

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

D. A. Kenny^{1†a}, C. Fitzsimons^{2a}, S. M. Waters¹ and M. McGee²

¹Animal and Bioscience Research Department, Animal & Grassland Research and Innovation Centre, Teagasc, Grange, Dunsany, Co. Meath, C15 PW93, Ireland;

²Livestock Systems Research Department, Animal & Grassland Research and Innovation Centre, Teagasc, Grange, Dunsany, Co. Meath, C15 PW93, Ireland

(Received 18 May 2017; Accepted 15 March 2018; First published online 21 May 2018)

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 (Saviotto *et al.*, 2014). Because the calculation of the RFI index forces it to be mathematically independent

^a These two authors contributed equally to this work.

[†] E-mail: david.kenny@teagasc.ie

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 \times 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 \times 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 (Saviotto *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 cattle¹

Studies	Animal type	Diet	Method	n	RFI group		Sig.	r ²
					High	Low		
Richardson <i>et al.</i> (1996)	Heifers/Bulls	Lucerne + concentrate	Alkanes	58	0.671	0.681	<0.10	–
Richardson <i>et al.</i> (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 <i>et al.</i> (2006)	Steers	HC	TFC	27	0.709	0.753	0.10	–0.33†
Krueger <i>et al.</i> (2009a)	Heifers	High roughage	AIA	152	0.735	0.762	<0.05	–0.51**
Cruz <i>et al.</i> (2010)	Steers	HC	Lignin	60	0.740	0.725	0.53	–
Lawrence <i>et al.</i> (2011)	Pregnant heifers	Grass silage	AIA	73	–	–	Ns	–
Lawrence <i>et al.</i> (2012)	Heifers	Grass silage + concentrate	AIA	18	0.567	0.582	Ns	–
Gomes <i>et al.</i> (2013)	Steers	HC	TFC	72	0.723	0.752	0.18	–
Lawrence <i>et al.</i> (2013)	Beef cows	Grass silage	AIA	39	0.700	0.690	0.74	–
Fitzsimons <i>et al.</i> (2013)	Heifers	Grass silage	AIA	22	0.730	0.730	0.83	–
Fitzsimons <i>et al.</i> (2014a)	Bulls	HC	AIA	67	0.720	0.740	0.41	–
Lines <i>et al.</i> (2014)	Heifers	Hay + concentrate	Titanium dioxide	16	0.683	0.684	Ns	–
McDonnell <i>et al.</i> (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.

¹Reference list for this table provided in Supplementary Material S1.

²r = correlation between RFI and DMD; †P < 0.10, *P < 0.05 and **P < 0.01.

³TMR (70 : 30 corn silage:concentrate on a dry matter basis).

⁴An 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 (CH₄) 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 CH₄ emissions (g/day), at least proportionate to their lower feed intake, however, the published literature does not support this expectation (Table 3). For example, CH₄ 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 CH₄ 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 CH₄ 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 cattle¹

Studies	Animal		RFI Group	pH	Lactate (mg/l)	NH ₃ (mg/l)	VFA (mM/l)	VFA			A:P
	type	Diet						Acetate ²	Propionate ²	Butyrate ²	
Guan <i>et al.</i> (2008)	Steers	HC	H	–	–	–	55.4 ^e	564	326	150 ^a	–
			L	–	–	–	96.7 ^d	544	259	60 ^b	–
Krueger <i>et al.</i> (2009a)	Heifers	High Roughage	H	–	–	–	–	Ns	H ^b > L ^a	Ns	H ^a < L ^b
			L	–	–	–	–	–	–	–	–
Krueger <i>et al.</i> (2009b)	Steers	HC	H	Ns	–	–	Ns	Ns	Ns	Ns	Ns
			L	–	–	–	–	–	–	–	–
Hernandez-Sanabria <i>et al.</i> (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 <i>et al.</i> (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 <i>et al.</i> (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 <i>et al.</i> (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 <i>et al.</i> (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 <i>et al.</i> (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 <i>et al.</i> (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

NH₃ = 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: $P < 0.10$).

¹Reference list for this table provided in Supplementary Material S1.

²Acetate, propionate and butyrate reported as mmol/mol of volatile fatty acid.

³NH₃ reported as millimolar (mM).

Table 3 Methane emissions and residual feed intake (RFI) in beef cattle¹

Studies	Animal model ²	Diet	Methodology	CH ₄	RFI group		
					High	Low	P-value
Nkrumah <i>et al.</i> (2006)	Phenotype study	High concentrate	Indirect calorimetry	g/day	129	126	0.04
				g/kg DM	14.9	11.3	0.04
Hegarty <i>et al.</i> (2007)	Selection lines	High concentrate	SF ₆	g/day	190	142	0.01
				g/kg DM	14.7	16.3	0.37
Jones <i>et al.</i> (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 <i>et al.</i> (2013)	Phenotype study	Grass silage	SF ₆	g/day	297	260	0.04
				g/kg DM	36	38	0.52
McDonnell <i>et al.</i> (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

CH₄, methane; DM = dry matter; SF₆ = sulphur hexafluoride tracer gas technique; OPFTIR = open path Fourier transform IR spectrophotometer technique; TMR = total mixed ration.

¹Reference list for this table provided in Supplementary Material S1.

²Animal model = phenotype study – cattle used were from a random population; selection lines – the progeny of cattle divergently bred and selected for RFI.

³No RFI × diet interaction was reported for this study.

⁴TMR (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 cattle¹

Studies	RFI group	Liver (kg)	Kidneys (kg)	GIT (kg)	Reticulo-rumen (kg)
Richardson <i>et al.</i> (2001)	H	–	–	15.9	–
	L	–	–	16.4	–
Basarab <i>et al.</i> (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 <i>et al.</i> (2009)	H	4.63 ^a	0.79 ^a	24.3 ^a	–
	L	4.16 ^b	0.67 ^b	21.8 ^b	–
Gomes <i>et al.</i> (2012)	H	4.78	–	18.9	–
	L	4.72	–	20.1	–
Bonilha <i>et al.</i> (2013)	H	4.58	0.77 ^a	25.0	–
	L	4.47	0.68 ^b	24.5	–
Fitzsimons <i>et al.</i> (2014a)	H	6.5	1.05	–	13.2 ^a
	L	6.2	1.04	–	12.1 ^b
Meale <i>et al.</i> , (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 ($P < 0.05$).

¹Reference list for this table provided in Supplementary Material S1.

²Entire 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 \times 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 \times 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 \times 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.

Acknowledgements

The authors gratefully acknowledge support from the Department of Agriculture, Food and the Marine, Research Stimulus Fund (Projects 13/S/519 and 05-224).

Declaration of interest

None.

Ethics statement

None.

Software and data repository resources

None.

Supplementary material

To view supplementary material for this article, please visit <https://doi.org/10.1017/S1751731118000976>

References

- Acetoze G, Weber KL, Ramsey JJ and Rossow HA 2015. Relationship between liver mitochondrial respiration and proton leak in low and high RFI steers from two lineages of RFI Angus bulls. *International Scholarly Research Notices* 2015, 1–5. article ID 194014.
- Allen MS 2014. Drives and limits to feed intake in ruminants. *Animal Production Science* 54, 1513–1524.
- Arthur PF, Archer JA, Johnston DJ, Herd RM, Richardson EC and Parnell PF 2001. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in Angus cattle. *Journal of Animal Science* 79, 2805–2811.
- Awda BJ, Miller SP, Montanholi YR, Vander Voort G, Caldwell T, Buhr MM and Swanson KC 2013. The relationship between feed efficiency traits and fertility in young beef bulls. *Canadian Journal of Animal Science* 93, 185–192.
- Basarab JA, Beauchemin KA, Baron VS, Ominski KH, Guan LL, Miller SP and Crowley JJ 2013. Reducing GHG emissions through genetic improvement for feed efficiency: effects on economically important traits and enteric methane production. *Animal* 7, 303–315.
- Basarab JA, Colazo MG, Ambrose DJ, Novak S, McCartney D and Baron VS 2011. Residual feed intake adjusted for backfat thickness and feeding frequency is independent of fertility in beef heifers. *Canadian Journal of Animal Science* 91, 573–584.
- Basarab JA, McCartney D, Okine EK and Baron VS 2007. Relationships between progeny residual feed intake and dam productivity traits. *Canadian Journal of Animal Science* 87, 489–502.
- Berry DP and Crowley JJ 2013. Cell biology symposium: genetics of feed efficiency in dairy and beef cattle. *Journal of Animal Science* 91, 1594–1613.
- Berry DP, Garcia JF and Garrick DJ 2016. Development and implementation of genomic predictions in beef cattle. *Animal Frontiers* 6, 32–38.
- Beef Improvement Federation 2010. Animal evaluation. In *Guidelines for uniform beef improvement programs* (ed. LV Cundiff, LD Van Vleck and WD Hohenboken), pp. 16–55. Beef Improvement Federation, North Carolina State University, Raleigh, NC, USA.
- Black TE, Bischoff KM, Mercadante VRG, Marquezini GHL, DiLorenzo N, Chase CC, Coleman SW, Maddock TD and Lamb GC 2013. Relationships among performance, residual feed intake, and temperament assessed in growing beef heifers and subsequently as 3-year-old, lactating beef cows. *Journal of Animal Science* 91, 2254–2263.
- Bolormaa S, Pryce JE, Kemper K, Savin K, Hayes BJ, Barendse W, Zhang Y, Reich CM, Mason BA, Bunch RJ, Harrison BE, Reverter A, Herd RM, Tier B, Graser HU and Goddard ME 2013. Accuracy of prediction of genomic breeding values for residual feed intake and carcass and meat quality traits in *Bos taurus*, *Bos indicus*, and composite beef cattle. *Journal of Animal Science* 91, 3088–3104.
- Bottje WG and Carstens GE 2012. Variation in metabolism: biological efficiency of energy production and utilization that affects feed efficiency. In *Feed efficiency in the beef industry* (ed. RA Hill), pp. 251–274. John Wiley & Sons, Inc., Ames, IA, USA.
- Carberry CA, Kenny DA, Han S, McCabe MS and Waters SM 2012. Effect of phenotypic residual feed intake and dietary forage content on the rumen microbial community of beef cattle. *Applied Environmental Microbiology* 78, 4949–4958.
- Carberry CA, Waters SM, Kenny DA and Creevey CJ 2014. Rumen methanogenic genotypes differ in abundance according to host residual feed intake phenotype and diet type. *Applied Environmental Microbiology* 80, 586–594.
- Cassady CJ, Felix TL, Beever JE and Shike DW 2016. Effects of timing and duration of test period and diet type on intake and feed efficiency of Charolais-sired cattle. *Journal of Animal Science* 94, 4748–4758.
- Connor EE 2015. Invited review: Improving feed efficiency in dairy production: challenges and possibilities. *Animal* 9, 395–408.
- Copping KJ, Accioly JM, Deland MPB, Edwards NJ, Graham JF, Hebart ML, Herd RM, Jones FM, Laurence M, Lee SJ, Speijers EJ and Pitchford WS 2016. Divergent genotypes for fatness or residual feed intake in Angus cattle. 3. Performance of mature cows. *Animal Production Science* 58, 55–66.
- Crowley JJ, Evans RD, Mc Hugh N, Kenny DA, McGee M, Crews DH and Berry DP 2011. Genetic relationships between feed efficiency in growing males and beef cow performance. *Journal of Animal Science* 89, 3372–3381.
- Crowley JJ, McGee M, Kenny DA, Crews DH, Evans RD and Berry DP 2010. Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance tested beef bulls. *Journal of Animal Science* 88, 885–894.
- Culbertson MM, Speidel SE, Peel RK, Cockrum RR, Thomas MG and Enns RM 2015. Optimum measurement period for evaluating feed intake traits in beef cattle. *Journal of Animal Science* 93, 2482–2487.
- Diskin MG and Kenny DA 2014. Optimising reproductive performance of beef cows and replacement heifers. *Animal* 8, 27–39.
- Donoghue KA, Arthur PF, Wilkins JF and Herd RM 2011. Onset of puberty and early-life reproduction in Angus females divergently selected for post-weaning residual feed intake. *Animal Production Science* 51, 183–190.
- Durruna ON, Colazo MG, Ambrose DJ, McCartney D, Baron VS and Basarab JA 2012. Evidence of residual feed intake reranking in crossbred replacement heifers. *Journal of Animal Science* 90, 734–741.
- Durruna ON, Mujibi FD, Goonewardene L, Okine EK, Basarab JA, Wang Z and Moore SS 2011. Feed efficiency differences and reranking in beef steers fed grower and finisher diets. *Journal of Animal Science* 89, 158–167.
- Fitzsimons C, Kenny DA, Fahey AG and McGee M 2013. Methane emissions, body composition and rumen fermentation traits of beef heifers differing in phenotypic residual feed intake. *Journal of Animal Science* 91, 5789–5800.
- Fitzsimons C, Kenny DA, Fahey AG and McGee M 2014b. Feeding behavior, rumen fermentation variables and body composition traits of pregnant beef cows differing in phenotypic residual feed intake. *Journal of Animal Science* 92, 2170–2181.
- Fitzsimons C, Kenny DA and McGee M 2014a. Visceral organ weights, digestion and carcass characteristics of beef bulls differing in residual feed intake offered a high concentrate diet. *Animal* 8, 949–959.
- Fitzsimons C, Kenny DA, Waters SM, Earley B and McGee M 2014c. Effects of phenotypic residual feed intake on response to an *in-vivo* glucose tolerance test and gene expression in the insulin signalling pathway in beef cattle. *Journal of Animal Science* 92, 4616–4631.
- Fitzsimons C, McGee M, Keogh K, Waters SM and Kenny DA 2017. Molecular physiology of feed efficiency in beef cattle. In *Biology of domestic animals* (ed. CG Scanes and RA Hill), pp. 120–163. CRC Press, Boca Raton, FL, USA.
- Fonseca L, Gimenez D, Mercadante M, Bonilha S, Ferro J, Baldi F, De Souza F and De Albuquerque L 2015. Expression of genes related to mitochondrial function in Nellore cattle divergently ranked on residual feed intake. *Molecular Biology Reports* 42, 1–7.
- Fontoura ABP, Montanholi YR, Diel de Amorim M, Foster RA, Chenier T and Miller SP 2015. Associations between feed efficiency, sexual maturity and fertility-related measures in young beef bulls. *Animal* 10, 96–105.
- Forbes JM 2005. Voluntary feed intake and diet selection. In *Quantitative aspects of ruminant digestion and metabolism* (ed. J Dijkstra, JM Forbes and J France), pp. 607–625. CAB International, University Press, Cambridge, UK.

- Gomes RC, Sainz RD, Silva SL, César MC, Bonin MN and Leme PR 2012. Feedlot performance, feed efficiency reranking, carcass traits, body composition, energy requirements, meat quality and calpain system activity in Nellore steers with low and high residual feed intake. *Livestock Science* 150, 265–273.
- Goonewardene LA, Okine E, Wang Z, Spaner D, Mir PS, Mir Z and Marx T 2004. Residual metabolizable energy intake and its association with diet and test duration. *Canadian Journal of Animal Science* 84, 291–295.
- Gregorini P, Gunter SA, Beck PA, Soder KJ and Tamminga S 2008. Review: The interaction of diurnal grazing pattern, ruminal metabolism, nutrient supply, and management in cattle. *Professional Animal Scientist* 24, 308–318.
- Hafila AN, Carstens GE, Forbes TDA, Tedeschi LO, Bailey JC, Walter JT and Johnson JR 2013. Relationships between postweaning residual feed intake in heifers and forage utilization, body composition, feeding behavior, physical activity and heart rate of pregnant beef females. *Journal of Animal Science* 91, 5353–5365.
- Hayes BJ, Bowman PJ, Chamberlain A and Goddard ME 2009. Invited review: Genomic selection in dairy cattle: progress and challenges. *Journal of Dairy Science* 92, 433–443.
- Hebart ML, Accioli JM, Copping KJ, Deland MPB, Herd RM, Jones FM, Laurence M, Lee SJ, Lines DS, Speijers J, Walmsley BJ and Pitchford WS 2016. Divergent breeding values for fatness or residual feed intake in Angus cattle. 5. Cow genotype affects feed efficiency and maternal productivity. *Animal Production Science* 58, 80–93.
- Hegarty RS, Goopy JP, Herd RM and McCorkell B 2007. Cattle selected for lower residual feed intake have reduced daily methane production. *Journal of Animal Science* 85, 1479–1486.
- Herd RM and Arthur PF 2009. Physiological basis for variation in residual feed intake. *Journal of Animal Science* 87, E64–E71.
- Herd RM, Arthur PF and Archer JA 2006. Repeatability of residual feed intake and interaction with level of nutrition in Angus cows. In Proceedings of the 26th Biennial Conference of the Australian Society of Animal Production. 10–14 July 2006, Short Communication no. 80 (ed. NR Adams, KP Croker, DR Lindsay, CA Anderson and LE Webb). Perth, WA, Australia.
- Herd RM, Dicker RW, Lee GJ, Johnston DJ, Hammond AJ and Oddy VH 2004. Steer growth and feed efficiency on pasture are favourably associated with genetic variation in sire net feed intake. *Animal Production in Australia* 25, 93–96.
- Jones FM, Accioli JM, Copping KJ, Deland MPB, Graham JF, Hebart ML, Herd RM, Laurence M, Lee SJ, Speijers J and Pitchford WS 2016. Divergent breeding values for fatness or residual feed intake in Angus cattle. 1. Pregnancy rates of heifers differed between fat lines and were affected by weight and fat. *Animal Production Science* 58, 33–42.
- Jones FM, Phillips FA, Naylor T and Mercer NB 2011. Methane emissions from grazing Angus beef cows selected for divergent residual feed intake. *Animal Feed Science and Technology* 166–167, 302–307.
- Kelly AK, Earley B, McGee M, Fahey AG and Kenny DA 2016. Endocrine and hematological responses of beef heifers divergently ranked for residual feed intake following a bovine corticotrophin-releasing hormone challenge. *Journal of Animal Science* 94, 1703–1711.
- Kelly AK, Lawrence P, Earley B, Kenny DA and McGee M 2017. Stress and immunological response of heifers divergently ranked for residual feed intake following an adrenocorticotropic hormone challenge. *Journal of Animal Science and Biotechnology* 8, 65.
- Kelly AK, McGee M, Crews DH, Fahey AG, Wylie AR and Kenny DA 2010a. Effect of divergence in residual feed intake on feeding behavior, blood metabolic variables, and body composition traits in growing beef heifers. *Journal of Animal Science* 88, 109–123.
- Kelly AK, McGee M, Crews DH, Sweeney T, Boland TM and Kenny DA 2010b. Repeatability of feed efficiency, carcass ultrasound, feeding behavior, and blood metabolic variables in finishing heifers divergently selected for residual feed intake. *Journal of Animal Science* 88, 3214–3225.
- Kelly AK, Waters SM, McGee M, Fonseca RG, Carberry C and Kenny DA 2011. mRNA expression of genes regulating oxidative phosphorylation in the muscle of beef cattle divergently ranked on residual feed intake. *Physiological Genomics* 43, 12–23.
- Kolath WH, Kerley MS, Golden JW and Keisler DH 2006. The relationship between mitochondrial function and residual feed intake in Angus steers. *Journal of Animal Science* 84, 861–865.
- Kong RSG, Liang G, Chen Y, Stothard P and Guan LL 2016. Transcriptome profiling of the rumen epithelium of beef cattle differing in residual feed intake. *BMC Genomics* 17, 592.
- Kowalski LH, Fernandes SR, DiLorenzo N, Moletta JL, Rossi P and de Freitas JA 2017. Residual feed intake and reproductive traits of growing Purunã bulls. *Journal of Animal Science* 95, 930–938.
- Lancaster PA, Carstens GE, Michal JJ, Brennan KM, Johnson KA and Davis ME 2014. Relationships between residual feed intake and hepatic mitochondrial function in growing beef cattle. *Journal of Animal Science* 92, 3134–3141.
- Lancaster PA, Carstens GE, Ribeiro FRB, Davis ME, Lyons JG and Welsh TH 2008. Effects of divergent selection for serum insulin-like growth factor-I concentration on performance, feed efficiency, and ultrasound measures of carcass composition traits in Angus bulls and heifers. *Journal of Animal Science* 86, 2862–2871.
- Lawrence P 2011. The effect of divergent selection for residual feed intake on the productivity of beef suckler cows and their progeny. PhD thesis, University College Dublin, Dublin, Ireland.
- Lawrence P, Kenny DA, Earley B, Crews DH and McGee M 2011. Grass silage intake, rumen and blood variables, ultrasonic and body measurements, feeding behavior and activity in pregnant beef heifers differing in phenotypic residual feed intake. *Journal of Animal Science* 89, 3248–3261.
- Lawrence P, Kenny DA, Earley B and McGee M 2012. Grazed grass herbage intake and performance of beef heifers with predetermined phenotypic residual feed intake classification. *Animal* 6, 1648–1661.
- Lawrence P, Kenny DA, Earley B and McGee M 2013. Intake of conserved and grazed grass and performance traits in beef suckler cows differing in phenotypic residual feed intake. *Livestock Science* 152, 154–166.
- Lindholm-Perry AK, Kuehn LA, Freetly HC and Snelling WM 2015. Genetic markers that influence feed efficiency phenotypes also affect cattle temperament as measured by flight speed. *Animal Genetics* 46, 60–64.
- Lu D, Sargolzaei M, Li C, Abo-Ismael M, Vander Voort G, Wang Z, Plastow G, Moore S and Miller SP 2013. Association analysis for feed efficiency traits in beef cattle using preserved haplotypes. *Genome* 56, 586–591.
- Manafiazar G, Basarab JA, Baron VS, McKeown L, Doce RR, Swift M, Undi M, Wittenberg K and Ominski K 2015. Effect of post-weaning residual feed intake classification on grazed grass intake and performance in pregnant beef heifers. *Canadian Journal of Animal Science* 95, 369–381.
- Manafiazar G, Basarab JA, McKeown L, Stewart-Smith J, Baron V, MacNeil MD and Plastow G 2017. Optimizing feed intake recording and feed efficiency estimation to increase the rate of genetic gain for feed efficiency in beef cattle. *Canadian Journal of Animal Science* 97, 456–465.
- Mao F, Chen L, Vinsky M, Okine E, Wang Z, Basarab J, Crews DH and Li C 2013. Phenotypic and genetic relationships of feed efficiency with growth performance, ultrasound, and carcass merit traits in Angus and Charolais steers. *Journal of Animal Science* 91, 2067–2076.
- McCann JC, Wiley LM, Forbes TD, Rouquette FM and Tedeschi LO 2014. Relationship between the rumen microbiome and residual feed intake-efficiency of Brahman bulls stocked on Bermudagrass pastures. *Plos One* 9, e91864.
- McDonnell RP, Hart KJ, Boland TM, Kelly AK, McGee M and Kenny DA 2016. Effect of divergence in phenotypic residual feed intake on methane emissions, ruminal fermentation, and apparent whole-tract digestibility of beef heifers across three contrasting diets. *Journal of Animal Science* 94, 1179–1193.
- McGee M and Drennan MJ 2006. Relationships between residual feed intake and maternal productivity and metabolic traits of beef suckler cows. In Proceedings of the Agricultural Research Forum, 15–16 March, Tullamore, Ireland, p. 100.
- McGee M, Ramirez JA, Carstens GE, Price WJ, Hall JB and Hill RA 2014. Relationships of feeding behaviors with efficiency in RFI-divergent Japanese Black cattle. *Journal of Animal Science* 92, 3580–3590.
- Meyer AM, Hess BW, Paisley SI, Du M and Caton JS 2014. Small intestinal growth measures are correlated with feed efficiency in market weight cattle, despite minimal effects of maternal nutrition during early to midgestation. *Journal of Animal Science* 92, 3855–3867.
- Meyer AM, Kerley MS and Kallenbach RL 2008. The effect of residual feed intake classification on forage intake by grazing beef cows. *Journal of Animal Science* 86, 2670–2679.
- Montanholi Y, Fontoura A, Swanson K, Coomber B, Yamashiro S and Miller S 2013a. Small intestine histomorphometry of beef cattle with divergent feed efficiency. *Acta Veterinaria Scandinavica* 55, 9.

- Montanholi YR, Lam S, Peripolli V, Vander Voort G and Miller SP 2013b. Short Communication: Associations between chemical composition and physical properties of milk and colostrum with feed efficiency in beef cows. *Canadian Journal of Animal Science* 93, 487–492.
- Montanholi YR, Swanson KC, Palme R, Schenkel FS, McBride BW, Lu D and Miller SP 2010. Assessing feed efficiency in beef steers through feeding behavior, infrared thermography and glucocorticoids. *Animal* 4, 692–701.
- Morris ST, Chan FY, Lopez-Villalobos N, Kenyon PR, Garrick DJ and Blair HT 2014. Growth, feed intake and maternal performance of Angus heifers from high and low feed efficiency selection lines. *Animal Production Science* 54, 1428–1431.
- Munro JC, Schenkel FS, Physick-Sheard PW, Fontoura ABP, Miller SP, Tennessen T and Montanholi YR 2017. Associations of acute stress and overnight heart rate with feed efficiency in beef heifers. *Animal* 11, 452–460.
- Myer PR, Smith TPL, Wells JE, Kuehn LA and Freetly HC 2015. Rumen microbiome from steers differing in feed efficiency. *PLOS ONE* 10, e0129174.
- Nascimento CF, Branco RH, Bonilha SFM, Cyrillo JNS, Negrão JA and Mercadante MEZ 2015. Residual feed intake and blood variables in young Nelore cattle. *Journal of Animal Science* 93, 1318–1326.
- Nielsen MK, MacNeil MD, Dekkers JCM, Crews DH, Rathje TA, Enns RM and Weaber RL 2013. Review: Life-cycle, total-industry genetic improvement of feed efficiency in beef cattle: Blueprint for the Beef Improvement Federation. *Professional Animal Scientist* 29, 559–565.
- Nkrumah JD, Okine EK, Mathison GW, Schmid K, Li C, Basarab JA, Price MA, Wang Z and Moore SS 2006. Relationships of feedlot feed efficiency, performance, and feeding behavior with metabolic rate, methane production, and energy partitioning in beef cattle. *Journal of Animal Science* 84, 145–153.
- Paradis F, Yue S, Grant JR, Stothard P, Basarab JA and Fitzsimmons C 2015. Transcriptomic analysis by RNA sequencing reveals that hepatic interferon-induced genes may be associated with feed efficiency in beef heifers. *Journal of Animal Science* 93, 3331–3341.
- Perkins SD, Key CN, Garrett CF, Foradori CD, Bratcher CL, Kriese-Anderson LA and Brandebourg TD 2014. Residual feed intake studies in Angus-sired cattle reveal a potential role for hypothalamic gene expression in regulating feed efficiency. *Journal of Animal Science* 92, 549–560.
- Pickering NK, Oddy VH, Basarab J, Cammack K, Hayes B, Hegarty RS, Lassen J, McEwan JC, Miller S, Pinares-Patiño CS and de Haas Y 2015. Animal board invited review: genetic possibilities to reduce enteric methane emissions from ruminants. *Animal* 9, 1431–1440.
- Ramos MH and Kerley MS 2013. Mitochondrial complex I protein differs among residual feed intake phenotype in beef cattle. *Journal of Animal Science* 91, 3299–3304.
- Richardson EC, Herd RM, Archer JA and Arthur PF 2004. Metabolic differences in Angus steers divergently selected for residual feed intake. *Australian Journal of Experimental Agriculture* 44, 441–452.
- Robinson DL and Oddy VH 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle. *Livestock Production Science* 90, 255–270.
- Saviotto D, Berry DP and Friggens NC 2014. Towards an improved estimation of the biological components of residual feed intake in growing cattle. *Journal of Animal Science* 92, 467–476.
- Seabury CM, Oldeschulte DL, Saatchi M, Beever JE, Decker JE, Halley YA, Bhattarai EK, Molaei M, Freetly HC, Hansen SL, Yampara-Iquise H, Johnson KA, Kerley MS, Kim JW, Loy DD, Marques E, Neibergs HL, Schnabel RD, Shike DW, Spangler ML, Weaber RL, Garrick DJ and Taylor JF 2017. Genome-wide association study for feed efficiency and growth traits in U.S. beef cattle. *BMC Genomics* 18, 386.
- Serão N, Gonzalez-Pena D, Beever J, Faulkner D, Southey B and Rodriguez-Zas S 2013. Single nucleotide polymorphisms and haplotypes associated with feed efficiency in beef cattle. *BMC Genetics* 14, 94.
- Shabat SKB, Sasson G, Doron-Faigenboim A, Durman T, Yaacoby S, Berg Miller ME, White BA, Shterzer N and Mizrahi I 2016. Specific microbiome-dependent mechanisms underlie the energy harvest efficiency of ruminants. *International Society for Microbial Ecology Journal* 10, 2958–2972.
- Shaffer KS, Turk P, Wagner WR and Felton EED 2011. Residual feed intake, body composition, and fertility in yearling beef heifers. *Journal of Animal Science* 89, 1028–1034.
- Stothard P, Liao X, Arantes AS, De Pauw M, Coros C, Plastow GS, Sargolzaei M, Crowley JJ, Basarab JA, Schenkel F, Moore S and Miller SP 2015. A large and diverse collection of bovine genome sequences from the Canadian Cattle Genome Project. *GigaScience* 4, 49.
- Taylor JF, Beever JE, Decker JE, Freetly HC, Garrick DJ, Hansen SL, Johnson KA, Kerley MS, Loy DD, Neibergs HL, Saatchi M, Schnabel RD, Seabury CM, Shike DW, Spangler ML and Weaber RL 2017. The genetic improvement of feed efficiency in beef cattle. *Journal of Animal Science* 95, 161.
- Wang Z, Colazo MG, Basarab JA, Goonewardene LA, Ambrose DJ, Marques E, Plastow G, Miller SP and Moore SS 2012. Impact of selection for residual feed intake on breeding soundness and reproductive performance of bulls on pasture-based multisire mating. *Journal of Animal Science* 90, 2963–2969.
- Wang Z, Nkrumah JD, Li C, Basarab JA, Goonewardene LA, Okine EK, Crews DH and Moore SS 2006. Test duration for growth, feed intake, and feed efficiency in beef cattle using the GrowSafe System. *Journal of Animal Science* 84, 2289–2298.
- Welch CM, Thornton KJ, Murdoch GK, Chapalamadugu KC, Schneider CS, Ahola JK, Hall JB, Price WJ and Hill RA 2013. An examination of the association of serum IGF-I concentration, potential candidate genes, and fiber type composition with variation in residual feed intake in progeny of Red Angus sires divergent for maintenance energy EPD. *Journal of Animal Science* 91, 5626–5636.