the feed face but do not consume any feed, was less in low- compared with high-RFI beef females (Kelly *et al.*, 2010a; Fitzsimons *et al.*, 2014b). The limited literature that has quantified eating rate indicates that low-RFI growing steers (Robinson and Oddy, 2004; Montanholi *et al.*, 2010) and heifers (Robinson and Oddy, 2004) and pregnant beef females (Hafla *et al.*, 2013; Fitzsimons *et al.*, 2014b) have a slower eating rate than their high-RFI counterparts.

It is important to note that the vast majority of aforementioned studies, by necessity, were conducted under confinement, despite the fact that beef systems worldwide are largely based on grazed pasture. Obviously, under grazing conditions, nutrient supply and herbage composition vary among grazing bouts; therefore, ingestive-digestive behaviours become very important (Gregorini *et al.*, 2008). Basarab *et al.* (2013) reported that low-RFI beef suckler cows managed under extensive grazing conditions had similar productive performance compared with their high-RFI contemporaries. A number of studies have examined the frequency of non-feed related activities in cattle varying in RFI status. For example, Lawrence *et al.* (2012) and Hafla *et al.* (2013) reported that there was no difference in the time spent standing, active or lying between high and low-RFI heifers and pregnant females, respectively, housed indoors. In contrast, however, there were no consistent feeding behaviour-related traits observed between divergent RFI phenotypes of heifers (Lawrence *et al.*, 2012) and lactating beef cows (Lawrence *et al.*, 2013) grazing pasture.

Digestion, rumen fermentation and microbiome
Increasing consumption of feed usually decreases diet digestibility, mainly as a result of a reduction in ruminal residency time. Consequently, a reduction in apparent digestibility *per se* would be expected in cattle classified as high- compared with low-RFI, but the literature does not support this speculation (Table 1). Nevertheless, several studies (including some of those that did not detect a difference in dry matter digestibility (DMD) between RFI classifications), reported that diet DMD was negatively correlated with RFI. It is unclear, however, whether the

Table 1 *The effect of residual feed intake (RFI) rank on apparent dry matter digestibility in beef cattle[1]*

Studies	Animal type	Diet	Method	n	RFI group		Sig.	r^2
					High	Low		
Richardson *et al.* (1996)	Heifers/Bulls	Lucerne + concentrate	Alkanes	58	0.671	0.681	<0.10	–
Richardson *et al.* (2004)	Steers	HC	TFC	38	0.660	0.660	Ns	− 0.44*
Brown (2005)	Steers	Alfalfa + concentrate	AIA	57	0.708	0.664	0.13	− 0.32*
Nkrumah *et al.* (2006)	Steers	HC	TFC	27	0.709	0.753	0.10	− 0.33†
Krueger *et al.* (2009a)	Heifers	High roughage	AIA	152	0.735	0.762	<0.05	− 0.51**
Cruz *et al.* (2010)	Steers	HC	Lignin	60	0.740	0.725	0.53	–
Lawrence *et al.* (2011)	Pregnant heifers	Grass silage	AIA	73	–	–	Ns	–
Lawrence *et al.* (2012)	Heifers	Grass silage + concentrate	AIA	18	0.567	0.582	Ns	–
Gomes *et al.* (2013)	Steers	HC	TFC	72	0.723	0.752	0.18	–
Lawrence *et al.* (2013)	Beef cows	Grass silage	AIA	39	0.700	0.690	0.74	–
Fitzsimons *et al.* (2013)	Heifers	Grass silage	AIA	22	0.730	0.730	0.83	–
Fitzsimons *et al.* (2014a)	Bulls	HC	AIA	67	0.720	0.740	0.41	–
Lines *et al.* (2014)	Heifers	Hay + concentrate	Titanium dioxide	16	0.683	0.684	Ns	–
McDonnell *et al.* (2016)	Heifers	Grass silage, grazed pasture, TMR[3]	AIA	28	0.706	0.716	0.13[4]	–

HC = high concentrate; TFC = total faecal collection, AIA = acid insoluble ash; TMR = total mixed ration; DMD = dry matter digestibility.
[1]Reference list for this table provided in Supplementary Material S1.
[2]r = correlation between RFI and DMD; †$P < 0.10$, *$P < 0.05$ and **$P < 0.01$.
[3]TMR (70 : 30 corn silage:concentrate on a dry matter basis).
[4]An interaction was reported in this study whereby low-RFI heifers had greater DMD than their high-RFI contemporaries when consuming a grass silage diet but this difference was not observed when the same animals grazed pasture or were offered a TMR indoors.

apparently improved digestive ability of more feed efficient animals is inherent, or simply a function of a slower passage rate of digesta through the rumen due to lower DMI. In some instances, the absence of differences in DMD between cattle of varying RFI phenotype may be related to the nature of the diets offered, as the effect of feed intake on digestion is less with forage than concentrate-based diets. In addition, in relation to the indirect marker methodologies employed in the majority of studies, these technologies may not be sufficiently sensitive to detect differences, where they exist and their accuracy may also be affected by the nature and homogeneity of the diet offered (Herd *et al.*, 2004).

Given the central nature of ruminal digestion to the profile of nutrients available for post-absorptive processes, it is surprising that few obvious differences in the primary rumen fermentation variables measured are evident between high- or low-RFI cattle and, in cases where variance was observed, results were not in agreement (Table 2). Consistent with studies showing no association between RFI and production and composition of volatile fatty acid (VFA), Kong *et al.* (2016) conducted transcriptome profiling of the rumen epithelium of steers differing in RFI and reported no differences in the expression of genes involved in VFA metabolism, however, concentration and absorption of ruminal VFA were not measured. Nevertheless, there is evidence for associations between the rumen microbiome, VFA and RFI phenotypes in growing beef cattle (Carberry *et al.*, 2012; Myer *et al.*, 2015; Shabat *et al.*, 2016). For example, the association between RFI ranking and bacterial profiles was more pronounced when a forage-only (grass silage), as opposed to a cereal-based diet, was offered to beef heifers (Carberry *et al.*, 2012). Furthermore, *Prevotella,* one of the most

dominant bacterial genera within the rumen microbiome, was more abundant in inefficient cattle (Carberry, *et al.*, 2012; McCann *et al.*, 2014; Myer *et al.*, 2015).

Although enteric methane (CH_4) production is an integral component of rumen fermentation, it constitutes what can be a significant loss of energy to the host animal (Pickering *et al.*, 2015). The well-documented strong positive relationship between DMI and ruminal methane production in cattle suggests that low-RFI cattle should have lower CH_4 emissions (g/day), at least proportionate to their lower feed intake, however, the published literature does not support this expectation (Table 3). For example, CH_4 emissions (g/day) were found to be lower for low- compared with high-RFI cattle, when offered unrestricted access to feed (Hegarty *et al.*, 2007; Fitzsimons *et al.*, 2013), but also where animals were offered an equal, though restricted, feed allowance (Nkrumah *et al.*, 2006). In contrast, McDonnell *et al.* (2016) found no effect of RFI status on CH_4 emissions (g/day) of beef heifers offered a grass silage diet followed by a high-starch cereal-based diet. These findings suggest that there is little evidence of a direct effect of RFI *per se* on ruminal CH_4 emissions (g/day) and that differences observed are likely a reflection of the variance in DMI between animals. This appears to be true regardless of whether cattle were the result of divergent selection for RFI (Hegarty *et al.*, 2007; Jones *et al.*, 2011) or not (Nkrumah *et al.*, 2006; Fitzsimons *et al.*, 2013; McDonnell *et al.*, 2016). In addition, other work from our laboratory (Carberry *et al.*, 2014) shows that with the exception of various genotypes of *Methanobrevibacter smithii* found to be more abundant in cattle of high- compared with low-RFI when compared across a number of contrasting diet types, overall methanogen abundance in rumen digesta was not affected by host feed efficiency status.

Table 2 *Rumen fermentation traits and residual feed intake (RFI) in beef cattle[1]*

Studies	Animal type	Diet	RFI Group	pH	Lactate (mg/l)	NH$_3$ (mg/l)	VFA (mM/l)	Acetate[2]	Propionate[2]	Butyrate[2]	A:P
Guan *et al.* (2008)	Steers	HC	H	–	–	–	55.4[e]	564	326	150[a]	–
			L	–	–	–	96.7[d]	544	259	60[b]	–
Krueger *et al.* (2009a)	Heifers	High Roughage	H	–	–	–	–	Ns	H[b] > L[a]	Ns	H[a] < L[b]
			L								
Krueger *et al.* (2009b)	Steers	HC	H	Ns	–	–	Ns	Ns	Ns	Ns	Ns
			L								
Hernandez-Sanabria *et al.* (2010)[3]	Steers	HC	H	–	–	0.096	58.6	546	315	95[d]	1.9
			L	–	–	0.110	64.2	549	334	73[e]	1.7
Lawrence *et al.* (2011)	Cows	Grass silage	H	6.8	20.2	73.5	85.2	683	189[a]	104	3.7[a]
			L	6.8	24.0	90.5	79.9	671	202[b]	103	3.3[b]
Hernandez-Sanabria *et al.* (2012)[3]	Steers	HC	H	–	–	0.15	86.0	523	340	87	1.7
			L	–	–	0.14	81.5	537	336	83	1.8
Lawrence *et al.* (2013)	Cows	Grass silage	H	6.9	33.1	105.5	71.3	613	241	109	2.6
			L	6.9	40.5	118.6	68.7	609	246	105	2.5
	Cows	Grazed grass	H	6.6	40.6[a]	110.6	87.6	669	241	106	3.3
			L	6.4	59.3[b]	134.8	93.4	657	246	113	3.1
Fitzsimons *et al.* (2013)	Heifers	Grass silage	H	6.9	29.4	38.2	80.0	623	141[d]	204	4.6[d]
			L	6.8	16.6	53.7	75.2	625	182[e]	161	3.5[e]
Fitzsimons *et al.* (2014a)	Bulls	HC	H	5.7	121.4	43.6	95.1	519	305	125	2.0
			L	5.8	127.2	52.2	91.3	540	275	139	2.3
Fitzsimons *et al.* (2014b)	Cows	Grass silage	H	6.8[a]	24.0	20.7[a]	54.3	680	166	103	4.1
			L	7.0[b]	18.9	10.2[b]	54.0	674	165	104	4.1

NH$_3$ = ammonia; VFA = volatile fatty acid; HC = high concentrate; H = high RFI; L = low RFI; A:P = acetate:propionate ratio.
[a,b,c,d,e]Least squares means within a column without a common superscript letter differ (a, b: $P < 0.05$; d, e: $P < 0.10$).
[1]Reference list for this table provided in Supplementary Material S1.
[2]Acetate, propionate and butyrate reported as mmol/mol of volatile fatty acid.
[3]NH$_3$ reported as millimolar (mM).

Table 3 *Methane emissions and residual feed intake (RFI) in beef cattle[1]*

Studies	Animal model[2]	Diet	Methodology	CH$_4$	RFI group High	RFI group Low	P-value
Nkrumah *et al.* (2006)	Phenotype study	High concentrate	Indirect calorimetry	g/day	129	126	0.04
				g/kg DM	14.9	11.3	0.04
Hegarty *et al.* (2007)	Selection lines	High concentrate	SF$_6$	g/day	190	142	0.01
				g/kg DM	14.7	16.3	0.37
Jones *et al.* (2011)	Selection lines	Low-quality pasture	OPFTIR	g/kg cow BW per day	0.26	0.26	Ns
		High-quality pasture		g/kg cow BW per day	0.46	0.34	<0.05
Fitzsimons *et al.* (2013)	Phenotype study	Grass silage	SF$_6$	g/day	297	260	0.04
				g/kg DM	36	38	0.52
McDonnell *et al.* (2016)	Phenotype study	Grass silage, grazed grass, TMR[4]	SF$_6$	g/day	146	156	Ns[3]
				g/kg DM	20.2	22.4	0.03

CH$_4$, methane; DM = dry matter; SF$_6$ = sulphur hexafluoride tracer gas technique; OPFTIR = open path Fourier transform IR spectrophotometer technique; TMR = total mixed ration.
[1]Reference list for this table provided in Supplementary Material S1.
[2]Animal model = phenotype study – cattle used were from a random population; selection lines – the progeny of cattle divergently bred and selected for RFI.
[3]No RFI × diet interaction was reported for this study.
[4]TMR (70 : 30 corn silage:concentrate on a DM basis).

Intestinal absorption and cell morphology

Enhanced intestinal absorption of nutrients may contribute to inter-animal variation in feed efficiency (Fitzsimons *et al.*, 2017). This hypothesis is supported by the findings of Meyer *et al.* (2014) who reported statistically significant correlations between jejunal mucosal density and RFI ($r = -0.33$) in cattle. Corroborating this, Montanholi *et al.* (2013a) found that cell number in duodenal and ileal epithelial tissue of low-RFI steers was higher than that of their high-RFI contemporaries. At a genomic level,

Table 4 *Visceral organ weights and residual feed intake (RFI) in beef cattle[1]*

Studies	RFI group	Liver (kg)	Kidneys (kg)	GIT (kg)	Reticulo-rumen (kg)
Richardson *et al.* (2001)	H	–	–	15.9	–
	L	–	–	16.4	–
Basarab *et al.* (2003)	H	6.57[a]	0.93	48.73[a]	18.6[2]
	L	6.06[b]	0.94	45.05[b]	17.9
Bonilha *et al.* (2009)	H	4.63[a]	0.79[a]	24.3[a]	–
	L	4.16[b]	0.67[b]	21.8[b]	–
Gomes *et al.* (2012)	H	4.78	–	18.9	–
	L	4.72	–	20.1	–
Bonilha *et al.* (2013)	H	4.58	0.77[a]	25.0	–
	L	4.47	0.68[b]	24.5	–
Fitzsimons *et al.* (2014a)	H	6.5	1.05	–	13.2[a]
	L	6.2	1.04		12.1[b]
Meale *et al.*, (2017)	H	6.29	1.13	29.86	10.09
	L	6.03	1.15	28.92	9.66

H, high RFI; L, low RFI; GIT, gastrointestinal tract.
[a,b]Least squares means within a column without a common superscript letter differ ($P < 0.05$).
[1]Reference list for this table provided in Supplementary Material S1.
[2]Entire stomach complex reported.

Serão *et al.* (2013) reported associations between feed efficiency and single nucleotide polymorphisms (SNP) that mapped to genes involved in small intestinal transport of phospholipids and cholesterol.

Size of and metabolic processes within the visceral organs
Due to the high metabolic cost associated with the gastrointestinal tract and liver, it is likely that inter-animal variation in the size and functionality of these organs may influence energy requirements for basal metabolism. However, the published literature that has examined variation in visceral organ size amongst animals of divergent feed efficiency status is inconsistent (Table 4). Likewise, in terms of energy expenditure of visceral organs, there are a number of recent molecular-based studies, such as that of Paradis *et al.* (2015), that have demonstrated inconsistencies in the association between RFI phenotype and transcript abundance for genes involved in metabolic processes within gastrointestinal tissues. For a more in-depth discussion on this topic, the reader is referred to the recent review of Fitzsimons *et al.* (2017).

Nutrient partitioning: protein and fat deposition

In addition to its central importance to the value of beef cattle, body content of both muscle and fat tissues make a significant contribution to overall energy status. The potential contribution of differences in energy utilisation relating to composition, maintenance and metabolic processes within muscle and adipose tissue depots to inter-animal variation for the RFI trait, has been reviewed by Fitzsimons *et al.* (2017). As highlighted earlier, there is currently much equivocation in the published literature on body compositional differences between cattle of divergent feed efficiency status

and this is consistent for both growing and pregnant beef cattle. For example, where the base model ($DMI = \beta BW + \beta ADG + (e = RFI)$) has been used to calculate RFI, studies have reported both positive (Hafla *et al.*, 2013) and negative (Lawrence *et al.*, 2011) associations between RFI status and ultrasonically measured *longissimus* muscle size. Similarly, positive (Arthur *et al.*, 2001; Basarab *et al.*, 2007; Berry and Crowley, 2013), though sometimes weak and close to zero (Mao *et al.*, 2013), or no association (Fitzsimons *et al.*, 2014a) between RFI status and ultrasonically measured fat depth in the live animal and carcass fatness traits have been reported. Discrepancies between studies may partly be due to variation in fat deposition in different breeds, differences in the site and technique for measurement of the traits between operators and also disparities in carcass classification methodologies that differ between countries. Similarly, inconsistencies in the literature exist for systemic metabolic indicator traits for body composition such as creatinine (negative association, Lawrence *et al.*, 2012; no association, Fitzsimons *et al.*, 2014a) and leptin (no association, Kelly *et al.*, 2010a). Reports on the effects of insulin and IGF-I, which are also indicators of body composition and overall metabolic status, on RFI status are equally in disagreement. In terms of circulating concentrations of IGF-I, some studies have reported higher (Nascimento *et al.*, 2015), others lower (Lancaster *et al.*, 2008) or no difference (Lawrence *et al.*, 2012; Welch *et al.*, 2013) in concentrations between low- and high-RFI cattle. Plasma concentrations of insulin at the end of a test period were found to be higher in the steer progeny of high- compared with low-RFI parents (Richardson *et al.*, 2004). Nevertheless, similar circulating concentrations of insulin (Kolath *et al.*, 2006; Lawrence *et al.*, 2012) and insulin response to a glucose tolerance test (Fitzsimons *et al.*, 2014c) suggest no differences in insulin sensitivity or insulin-mediated body composition between cattle divergent for RFI.

To evaluate the relationship between RFI status and measures of body composition we conducted meta-analyses of studies that used growing beef cattle offered energy-dense diets. Although numerous individual studies have examined this relationship, the huge variation in reporting of results severely limited the number of studies that could be included in our meta-analyses. In relation to muscle accretion, we found no difference in either live animal ($n = 5$; $P = 0.36$) or carcass ($n = 8$; $P = 0.39$) measures between cattle of high- or low-RFI status. An additional meta-analysis was conducted to quantify the relationship between variation in RFI and ultrasonically measured back fat depth and again we failed to observe a difference ($P = 0.65$) between growing high- and low-RFI cattle (references for these meta-analyses in Supplementary Material S1). This suggests that RFI rank in growing cattle is not associated with final muscle area, carcass muscle area and change in back fat depth during the linear phase of the growth curve, typical of RFI test periods in many studies. These findings are in contrast to those of Berry and Crowley (2013) who reported a genetically based tendency for RFI status to be negatively correlated with muscularity and positively associated with body fat in the live

animal or in the carcass. Equivocation amongst literature reports is undoubtedly contributed to by variation between studies in the breed, gender and stage of physiological maturity of the cattle employed. In addition, while an explicit relationship between RFI status and body composition could not be established in our meta-analyses, the well-established influence of body fatness, in particular on key reproductive events (i.e. onset of puberty and resumption of *postpartum* ovarian cyclicity; Diskin and Kenny, 2014) must be borne in mind in any attempt to select animals for improved energetic efficiency. Indeed, the potential for antagonistic relationships amongst economically important traits is most appropriately catered for within the context of multi-trait economically weighted selection indices, the basis of beef cattle genetic improvement programmes, worldwide.

Maintenance requirements, mitochondrial function and stress physiology

Typically, total dietary energy intake required for body maintenance far exceeds 50% in adult cattle and in most cases is in excess of 40% in growing cattle consuming forage diets. The large energetic requirement of maintaining homeorhesis is contributed to by a number of physiological and biochemical processes, which may have implications for feed efficiency status, some of which are discussed below.

Mitochondrial function
Mitochondria are cellular organelles, responsible for approximately 90% of oxygen consumption (Bottje and Carstens, 2012). Consistent with this premise, the respiratory control ratio (indicative of the level of coupling between respiration and oxidative phosphorylation and in turn, the degree of efficiency of electron transfer) in *longissimus* muscle tissue was superior in low- RFI relative to high-RFI steers (Kolath *et al.*, 2006). However, using citrate synthase activity as an indicator of mitochondrial number and tissue samples from young beef bulls (provided from the study of Fitzsimons *et al.*, 2014a), we failed to observe a relationship between RFI status and mitochondrial number in either muscle or liver tissue (McKenna *et al.*, unpublished results).

However, Lancaster *et al.* (2014), using a protein assay conducted with hepatic bovine tissue have shown that, compared with feed efficient steers, ADP-control of oxidative phosphorylation is lower in their energetically inefficient counterparts. Studies investigating bovine hepatic mitochondrial function using cattle phenotypically divergent for RFI (Lancaster *et al.*, 2014) and steer progeny of sires divergent for RFI (Acetoze *et al.*, 2015) found that while RFI status did not affect state 2, 3 or 4 respiration rates or indices of proton leakage rates, acceptor control ratio (indicator of respiratory rate within the mitochondrion) was greater (Lancaster *et al.*, 2014) in low-RFI cattle. In addition, greater mitochondria complex I was found in lymphocytes of low- compared with high-RFI steers suggesting greater production of ATP in feed efficient cattle (Ramos and Kerley, 2013). At the cellular transcript level, the results of studies

which have examined differential mRNA expression of genes involved in oxidative phosphorylation in either muscle or liver tissue of beef cattle divergent for RFI, have been inconsistent (Kelly *et al.*, 2011; Fonseca *et al.*, 2015).

Stress physiology
There is some evidence for differences in the stress response between high- and low-RFI animals and this has led to speculation that this process may contribute to observed differences in energetic efficiency (Montanholi *et al.*, 2010). In a recent study from our own group, low-RFI Simmental heifers tended to have reduced sensitivity to the exogenous ACTH, suggesting that hypothalamic–pituitary–adrenal axis function may be related to RFI status in cattle (Kelly *et al.*, 2017). However, in another recent study investigating endocrinological responses to a corticotropin-releasing hormone challenge, Kelly *et al.* (2016) found no difference in systemic concentrations of cortisol between high- or low-RFI Limousin heifers. Munro *et al.* (2017) investigating the relationship between RFI and heart rate, found that low-RFI heifers had an increased heart rate in response to an acute stressor, however plasma cortisol was not measured in that study.

Maternal traits and fertility

Despite the fact that the greatest benefits of improved RFI may be realised in the cow herd when compared with growing cattle, there are relatively few studies that have examined the effect of RFI status on fertility and maternal productivity traits. Colostrum and milk yield are the principle factors influencing beef calf passive immunity and pre-weaning growth, respectively. In our own studies we have not established any association between RFI ranking and cow serum immunoglobulin concentration *prepartum*, colostrum yield or total Ig concentration in colostrum of beef cows (McGee and Drennan, 2006) or indeed subsequent measures of calf passive immunity (McGee and Drennan, 2006; Lawrence *et al.*, 2011). Although Montanholi *et al.* (2013b) reported a tendency for a positive effect of RFI status on colostrum specific gravity (an indicator of higher immunoglobulin), these authors failed to establish any relationship between RFI and colostrum protein, fat, lactose or total solids concentrations.

Residual feed intake ranking had no significant effect on milk yield of beef cows (McGee and Drennan, 2006; Lawrence *et al.*, 2011; Morris *et al.*, 2014). In terms of milk composition, Montanholi *et al.* (2013b) reported a negative relationship between RFI and milk lactose concentration ($r = -0.29$) in beef cows but no association with other milk constituents. Consistent with reported results on cow milk yield, calf pre-weaning growth was not associated with maternal status for RFI (Lawrence *et al.*, 2013; Morris *et al.*, 2014). Given that maternal weaning weight is representative of dam milk yield and, at a genetic level, Crowley *et al.* (2011) found no relationship between maternal weaning weight and RFI of growing males, these findings corroborate

the absence of a phenotypic association between cow RFI ranking and milk yield or progeny performance pre-weaning.

Calving difficulty contributes heavily to production losses and labour costs on beef farms. However, calving difficulty score was not found to differ between cows divergent for RFI (Basarab et al., 2011; Lawrence et al., 2011 and 2013; Fitzsimons et al., 2014b). There is some evidence, however, to indicate that perinatal calf mortality may be lower for more feed efficient cows (Basarab et al., 2007 and 2011), though more work is required on the relationship between RFI status and animal health and immunocompetence.

In terms of reproductive performance, no differences were found between high and low-RFI beef females with regard to pregnancy, calving and/or weaning rates (Basarab et al., 2007; Morris et al., 2014; Jones et al., 2016), although in other studies a lower pregnancy and calving rate (Basarab et al., 2011) and lower weaning rate (Copping et al., 2016; Hebart et al., 2016) was observed for low-RFI females. Donoghue et al. (2011) and Hebart et al. (2016) reported that low-RFI females calved later in the calving season than their high-RFI contemporaries; however, this was not evident in other studies (Morris et al., 2014). Crowley et al. (2011) reported a negative, but not statistically significant, genetic correlation ($r = -0.29$) between age at first calving and RFI status in beef cattle. The later calving date of low-RFI females recorded in some studies could be attributable to a delay in the onset of puberty (Shaffer et al., 2011), although age at puberty was not always different between RFI classifications (Basarab et al., 2011; Donoghue et al., 2011). The positive association between body fatness and the timing of onset of puberty and postpartum ovarian cyclicity has been well documented and has been proposed as a reason for delayed calving date in more efficient and often leaner animals. In the study of Basarab et al. (2011), when the DMI prediction model was adjusted for back fat thickness (and feeding event frequency), low-RFI heifers were found to be older at puberty than their less efficient contemporaries. Despite this, however, the above-mentioned adjustments negated the adverse effects of low-RFI on pregnancy rate, calving rate and the proportion of calves born in the first 28 days of the calving season. Indeed, Basarab et al. (2011) suggested that on-going selection for low-RFI within cohorts of heifers of mixed pubertal status may negatively impact long-term fertility in low-RFI heifers by favouring later-maturing animals that have not incurred the additional energy expenditure associated with sexual activity.

Bull fertility has a central role in herd productivity and is an important trait to include in genetic selection programmes for beef cattle. Certain studies have reported an unfavourable relationship between RFI status and some (Wang et al. 2012; Awda et al., 2013) but not all (Awda et al., 2013) estimates of semen quality. In addition, other studies have shown no effect of RFI rank on scrotal circumference, a measure of spermatogenic potential (Awda et al., 2013; Fontoura et al., 2015, Kowalski et al., 2017) or indeed systemic concentrations of testosterone (Kowalski et al., 2017). Within the context of multi-sire groups on pasture, Wang et al. (2012) concluded that there was no evidence for a detrimental effect of selection for improved feed efficiency on the reproductive performance of beef bulls. Similar to heifers (discussed above) the influence of factors such as fatness and sexual activity must be considered in any interpretation of the relationship between RFI status and age at onset of puberty in bulls.

Repeatability and genotype × environment interaction for residual feed intake

Clearly, if RFI is to be included as an economically important trait worthy of consideration in selection programmes, an animal's status for the trait must be repeatable across the various phases and physiological states of its productive life, as well as across different dietary regimens. High repeatability for a trait is also important in breeding animals where predictions of performance can only be made early in life. Furthermore, genotype × environment interactions are particularly relevant if estimates of genetic merit for improved productivity or feed efficiency are derived under conditions different from that under which progeny are reared (Berry and Crowley, 2013). Worldwide, performance testing of beef breed bulls is usually carried out using high-energy, concentrate-based diets, whereas the majority of beef cattle are largely produced on predominantly forage-based diets, often grazed pasture, which have very different intake characteristics (as discussed earlier).

Studies examining the repeatability of RFI in growing beef cattle offered the same diet across two 'separated' periods have found that RFI was moderately repeatable ($r = 0.62$, Kelly et al., 2010b; $r = 0.40$, Gomes et al., 2012) and had a moderate rank correlation of 0.52 in cattle offered the same diet across two 'consecutive' periods (Durunna et al., 2012). Similar findings were obtained by Herd et al. (2006) evaluating females post-weaning and subsequently as non-pregnant, non-lactating beef cows 4 to 4.5 years old. However, in commercial practice cattle are usually not offered the same diet throughout life and productive cows are usually pregnant and/or lactating. Nevertheless, moderate phenotypic correlations were reported between RFI measured in steers offered a grower diet and subsequently offered a finisher diet (Durunna et al., 2011; Cassady et al., 2016). Lawrence (2011) and Hafla et al. (2013) found that RFI status was correlated when measured in heifers offered a diet of forage and concentrates and subsequently in the same animals as cows offered a forage-only diet. Conversely, Black et al. (2013) using a similar animal model found no such relationship, though low-RFI weanlings did consume less feed as cows.

A number of studies have reported on the effect of RFI classification, when feed intake of female cattle was measured in confinement and subsequently, at pasture. Beef females previously ranked as divergent for RFI indoors offered a grass silage diet (Lawrence et al., 2012 and 2013) or hay (Meyer et al., 2008) did not differ in herbage intake when subsequently grazing pasture during first pregnancy (Lawrence et al., 2012), during gestation or late lactation (Meyer et al., 2008) or during lactation (Lawrence et al.,

2013). Similarly, Morris *et al.* (2014) reported no difference in herbage intake in grazing lactating beef heifers from high- and low-RFI selection lines. In contrast, Manafiazar *et al.* (2015) reported that heifers ranked as low-RFI in an outdoor drylot offered a barley silage-based diet had a lower intake of grazed herbage when subsequently measured as pregnant replacement heifers. Reasons for the discrepancies in DMI between the confined and grazing dietary phases in the majority of the aforementioned studies may be attributed to: (i) the re-ranking *per se* of animals for RFI over time (maturity); (ii) differences in diet type and thus, associated intake and digestion characteristics; (iii), changes in the physiological state of the animals and, finally, and perhaps most importantly (iv) the inherent difficulty in accurately quantifying herbage intake in grazing cattle (Lawrence *et al.*, 2012).

Together, the results of these studies suggest that RFI is a moderately repeatable trait across time (maturity), stages of production and different diet types in beef cattle. However, it is evident that some animal re-ranking occurs, suggesting the existence of a genotype × environment interaction for the trait.

Genetics of residual feed intake

The main obstacles to widespread adoption of feed efficiency in cattle breeding programmes are the large cost and technical difficulty associated with measuring the trait (Nielsen *et al.*, 2013). The advent of genomically assisted selection approaches, where genomic information is employed to aid the prediction of the breeding merit of an animal, should increase selection accuracy and accelerate genetic improvement (Berry *et al.*, 2016). From their meta-analysis, Berry and Crowley (2013) reported a pooled heritability for RFI in growing cattle of 0.33 (range of 0.07 to 0.62). Coupled with its considerable genetic variance (Crowley *et al.*, 2010), the RFI trait is likely to respond favourably to genomic selection. However, genomic prediction accuracy in beef cattle is still not sufficiently high to allow selection of candidates without an appropriate phenotypic measurement (Bolormaa *et al.*, 2013). The calculation of genomically informed estimated breeding values depends on the generation of a reference population where the trait of interest (i.e. feed efficiency) has already been measured and animals genotyped for appropriate genomic markers (Hayes *et al.*, 2009; Stothard *et al.*, 2015; Seabury *et al.*, 2017). Such a reference population does not currently exist in beef cattle (Fitzsimons *et al.*, 2017) and its assembly would have to overcome factors such as contrasting breeds, age and nutritional management of cohorts of cattle between, and even within, collaborating research groups.

At present, research on the genomic control of feed efficiency in cattle is focused on the identification of panels of genetic variants of biological significance to the trait (Lu *et al.*, 2013; Lindholm-Perry *et al.*, 2015; Fitzsimons *et al.*, 2017). However, if ultimately of benefit to industry, it is essential that these polymorphisms are sufficiently robust across breed, phase of development and dietary regimen.

A recent genome-wide association study (Seabury *et al.*, 2017) comparing quantitative trait loci (QTL) and utilising the Illumina Bovine HD (778K) and SNP50 assay platforms has reported QTLs associated with and influencing feed efficiency-related traits which could potentially be used for genomic selection. Furthermore, projects with the objective of combining international DNA sequence information, such as the Canadian Cattle Genome Project (Stothard *et al.*, 2015), aim to develop genomics-based tools to enhance the efficiency and sustainability of beef production. The focus of such collaborative projects should be on the identification of functional variants supported by imputation, where necessary, so that the association between these variants and traits of economic importance such as feed efficiency and related traits can be determined (Taylor *et al.*, 2017). Future success in breeding for improved feed efficiency in beef cattle will depend on the incorporation of such genetic information into national and international multi-trait genomic selection based breeding programmes.

Conclusion

This review has highlighted some of the many biological processes that may regulate inter-animal variation for feed efficiency. It is clear that expression of feed efficiency potential is multifaceted and will depend on the interaction of numerous biochemical pathways across a multitude of tissues and will also be highly dependent on the prevailing management regimen. Although numerous studies have examined RFI across a variety of breeds, genders and management systems there is still a distinct lack of published experimental information of sufficient depth to unravel the biological regulation of the trait. In particular, a paucity of data exists on the contribution of key processes including appetite control, gastrointestinal function as well as cellular energetics and metabolism. Interpretation of effects of RFI status on body composition are potentially impacted upon by stage of maturity, and deciphering these relationships will be important to sustain the dual goals of improved meat quality and reproductive efficiency. The RFI trait has been shown to be moderately repeatable across time (maturity), stages of production and different diets in beef cattle, at least in studies where animals were in confinement. There are relatively few studies, however, that have addressed the relationship between RFI status and productivity-related traits at pasture, a concept critical to the overall lifecycle of beef production systems. The difficulty in determining such relationships lies in the complexities of attaining precise and repeated or prolonged measures of feed intake at pasture. Sustained progress in improving the feed efficiency potential of beef cattle will rely, in the short to medium term on continued assembly of accurate feed intake and efficiency phenotypes and in the medium to longer term on the combination of these data with appropriate genotypic information, eventually circumventing the requirement for expensive and logistically difficult feed intake recording.

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Declaration of interest

None.

Ethics statement

None.

Software and data repository resources

None.

Supplementary material

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