

Biological basis for variation in energetic efficiency of beef cattle

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Introduction

Substantial improvements in the efficiency of poultry and livestock meat-production systems have been achieved in the past 50 years. In comparing the performance of broilers from a 1957 random-bred strain with a modern commercial strain while fed diets typical for each time period, Havenstein et al. (2003) found that modern broilers required one-third less time (32 vs 101 days), and 3-fold less feed (1.47 vs 4.42 feed:gain ratio) to reach a similar market weight of 4 pounds than 1957 broilers. They concluded that 85 to 90% of these production efficiency gains were due to genetic selection, whereas the other 10 to 15% was due to improvements in nutrition. Total U.S. production of beef has doubled in the past 50 years, from 13.2 to about 27 billion pounds even though today's beef cow inventory is roughly the same as it was in 1955. Production efficiency has increased more than 80% from 137 to over 250 lb of beef per total cow inventory (Elam and Preston, 2004). Most of these production efficiency gains were realized through the use of grain-feeding production systems, adoption of nutrition, reproductive and pharmaceutical-based technologies, and the application of crossbreeding and selection programs that focused on output traits. In contrast to the poultry industry, beef productivity gains have been achieved in the absence of direct selection to improve feed efficiency. Indeed there is little evidence to indicate that genetic merit for feed efficiency or maintenance energy requirements have been favorably altered in the past 50 years (Archer et al., 1999; Johnson et al., 2003).

While considerable genetic variation both among and within beef cattle populations is known to exist for feed efficiency, the absence of genetic progress is not surprising given the industry's focus on output traits, inconsistent selection goals, cost of measuring feed intake and the complex interactions that exist between various biotypes and production environments used to produce beef. The lack of an appropriate trait for use in selection programs has also curtailed genetic progress in feed efficiency. Residual feed intake (RFI) is a feed efficiency trait that quantifies inter-animal variation in feed intake beyond that expected to meet energy requirements for maintenance and production—efficient animals are those that eat less than expected for a given body weight and level of production. Unlike ratio-based efficiency traits (e.g., feed:gain) that are highly influenced by growth and maturity patterns, RFI is phenotypically independent of the production traits used to compute expected intake so that favorable selection for RFI will improve feed efficiency with minimal affects on growth or mature size. Consequently, RFI better reflects inherent variation in metabolic processes associated with inter-animal differences in net feed efficiency rather than level of production. In growing beef cattle, variation in RFI has been linked to differences in heat production, methane production, composition of gain and digestibility demonstrating that numerous biological processes are responsible for genetic variation in RFI. While our understanding of RFI in growing cattle has advanced in recent years, we have limited knowledge about the associations between RFI in growing calves and biological

efficiency of mature cows. Further, we have limited knowledge regarding the influence of diet quality or stage of growth on genetic rank of animals for RFI. A more complete understanding the biological mechanisms responsible for inter-animal variation in RFI will provide insight into these questions, and will help drive the search for indicator traits and major genes associated with RFI in order to more cost-effectively identify cattle with favorable phenotypes for feed efficiency.

Genetic Variation in Feed Efficiency

Regulation of feed intake and efficiency of feed utilization by animals involves a complex set of biological processes and metabolic pathways, which can be influenced by numerous management and environmental factors. Moreover, feed intake is highly correlated in a positive manner with animal size and productivity, such that single-trait selection for increased growth will lead to higher feed intakes and maintenance energy requirements (Herd et al., 1991; Almeida et al., 2007). Similarly, single-trait selection for lower feed intake will reduce genetic merit for growth resulting in undesirable affects on productivity. Most of the early research that focused on the genetics of feed efficiency in cattle focused on ratio-based traits like feed conversion ratio (**FCR**; feed:gain ratio), which is moderately heritable (Crews 2005). Feed conversion ratio is strongly correlated ($r_g > -0.50$) with growth traits so that favorable selection for FCR in cattle will increase genetic merit for growth and mature size of breeding females (Archer et al., 2002; Herd and Bishop, 2000).

An alternative approach to measuring feed efficiency involves partitioning feed inputs into maintenance and production components. Linear regression methods can be used to compute expected feed intake based on average weight and gain on test, and the difference between actual and expected feed intake defined as RFI. Studies across multiple species have generally found that 60 to 80% of the inter-animal variation in feed intake is accounted for by differences in BW and level of production, which means that RFI typically accounts for approximately 20 to 40% of the phenotypic variation in feed intake. Residual feed intake has been shown to be moderately heritable in laying hens, growing pigs and growing beef cattle. With a few exceptions, RFI has been shown to be genetically independent of BW and level of production. Thus, in selection studies with hens (Luiting and Urf, 1991), pigs (Cai et al., 2008) and beef cattle (Arthur et al., 2001b), progeny from parents divergently selected for RFI had substantial differences in feed intake, but similar BW and production. These studies indicate that selection for low RFI will lead to reductions in feed inputs without compromising level of production, thereby improving feed efficiency.

Biological Basis for Variation in RFI

Residual feed intake is a feed efficiency trait that quantifies the deviation in feed energy intake above or below the energy requirements for maintenance and production derived for a contemporary group of animals of similar biotype and management. Since RFI is phenotypically independent of body weight and level of production, RFI better reflects inherent inter-animal variation in biological processes associated with feed efficiency, such as nutrient digestion, body composition, heat increment of feeding, or

energy expenditures associated with basal metabolism, physical activity and thermoregulation. Using slaughter-balance technique, Basarab et al. (2003) found that heat production was 10% higher and proportional liver mass (g/kg empty body weight) 7% heavier in steers with high compared to low RFI phenotypes. Nkrumah et al. (2006) measured heat production of steers with divergent phenotypes for RFI using indirect calorimetry, and found that steers with low RFI produced 21% less heat than steers with high RFI. In adult hens (Gabarrou et al., 1998) that were divergently selected for RFI over multiple generations, birds selected for high RFI consumed 48% more feed and had 32% higher total energy expenditures than those selected for low RFI. These studies demonstrate that variation in whole-animal energy expenditure contributes to observed differences in RFI. Richardson and Herd (2004) summarized results from several studies conducted with steer progeny from a single generation of divergent selection for RFI. They estimated that approximately one-third of the biological variation in RFI of these calves could be explained by differences in digestion (10%), heat increment (9%), composition of gain (5%) and activity (5%), and surmised that the remaining variation in RFI was related to differences in protein turnover, stress and tissue metabolism (37%) and differences in cellular energy expenditures such as ion pumping and mitochondrial proton leakage (27%).

Inter-animal variation in total energy expenditures by animals that have similar biotype and management backgrounds may arise from a host of cellular energy-consuming processes. Possible physiological processes suggested to account for variation in energy expenditures include ion pumping (Na⁺/K⁺ATPase), mitochondrial proton leak, thyroid hormones, leptin, IGF-1, lipid metabolism enzymes or sympathetic activity (Johnson et al., 2003). Of these physiological processes, it has been estimated that mitochondrial proton leak, ion pumping associated with Na⁺/K⁺ATPase, and protein turnover each contribute approximately 20% to the total inter-animal variation in basal energy expenditures (Rolfe and Brown, 1997; Ramsey et al., 2000). Mitochondria are the “energy powerhouse” of cells responsible for capturing over 90% of the energy in the form of adenosine triphosphate (ATP). Oxidation of fuel substrates (e.g., glucose, propionate) generates reducing equivalents (e.g., NADH) that feed into the electron transport chain (ETC), which in turn pumps protons into the intermembrane space of mitochondria. The resulting protomotive force created by the ETC then drives the activity of an enzyme that produces ATP. Occasionally this protomotive force is uncoupled from oxidative phosphorylation, and protons “leak” into the mitochondrial matrix to generate heat rather than ATP. Harper et al. (2002) concluded that approximately 26 and 52% of variation in basal energy expenditures are related to inter-animal differences in proton-leak-dependent O₂ consumption in liver and skeletal muscle tissues, respectively. Thus, variation in mitochondrial proton leak can be a major contributor to variation in whole-animal energy expenditures.

Using broilers with divergent phenotypes for gain:feed ratios, Bottje (2002) found that respiratory-chain coupling of muscle mitochondria was higher in broilers with high gain:feed (more efficient) than broilers with low gain:feed ratios. In mice divergently selected for heat loss, McDonald and Nielsen (2008) presented evidence that mitochondrial efficiency was enhanced by selection for low heat loss (more efficient).

Kolath et al. (2006) and Lancaster et al. (2007) assessed mitochondrial function in calves with divergent phenotypes for RFI. Calves with low RFI had higher respiratory-chain coupling in muscle mitochondria (Kolath et al., 2006) and liver mitochondria (Lancaster et al., 2007) compared to calves with high RFI. However, there was no evidence from these studies to indicate that differences in mitochondrial proton leak contributed to observed variation in RFI. Bottje et al. (2006) found that site-specific defects in the ETC of mitochondria that induce electron leak and protein oxidation can also contribute to observed differences in feed efficiency of broilers. Although, Kolath et al. (2006) did not find similar differences, mitochondria from low RFI calves had more rapid uptake of oxygen than calves from high RFI calves. Recent research findings from Kerley's laboratory indicate that the concentrations of mitochondrial proteins in the ETC, specifically complex I and III, are associated with observed differences in RFI of growing calves. The ratio of mitochondrial complex I to III was found to be 1.3-fold higher in calves with low RFI compared to calves with high RFI. Interestingly, the magnitude difference in feed intake and feed:gain ratio between calves with divergent RFI phenotypes was also 1.4 and 1.3-fold different, respectively, suggesting that this measure of mitochondrial efficiency may be predictive of observed differences in RFI. These results suggest that more low RFI calves have mitochondria that possess higher respiratory-chain coupling that are capable of more rapid rates of oxidative phosphorylation than mitochondria from inefficient animals.

Body Composition. Differences in body composition may also contribute to variation in RFI because lean tissue requires less energy per unit of gain than fat, due to a lower energy density as protein, water and mineral compared to fat (1.24 vs 9.39 kcal/g). However, the partial efficiency of metabolizable energy utilization to deposit protein is actually lower and more variable compared to the efficiency of fat tissue deposition due to higher rates of protein turnover. This is especially true in non-carcass tissues like visceral organs (e.g., liver, heart). In Angus bulls fed moderate-energy diets, Lancaster et al. (2009) found weak positive correlations between RFI and final ultrasound ribfat depth, such that more efficient bulls were leaner. Similarly, Arthur et al. (2001) and Schenkel et al. (2004) reported weak positive correlations between RFI and carcass fat traits in growing bulls. Slightly higher positive correlations between RFI and carcass fat traits have been reported in finishing steers (Basarab et al., 2003; Nkrumah et al., 2004). Robinson and Oddy (2004) reported strong genetic correlations between RFI and rib (0.48) and rump fat (0.72) in yearling steers fed a finishing diet. These data suggest that differences in carcass composition may account for more of the variation in RFI of cattle that are fed high-energy diets than cattle fed low-energy diets. Lancaster et al. (2009) found that variation in carcass ultrasound traits accounted for 9% of the variation in RFI, which is similar to what Basarab et al. (2003) in feedlot steers. Richardson and Herd (2004) concluded that individual animal variation in carcass composition explained only 5% of the variation in RFI of Angus cattle fed a pelleted alfalfa-based diet. Differences in energy expenditures associated with growth of visceral organs such as liver, gastrointestinal tract and heart can also contribute to observed differences in RFI as the metabolic activity of these tissues is much higher compared to carcass tissues. Basarab et al. (2003) found that steers with low RFI steers had 8% lower liver weights and total gastrointestinal tract than steers with high RFI. Ribeiro et

al. (2007) also reported that rumen weights were slightly lighter in low RFI Angus calves. However, Richardson et al. (2001) found that the proportional weights of visceral organs were similar in steer progeny from parents divergently selected for RFI. More research is warranted to determine if differences in proportional visceral organ growth accounts for significant variation in RFI.

Activity-Related Energy Expenditures. In cattle, the energetic costs associated with eating, chewing and ruminating can account for 10 to 33% of the total metabolizable energy derived from forages (Susenbeth et al., 2003). Energy expenditures associated with consuming feed are strongly related to the amount of time spent eating, but minimally affected by ingestion rate (feed consumed per unit time). Thus, differences in time spent eating and frequency of meals consumed may contribute to variation in RFI due to differences in energy expenditures related to feeding activities as well as activities such as standing and walking that are associated with consuming feed. In pigs, de Haer et al. (1993) found that daily time spent eating and frequency of bunk visits was positively correlated with RFI, but not feed:gain ratio. Lancaster et al. (2009) also found that RFI, but not feed:gain ratio, was positively correlated with meal duration and meal frequency. Bulls with low RFI spent 13% less time consuming meals and consumed 11% fewer meals per day, but consumed feed at a similar rate (lb per minute) compared with bulls with high RFI phenotypes. The variation in feeding activities associated with meal duration and frequency accounted for 35% of the variation in feed intake that was not attributed to BW, ADG and carcass composition. Likewise, variation in energy expenditures associated with physical activity (lying vs. standing, locomotion) may also contribute to variation in RFI. In cattle, Susenbeth et al. (1998) found that total energy expenditure was positively correlated with time spent standing, and that energy expenditures were 19% greater when cattle were standing compared with lying. Based on pedometer measurements in cattle, Herd et al. (2004) estimated that approximately 10% of the variation in RFI of growing cattle was due to differences in energy expenditures related variation in physical activity. Luiting et al. (1991) found that activity-related energy expenditures accounted for 29 to 54% of the difference in total energy expenditure between laying hens that were divergently selected for RFI. These results demonstrate that there may be merit in using feeding behavior traits as indicator traits for RFI.

Digestion. In calves with divergent RFI fed a high-grain diet, Nkrumah et al. (2006) found that methane energy losses were 28% lower and apparent digestibilities 6% higher in calves with low compared to high RFI. Richardson et al. (1996) also reported that apparent digestibilities tended to be 1% higher in calves with low RFI fed a pelleted roughage-based diet. They estimated that this difference in digestibility accounted for about 14% of the variation in RFI between the calves with divergent RFI phenotypes. Krueger et al. (2009) found that low-RFI Brangus heifers fed a roughage-based diet had 3% higher apparent digestibilities than Brangus heifers with high RFI. This difference in apparent digestibility accounted for approximately 19% of the variation in RFI. Based on observed differences in feed intake and differences in apparent digestibilities for nitrogen and phosphorus, Krueger et al. (2009) estimated that fecal excretion rates were 36 and 32% lower, respectively, in heifers with low RFI. Increases

in level of intake relative to maintenance are in some cases associated with depressions in apparent digestibility (NRC, 1996), which may account for some of the differences in digestibility between calves with divergent RFI. In the case of the Brangus study, this did not appear to be the case. In contrast to these studies with beef cattle, variation in RFI of poultry (Gabarrou et al., 1998) and pigs (de Haer et al., 1993) was not found to be associated with differences in digestibility, indicating that species differences exist in the biological mechanisms responsible for variation in RFI.

Conclusions

There is now considerable evidence that genetic variation exists in beef cattle for feed intake unaccounted for by differences in weight and growth rate—residual feed intake, thereby providing opportunities to improve profitability of beef production systems through reductions in feed inputs, with minimal influences on growth or mature size. In growing beef cattle, variation in RFI has been linked to differences in heat production, methane production, composition of gain and digestibility, indicating that cattle with more efficient RFI phenotypes are leaner, have lower maintenance energy requirements and methane emissions, and improved diet digestibility. A more complete understanding the biological processes that contribute to the inter-animal variation in RFI is need to more effectively exploit the genetic variation in feed efficiency that exist in beef cattle. Significant reductions in manure nitrogen and phosphorus excretion as well as in greenhouse gas emissions (methane, nitrous oxide) are achievable through selection for improved RFI.

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