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CELL BIOLOGY SYMPOSIUM:
Genetics of feed efficiency in dairy and beef cattle[1]

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ABSTRACT: Increasing food production for the growing human population off a constraining land base will require greater efficiency of production. Genetic improvement of feed efficiency in cattle, which is cumulative and permanent, is one likely vehicle to achieving efficiency gains. The objective of this review is to summarize genetic parameters for feed efficiency traits in dairy and beef cattle and also to address some of the misconceptions associated with feed efficiency in these sectors, as well as discuss the potential use of feed efficiency in breeding programs. A meta-analysis of up to 39 scientific publications in growing cattle clearly showed that genetic variation in feed efficiency exists with a pooled heritability for residual feed intake (RFI) and feed conversion efficiency of 0.33 ± 0.01 (range of 0.07 to 0.62) and 0.23 ± 0.01 (range of 0.06 to 0.46), respectively. Heritability estimates for feed efficiency in cows were lower; a meta-analysis of up to 11 estimates revealed heritability estimates for gross feed efficiency and RFI of 0.06 ± 0.010 and 0.04 ± 0.008, respectively. Meta-analysis of genetic correlations between feed intake, feed efficiency and other performance traits are presented, and selection index theory is used to calculate the proportion of genetic variation in feed intake that can be explained by easy to measure, and often already collected, data. A large proportion of the genetic variation in feed intake could be explained in both growing animals and lactating animals using up to 5 predictor traits, including BW, growth rate, milk yield, body composition, and linear type traits reflecting body size and muscularity. Knowledge of genetic merit for feed intake can be used, along with estimates of genetic merit for energy sinks, to calculate genetic merit for feed efficiency. Therefore, the marginal benefit of collecting actual feed intake data, using the genetic parameters used in this study, appears to be low. There is now sufficient information available to develop a road map on how best to direct research to ensure long-term food security for a growing human population. Gaps in knowledge are identified here, and possibilities to address these gaps are discussed.

Key words: beef, cattle, dairy, efficiency, genetics

INTRODUCTION

The world human population is increasing, and the demand for food in 2050 is expected to be approximately 70% greater than the demand in 2010 [Food and Agriculture Organization (**FAO**), 2009]. This increase in food demand can only be met by increased efficiency of food production, both animal and crop derived. Production efficiency may be described at a lifetime or herd level and may be defined as the saleable output per unit input, each appropriately weighted by their relative economic importance. Although feed efficiency, as currently defined, is not synonymous with production efficiency, it undoubtedly has a major role to play in increasing production from an ever-decreasing food-producing land base. Monitoring individual animal or herd feed efficiency has many uses other than as a breeding tool, including the evaluation of alternative management strategies (e.g., diet) or monitoring animal or herd health. Some measures of feed efficiency facilitate comparison across herds, which can be useful

for benchmarking. Measures of feed efficiency also have uses in research projects to help elucidate the possible factors contributing to differences in efficiency among animals. Achieving improved efficiency of production through genetic selection can be best achieved through a balanced breeding goal selecting on all traits influencing profitability simultaneously rather than selection on individual traits. This review summarizes the literature on feed efficiency, with particular reference to the genetics of feed efficiency in growing and lactating beef and dairy cattle. Misconceptions about feed efficiency, as well as the usefulness of feed efficiency in breeding strategies, are also addressed.

DEFINITIONS OF FEED EFFICIENCY

Feed efficiency has generally been defined in either growing animals or lactating animals, with most studies undertaken on the former.

Growing Animals

Feed efficiency variables can be loosely described as 1) ratio traits or 2) regression or residual traits. The time period of measurement required to obtain accurate estimates of feed efficiency has been discussed in detail elsewhere (Archer et al., 1997; Wang et al., 2006). Archer et al. (1997) concluded that a 70-d test period (after acclimatization), with animals weighed at least every 2 wk, was sufficient for a performance test for feed efficiency. Archer et al. (1997) also suggested that a shorter period of intake measurement of 35 d would result in little reranking of animals for genetic merit of feed efficiency but did result in considerable reranking of animals on phenotypic efficiency. Kearney et al. (2004) reported that using automatic weighing when animals were feeding could be used to reduce the duration of the test period to 56 d without affecting the precision of estimating ADG. It is prudent to mention the huge importance of accurate measures of the variables included in the definition of feed efficiency as discussed in detail by Robinson (2005).

Ratio Traits. Feed conversion ratio (**FCR**) was traditionally the most commonly used measure of feed efficiency in beef cattle and is generally defined as DMI divided by ADG. Animals with a lower FCR are reported to be more efficient.

Partial efficiency of growth (**PEG**; Kellner, 1909) is the efficiency of growth (i.e., the ratio of BW gain to feed) after accounting for energy requirements for maintenance and may be calculated as ADG divided by average feed intake less the feed intake required for maintenance. Maintenance requirements can be estimated using feed tables (e.g., NRC, 2001) and average

BW during the measurement period. However, neither FCR nor PEG assume differences exist among animals in maintenance efficiency, which is not necessarily true (see Archer et al., 1999); maintenance efficiency may be defined in growing animals as the ratio of BW to feed intake at zero BW change (Archer et al., 1999).

Although not a measure of feed efficiency per se, relative growth rate (**RGR**; Fitzhugh and Taylor, 1971) is nonetheless a measure of efficiency. Relative growth rate is defined as growth relative to instantaneous body size and is calculated as the logarithm of BW at the end of the test period less the logarithm of BW at the start of the test period divided by the days on test, all multiplied by 100. Also not a direct measure of feed efficiency per se, the Kleiber ratio (**KR**; Kleiber, 1961) is defined as ADG per unit metabolic BW. As ADG increases for the same metabolic BW, more growth is obtained without increasing maintenance energy cost. Although RGR and KR are not feed efficiency measures in their own right, they can be used as measures of feed efficiency if all animals on test are fed the same restricted diet.

Residual Traits. Residual feed intake (**RFI**), also known as net feed efficiency (Exton et al., 2000), is increasing in popularity as a measure of feed efficiency in growing animals. Residual feed intake may be defined as the difference between actual and predicted intake. Although Koch et al. (1963) is generally credited as the original proposer of RFI, Byerly (1941), in a technical article, actually previously described such a trait in laying hens. Residual feed intake, as proposed by Koch et al. (1963), is represented as the residuals from regression of intake on the various energy sinks. The regression model may be developed using a least squares regression approach. Alternatively, RFI may be generated using standard feed tables (e.g., NRC, 2001) or other information sources to allocate the energy demand for each of the energy sinks and subtract the total from the energy intake; this measure of RFI is sometimes termed "nutritional RFI". If calculated using a least squares approach, the average RFI of the study population will be zero, in line with the mathematical properties of least squares regression; this may not be the case if RFI is derived using feed tables. Furthermore, correlations between RFI and the energy sinks may exist unless RFI is generated using least squares regression. Nevertheless, irrespective of the method used to derive RFI, animals of more negative RFI are deemed to be more efficient during the test period; these animals eat less than expected.

Traditionally, the energy sinks used in the calculation of RFI in growing cattle were ADG and metabolic BW. Metabolic BW is usually defined as BW midway through the test period to the power of 0.75 (Nkrumah et al., 2007b; Crowley et al., 2010; Durunna et al., 2011a), although a value of 0.73 has also been used

(Arthur et al., 1996; Archer et al., 2002). Because of the differences among animals in the composition of ADG and the differential in energy demands of both fat and protein gain (Australian Feeding Standards, 1990), it is now recommended to include (ultrasound measures of) fat and protein (gain) as regressor variables in the multiple regression model when deriving RFI (Baker et al., 2006; Basarab et al., 2011). This is particularly important because, all else being equal, animals depositing proportionally more protein than fat for the same ADG will, on average, be deemed more efficient, and if all animals are of similar age, then this may result in long-term selection for later maturing animals, which may have implications for the overall efficiency of the cow herd. Crowley et al. (2010), comparing breeds of animals managed similarly and of similar age, reported poorer RFI in the early maturing breeds (i.e., Angus and Hereford) compared with the later maturing breeds (i.e., Charolais and Limousin), with the Simmental breed being intermediate; similar results were reported in performance-tested bulls in Canada (Schenkel et al., 2004). Therefore, all calculations of RFI should account for differences in the composition of growth, and this can be best achieved through ultrasound measures of body fat (in a 2-way interaction with BW change).

Including ultrasound fat depth in the multiple regression model for RFI, alongside ADG and metabolic BW, explains only an additional 0% to 7% of the variation in DMI (Basarab et al., 2003, 2011; Baker et al., 2006; Crews et al., 2006; Durunna et al., 2011a, 2012). A similar conclusion is evident from the weak phenotypic correlations between different measures of animal fat and RFI calculated without body composition in the multiple regression model for RFI (Robinson and Oddy, 2004; Bouquet et al., 2010; Crowley et al., 2011b). However, calculations based on the information provided by Hoque et al. (2006) showed that the proportion of phenotypic variance in feed intake increased from 32% with just ADG and BW to 45% when back fat was also included in the multiple regression model in Japanese Black cattle; Japanese Black cattle have been genetically selected for greater fat marbling.

Other energy sinks that may also be included in the RFI models include "activity," which can be approximated by frequency of feeding (Basarab et al., 2011; Durunna et al., 2012); only 3% to 4% additional variation in DMI is explained with feeding activity over and above that already accounted for by ADG, metabolic BW, and ultrasound body fat (Basarab et al., 2011; Durunna et al., 2012). A similar conclusion (2.9% increase in variation in DMI explained) was evident when the correlation matrix among a series of traits reported by Robinson and Oddy (2004) was used to quantify the increase in the variation in feed intake explained by both

feeding time and number of eating sessions over and above that explained by ADG, metabolic BW, plus rump fat estimated by ultrasound.

Koch et al. (1963) also proposed residual BW gain (**RG**) as an alternative measure of identifying interanimal variation in feed efficiency among growing animals. Using a similar principle to that for RFI, Koch et al. (1963) defined RG as the residuals from regression of ADG on feed intake and metabolic BW. Unlike RFI, where negative values are deemed to indicate more efficient animals, more positive RG values (i.e., animals growing faster than expected) are deemed to be more efficient.

Interestingly, there appears to be no recent studies that investigated whether or not nonlinear associations between feed intake and either BW or ADG existed; most studies appear to just assume linearity, which may be true in populations of animals performing similarly, but Koch et al. (1963) reported nonlinear associations in some populations. Biologically, however, nonlinear associations, especially in diverse populations and/or animals with inferior genetic merit for ADG, may exist; for example, ADG may eventually start to plateau as feed intake reaches relatively high levels. This is, however, more likely to be the case in older animals where an increased proportion of feed intake is used for maintenance rather than growth. Furthermore, in the equation to predict RFI, DMI is regressed on ADG, and metabolic BW is usually assumed to be the midtest BW estimated from regressing BW on day of test (Nkrumah et al., 2007b; Montanholi et al., 2009; Durunna et al., 2011a). However, the regression model,

$$\overline{FI} = \mu + b_1 ADG + b_2 MWT^{0.75} + e,$$

is intended to represent

$$\overline{FI} = \mu + b_1 \frac{\sum_{d=0}^{length}(WT_{d+1} - WT_d)}{length} + b_2 \frac{\sum_{d=0}^{length}(WT_d)^{0.75}}{length} + e,$$

where $\overline{FI}$ is mean feed intake during the test period, μ is the intercept of the model (which may also include a contemporary group effect), ADG is average daily BW gain, MWT is midtest BW, WT_d and WT_{d+1} are BW at days d and d + 1 of test, respectively, b_1 and b_2 are the regression coefficients on the first and second energy sink components, respectively, length is the length of the test, and e is the residual of the model (i.e., RFI). Although very similar, $MWT^{0.75}$ is, however, not mathematically equivalent to

$$\frac{\sum_{d=0}^{length}(WT_d)^{0.75}}{length}.$$

The phenotypic CV for feed intake in cattle varies from 9% to 14% (Nieuwhof et al., 1992; Herd and Bishop, 2000; Arthur et al., 2001a; Robinson and Oddy, 2004; Hoque et al., 2007; Bouquet et al., 2010; Crowley et al., 2010), and for growth rate it varies from 7% to 19% (Nieuwhof et al., 1992; Herd and Bishop, 2000; Arthur et al., 2001a; Robinson and Oddy, 2004; Hoque et al., 2007; Crowley et al., 2010). The CV for RFI or RG, when estimated using least squares regression, is undefined because the mean of the residuals is zero. However, when mean feed intake and mean ADG were used in the denominator for the calculation of the CV for RFI and RG, respectively, excluding the study of Nieuwhof et al. (1992), the range in CV for RFI was 4% to 8%, whereas the range for RG, which was always larger than for RFI, varied from 10% to 14% (Arthur et al., 2001a; Robinson and Oddy, 2004; Hoque et al., 2007; Bouquet et al., 2010; Crowley et al., 2010). The corresponding CV for RFI and RG in the study of Nieuwhof et al. (1992) were 11% and 6%, respectively. Therefore, considerable phenotypic variation exists in both RFI and RG, but the variation in RG seems to be, on average, greater than the variation in RFI.

There is nonetheless a perception that all of the variation in DMI not accounted for by the energy sinks is variation in feed efficiency or, equivalently, variation in ADG not accounted for by differences in feed intake and metabolic BW. However, differences in contemporary groups and other systematic environmental effects (e.g., age of animal) also contribute to the observed variation. For example, Crowley et al. (2010), using a model to calculate RFI, increased the proportion of variation in feed intake explained from 38% when the regression included only ADG and metabolic BW (calculated using the correlation matrix provided) to 72% when the regression model also included a contemporary group effect. Similarly, the proportion of variation in ADG explained by differences in feed intake and metabolic BW increased from 16% to 51% when contemporary group was also included in the statistical model (Crowley et al., 2010). Therefore, when quantifying the variation in any trait that is exploitable, it should be quantified after adjustment for fixed effects.

Berry and Crowley (2012) proposed an amalgamation of both RFI and RG to generate an alternative feed efficiency trait, residual intake and gain (**RIG**). They simply standardized both RFI and RG to have equal variances and then summed both standardized traits after inverting the sign of RFI so that a positive value was more favorable, and therefore, a positive RIG value was more favorable. Berry and Crowley (2012) cited the lack of a correlation between RFI and ADG as a possible reason for poor acceptance by industry of RFI because individual animals growing slowly may rank highly on RFI, yet these animals may not be desirable. In addition, the lack of a correlation between RG and feed intake creates a similar situation. By combining both RFI and RG into RIG, the independence between RIG and metabolic BW was maintained (i.e., mathematical properties of the least squares regression approach they used), but RIG was negatively phenotypically correlated with feed intake and positively phenotypically correlated with ADG (Berry and Crowley, 2012). This therefore reduces (but does not eliminate) the likelihood of a slower-growing animal ranking highly on RIG. Moreover, Berry and Crowley (2012) showed, using a simple example, that although animals ranking highly on RIG consumed more per day than animals from the sample population ranking highly on RFI, the total quantity of feed consumed during a hypothetical finishing period was less in the superior RIG animals compared with the superior RFI or RG animals.

Comparison of Definitions of Feed Efficiency in Growing Animals. The main disadvantage of the vast majority of feed efficiency traits described (exceptions are KR and RGR, which may actually be classified as "comparative growth traits" as opposed to "feed efficiency traits" per se) is the requirement for individual animal feed intake information. Accuracy of data recording for all traits is also important (Robinson, 2005), as is the case for all performance measures.

The main advantage of most of the ratio traits is their ease of calculation (once the appropriate performance measures are available) and interpretation, as well as the ability to easily compare feed efficiency statistics across populations. The main disadvantages, however, of the ratio traits are 1) an increase in the error variance as a proportion of the total variance in the statistical analysis may result (Lison, 1958), 2) strong correlations exist between the ratio trait and its component traits, and 3) no distinction is made between the energy used for separate functions. The expected responses to selection on ratio traits are difficult to ascertain (Gunsett, 1984) because of the poor statistical properties of ratio traits due to the antagonism between the desirable response in the numerator (i.e., decreased feed intake in the case of FCR) and the denominator (i.e., increased growth rate in the case of FCR) and the unknown relative selection pressures on each.

Residual feed intake and RG, in contrast, if calculated using least squares regression, are independent of their regressors. In general, RFI and RG are generated at the phenotypic level and are thus phenotypically independent of the regressors. However, this does not necessarily imply genetic independence (Kennedy et al., 1993). Although most estimates of genetic correlations between RFI derived from phenotypic regression and the regressor traits are not significantly different

from zero (Herd and Bishop, 2000; Arthur et al., 2001a; Barwick et al., 2009; Crowley et al., 2010), genetic regression is also possible (Kennedy et al., 1993) to ensure zero genetic covariances between RFI and the regressors. Estimation of RFI using genetic variance and covariances will avoid the possibility that identified genetic variance in RFI is a consequence of the genetic correlations between feed intake and the energy sinks (Veerkamp, 2002). Residual feed intake and RG-type traits can also be derived using restricted selection indexes (Eisen, 1977). Defining RFI (or RG) at the phenotypic level does, however, provide greater flexibility in that the regression can be fit within contemporary group to account for differences in diet and also to more easily account for nonlinear associations among variables.

A common misconception, relevant to all measures of feed efficiency but particularly cited for RFI, is that the unexplained feed intake or "residual" is assumed to represent true feed efficiency. In fact, this residual component can be due, in part, to random noise, such as measurement and prediction error, or due to inaccurate recording, feed losses, or bias in the regression coefficients for the respective regressors (Robinson, 2005). The contribution of error variation to the phenotypic variation is reflected in the heritability of the trait. However, there can also be heritable variation in measurement error; for example, there may be heritable variation in food spillage influencing measured feed intake or a heritable variable in the deposition site of adipose tissue that thereby influences "measurement error" in ultrasound measurement of back fat thickness. Although measurement error is a phenomenon experienced by (almost) all phenotypic measures, many definitions of feed efficiency, such as RFI, RG, and RIG, are an accumulation of these error terms, thereby exacerbating the problem. Explaining a large proportion of the variation in RFI with different animal measures (Robinson and Oddy, 2004; Basarab et al., 2011) has proven difficult, substantiating the fact that true residual noise is probably contributing to differences in RFI. Furthermore, where genetic independence between RFI and the regressor traits does not exist, a proportion of the heritability of RFI may simply be an artifact of "picking up" the genetic correlations (Veerkamp, 2002); the contribution to the heritability of RFI will be dictated by the strength of the genetic correlation between RFI and the regressor traits and can be derived using selection index methodology. To illustrate this, we simulated the daily DMI of the 2,605 performance-tested bulls analyzed by Crowley et al. (2010) from a normal distribution N(10.73, 1.52) with a phenotypic correlation structure with the observed ADG and BW, as reported by Crowley et al. (2010). Residual feed intake was calculated on the basis of a least squares phenotypic regression on both ADG and metabolic BW, and

its variance components were estimated exactly as defined by Crowley et al. (2010). The heritability for RFI was 0.06 ± 0.03. The genetic correlations between the simulated RFI and ADG and metabolic BW were -0.12 and -0.22, respectively. Therefore, the observed heritability of RFI and similar traits must be interpreted with caution in the context of how RFI was computed.

One of the main disadvantages of the residual traits, compared with the aforementioned ratio traits, is the greater difficulty associated with calculating these traits. Once the data are available, ratio traits can easily be calculated, but residual traits must be calculated by individuals familiar with least squares regression unless feed tables are used. Using least squares approaches, residual traits cannot be calculated for a single animal and need at least as many animals as there are factors in the regression model. Wulfhorst et al. (2010), in their social assessment of perception of producers about RFI in the United States, concluded that "the RFI concept is complex and not readily understood when first encountered, even for trained scientists." Furthermore, if RFI is generated using least squares regression, comparing populations without access to the original data is not possible; this can, however, be overcome by predicting feed intake using regression coefficients from feed tables and using these to derive RFI or by publishing the regression coefficients from the least squares analysis. Therefore, to facilitate comparison of populations, all studies should report regression coefficients from their least squares prediction models used to generate RFI, and ideally, the units of measurement of the traits should be standardized. Alternatively, variance and covariance components between feed intake and the energy sinks should be presented, which will facilitate the calculation of different definitions of feed efficiency. It should be noted, however, that even with ratio traits, comparison of populations should be undertaken with caution, especially where differences in systematic environmental effects exists.

Lactating Animals

Defining feed efficiency in lactating animals is more complicated than defining feed efficiency in growing animals during the linear phase of growth because lactating cows undergo lactation cycles characterized by rapid catabolism of body reserves immediately postcalving, followed by anabolism of body reserves until next calving (Roche et al., 2009). Any proposed measure of feed efficiency in lactating animals must take note of the contribution of mobilization of body reserves to the energy supply of the animal. Not properly accounting for changes in body weight or BCS in the derivation of RFI is mathematically equivalent to energy balance (Veerkamp, 2002).

Ratio trait measures of feed efficiency used in lactating animals include milk production per unit intake (this trait is commonly referred to as feed conversion efficiency; Nieuwhof et al., 1992; Coleman et al., 2010; Prendiville et al., 2011; Vallimont et al., 2011), milk production per kilogram BW (Coleman et al., 2010; Prendiville et al., 2011), and intake per kilogram BW (Coleman et al., 2010; Prendiville et al., 2011). Although not a feed efficiency trait per se, the BW of a calf weaned relative to the BW of the cow is a commonly used measure of efficiency in beef production systems.

Coleman et al. (2010), in their derivation of feed efficiency in lactating Irish Holstein-Friesian dairy cows, applied similar mathematical procedures in defining RFI to those previously used in growing animals, but differences in body tissue mobilization were accounted for (as far as was possible). Coleman et al. (2010) defined RFI as the residuals from a least squares regression model that regressed daily DMI on daily milk yield, fat yield, protein yield, lactose yield, metabolic BW, BCS, and change in BW. They also included year as a fixed effect in the multiple regression model to remove temporal effects. Because the energy generated from a 1-kg loss in BW is less than the energy required for a 1-kg gain in BW (O'Mara, 2000). Coleman et al. (2010) applied piecewise regression to BW change in the RFI model to account for this phenomenon. Vallimont et al. (2011), in their model to define RFI, also included an interaction between BW and BCS change as well as days in milk; multicolinearity between variables should be monitored in other populations when such a large number of correlated variables are included in a multiple regression model. Veerkamp et al. (1995), in one of their definitions of RFI, also included interactions between BCS and BW as well as between BCS and BW change. When defining feed efficiency in lactating animals, it is important to measure BW and fatness regularly to be able to appropriately account for body tissue mobilization. For example, 2 lactating animals starting and ending a test period with the same BW and fatness level may actually have considerably different body tissue mobilization profiles, and this has implications for their energy use kinetics.

Analogous to the similarities in the definition of both RFI and RG in growing animals, Coleman et al. (2010) proposed an alternative definition of feed efficiency in lactating animals, which they termed residual solids production (**RSP**). Instead of this trait representing the residuals of a multiple regression model regressing DMI on energy sinks, RSP was represented by the residuals from a least squares model regressing milk solids production on the remaining energy sinks plus DMI. Residual solids production may be defined as the actual milk solids produced relative to expected solids production based on the feed intake of an individual animal and other energy sinks (e.g., maintenance, growth) or energy sources (e.g., body tissue mobilization). In contrast to RFI, positive RSP values are indicative of more feed efficient animals during the time period under investigation.

Comparison of Definitions of Feed Efficiency in Lactating Animals. Other than the aforementioned disadvantages of ratio traits (e.g., difficult to predict response to selection and strong correlations with component traits), the ratio traits in lactating cows take no cognizance of body tissue mobilization that may have implications for subsequent health and fertility (Roche et al., 2009). Residual feed intake and RSP in lactating animals, although measuring feed efficiency per se, does not accurately reflect production efficiency. Production efficiency here may be used to describe output per unit input or simply profit over the lifetime of the animal. This is because the models used to calculate both residual traits do not account for the partitioning of energy into the individual components, some of which are more economically important (e.g., milk fat and protein yield) than others (metabolic BW). For example, if the regression coefficient from regressing DMI on metabolic BW in the multiple regression used by Coleman et al. (2010) in their definition of RFI (multiple regression equation also included other energy sinks) was 0.20, then all else being equal (e.g., energy corrected milk is identical), a cow weighing 500 kg (i.e., metabolic BW of 106 $kg^{0.75}$) eating 15.0 kg DM will have the same RFI as a cow weighing 600 kg (i.e., metabolic BW of 121 $kg^{0.75}$) and eating 18.1 kg DM. Although feed efficiency, defined by RFI, of both animals was identical, the production efficiency of the latter animal is obviously inferior because more energy is being used for maintenance.

Gaps in Knowledge on Definitions of Feed Efficiency

Undoubtedly, one of the greatest gaps in knowledge hindering the widespread use of feed intake or feed efficiency measures in both animal breeding and animal management is the availability of routine cost-effective access to large quantities of feed intake information on individual animals. However, several methods to predict feed intake are currently under research, some of which show promise. McParland et al. (2011) proposed the use of the spectra generated from mid-infrared spectroscopy analysis of individual milk samples as predictors of energy intake (as well as energy balance) in lactating dairy cows. Near-infrared spectroscopy analysis of fecal samples in growing Angus bulls has also been proposed (Huntington et al., 2011). Moreover, methods such as infrared thermography (Montanholi et al., 2009), although at an early stage of research, may have some potential in explaining at least some of the variation in RFI among animals.

Moderate phenotypic correlations have been reported between feeding behavior and DMI, RFI, and FCR (Robinson and Oddy, 2004; Nkrumah et al., 2007a). Using the phenotypic correlation matrices provided in their study, 6% (Robinson and Oddy, 2004) to 25% (Nkrumah et al., 2007b) of the phenotypic variance in RFI in growing animals could be explained by daily feeding duration and feeding frequency, and 12% to 14% of the phenotypic variance in DMI could be explained. Automatic measurement of these two traits is relatively simple using an electronic identification sensor on the animal and a receiver at the feed bunk.

Basarab et al. (2011) noted that many of the studies on feed efficiency in males occur around the period when bulls are reaching sexual maturity. Not taking cognizance of this may result in the selection of bulls that have not yet reached sexual maturity (i.e., later maturing bulls) because of the increased activity associated with young bulls after puberty and its implications on energy usage and thus feed efficiency. This substantiates further the hypothesis that selection for RFI alone may delay maturity and result in larger mature size. However, such antagonistic responses to selection can be negated through the use of breeding goals that include traits such as age at first calving and/or mature cow size with the appropriate weighting. Nonetheless, Basarab et al. (2011) reported no association between RFI in heifers and age at puberty, BW at puberty, or the rate at which puberty was reached, although the low-RFI animals reached puberty at a numerically older age (353 d in low-RFI animals compared with 347 d in high-RFI animals); the difference, however, was significant when ultrasound fat was included in the multiple regression model for the derivation of RFI, corroborating the negative correlation (-0.16; $P = 0.06$) between RFI and age at puberty in heifers reported by Shaffer et al. (2011).

Also lacking is information on the repeatability and genetic correlations between feed intake and feed efficiency between nulliparae and lactating animals or, in other words, the extent of genotype-by-environment (i.e., physiological state, **G×E**) interactions. Albeit from a very limited-sized, yet well-designed experiment, Nieuwhof et al. (1992) reported that selection for RFI in growing animals was genetically correlated ($r = 0.58$) with RFI in lactating mature animals in early lactation; however, no SE of the genetic correlations were provided. Moreover, although RFI was not calculated on growing bulls in the same study, Nieuwhof et al. (1992) reported a weak genetic correlation between gross feed efficiency in growing bulls and both growing heifers (0.21) and first lactation animals (0.40); bulls were fed a high-energy density diet, whereas the heifers were fed roughage. Therefore, it was not possible to elucidate whether the G×E interaction was due to different diets, gender, or

physiological state. Accurate knowledge of the genetic correlations between growing and lactating animals has implications for breeding programs, especially in dairy cattle. Preselection of animals for feed efficiency during the growing phase may impact the true selection intensity (i.e., before preselection) on the breeding goal usually derived for lactating animals. This could result in reduced overall genetic gain and thus profitability.

Additional research is required on the most appropriate definition of feed efficiency in lactating cows. Coleman et al. (2010) documented several different definitions of feed efficiency in lactating dairy cows, as previously outlined. However, their definitions of feed efficiency did not differentiate between alternative partial efficiencies and therefore does not necessarily equate to production efficiency. Defining feed efficiency in lactating beef cows where milk yield information is generally not available also requires attention and should probably be based on calf growth rate, although cognizance must be taken of the additive genetic merit for growth rate (i.e., direct weaning weight) of the calf.

Although considerable research has been undertaken on the most appropriate length of the test period to obtain accurate predictions for feed efficiency in growing animals (Archer et al., 1997; Kearney et al., 2004; Wang et al., 2006), little research is available in lactating cows. Prendiville et al. (2011) and Connor et al. (2012), albeit both using limited data sets, reported that RFI measured in middle to late lactation was more strongly phenotypically correlated with RFI averaged across lactation than RFI measured in early lactation. However, animals in middle to late lactation are generally all increasing in BW and BCS (Roche et al., 2009), unlike in early lactation, where body tissue mobilization profiles differ considerably. Therefore, the modeled RFI in early lactation is likely to contain more true residual (i.e., random) noise than in later lactation, and therefore, 1) the appropriate statistical model for RFI must be used that properly accounts for body tissue mobilization, and 2) a sufficiently long time period must be used to quantify RFI, which accounts for the necessity of cows to replenish lost body condition.

The appropriateness of measuring feed efficiency indoors on an energy-rich diet as an indication of feed efficiency in grazing animals needs to be quantified, especially given the contribution of activity and feeding behavior to differences in feed efficiency (Robinson and Oddy, 2004; Nkrumah et al., 2007b). Meyer et al. (2008) failed to detect a difference in forage intake between high- and low-RFI grazing beef cows (measured during both gestation and late lactation); cows were characterized as high or low RFI on the basis of their earlier measured performance on a feeding trial (fed on alfalfa grass mixed hay) as heifers.

GENETIC VARIATION
IN FEED EFFICIENCY MEASURES

Table 1 summarizes heritability estimates of feed efficiency traits across several breeds and populations for growing animals, and heritability estimates for mature cows are summarized in Table 2. The heritability estimates for the feed efficiency traits in growing animals varied from 0.06 (Robinson and Oddy, 2004) to 0.62 (Archer et al., 1997). Heritability estimates for either RFI or FCR varied from 0.00 (Svendsen et al., 1993) to 0.38 (Veerkamp et al., 1995) in cows. The minimum heritability estimates in growing animals for ADG, BW, DMI, RFI, and FCR were 0.06, 0.30, 0.14, 0.07, and 0.06, respectively; the respective maximum estimates in growing animals were 0.65, 0.77, 0.70, 0.62, and 0.46. Heritability estimates for KR varied from 0.21 to 0.52 in growing animals (5 studies), whereas the heritability estimates for RGR in growing animals varied from 0.14 to 0.33 (4 studies). Only 2 heritability estimates for RG existed in the literature for growing cattle, and these were 0.28 and 0.62 (Koch et al., 1963; Crowley et al., 2010). However, using the necessary (co)variance components provided in some studies, it was possible to calculate the heritability of RG. Heritability for RG varied from 0.17 to 0.23 (Arthur et al., 2001a,c; MacNeil et al., 2011; Rolfe et al., 2011). Using a similar approach and the necessary parameters for feed intake, milk yield, and BW in lactating dairy cattle, the heritability for RFI was calculated as 0.05 to 0.08 (Parke et al., 1999; Søndergaard et al., 2002; Vallimont et al., 2011).

The pooled heritability (and pooled SE) across all studies was calculated, as defined by Koots et al. (1994a). The pooled heritability for ADG, BW, feed intake, RFI, FCR, RG, KR, and RGR in growing animals was 0.31 ± 0.014, 0.39 ± 0.010, 0.40 ± 0.012, 0.33 ± 0.013, 0.23 ± 0.013, 0.28 ± 0.030, 0.35 ± 0.030, and 0.26 ± 0.041, respectively. The heritability estimates for the feed efficiency traits in cows (Table 2) were considerably less than those reported in growing animals (Table 1), albeit the number of studies was considerably fewer for cows. Mean heritability for feed intake, BW, RFI, and FCR across studies in the cows was 0.06 ± 0.008, 0.63 ± 0.008, 0.04 ± 0.008, and 0.06 ± 0.010, respectively. Only studies that also presented heritability estimates for feed efficiency variables are included here in the pooled heritability estimate of feed intake and BW. The heritability of feed intake in these studies is, however, somewhat lower than estimates of feed intake in most studies, especially in dairy cows (Berry et al., 2007; Hüttmann et al., 2009; Buttchereit et al., 2011).

Genetic and phenotypic correlations among the different measures of feed efficiency in growing animals are summarized in Table 3. The correlations with RFI reported in Table 3 are when RFI was defined from

regressing feed intake on ADG and BW. The correlation between RFI defined from regressing feed intake on both ADG and BW and RFI defined from regressing feed intake on ADG, BW, and body fat was 0.99 (Schenkel et al., 2004). The average genetic correlation was estimated using an approach similar to Koots et al. (1994b), except that the approximated SE of the genetic correlation using information on the number of sires in the analysis was replaced by the actual published standard error of the genetic correlation. A similar approach was undertaken for phenotypic correlations with the exception that because SE are not always provided in the literature, the SE of the pooled phenotypic correlation was estimated as outlined by Koots et al. (1994b).

Both FCR and RFI were positively genetically correlated with feed intake (0.39 and 0.72, respectively), but only FCR was genetically correlated with ADG (−0.62), indicating that improved FCR was associated with greater ADG. However, neither FCR nor RFI was genetically correlated with midtest BW, although considerable variation in the genetic correlations existed, especially for FCR. The genetic correlation between FCR and RFI was 0.75, with a range in correlations from −0.21 to 0.93. The phenotypic and genetic correlations between RG and RFI were −0.40 and −0.46, respectively, and the respective correlations between RG and FCR were −0.39 and −0.89. Residual feed intake was weakly correlated with KR and RGR. Nevertheless, large variation existed in the correlations among traits, which could be due to sampling variation but also G×E interactions.

In lactating dairy cattle, Veerkamp et al. (1995), using alternative definitions of RFI (i.e., without accounting for body state change), reported positive genetic (0.63 to 0.69) and phenotypic (0.68 to 0.76) correlations between RFI and DMI; similar correlations were reported between RFI and both ME intake and CP intake. Genetic and phenotypic correlations between RFI and milk production traits in lactating dairy animals were close to zero (Veerkamp et al., 1995), substantiating the lack of any difference ($P > 0.96$) in milk production between lactating dairy cows stratified on RFI (Coleman et al., 2010); the lack of an association was because milk production-related traits were included in the least squares multiple regression defining RFI, and therefore, RFI was phenotypically independent of these traits. Interestingly, however, RFI, even when traits related to BCS and BW change were included in the phenotypic regression defining RFI, was genetically correlated with BW change and BCS (Veerkamp et al., 1995), indicating different residual and genetic relationships between these traits and feed intake (Kennedy et al., 1993); correlations with BW and BCS (change) may have implications for animal health and fertility because of the known genetic (Berry et al., 2003) and phenotypic (Roche et al., 2009) asso-

Table 1. Heritability estimates (SE in parentheses) for ADG, BW, feed intake (FI), residual feed intake (RFI), and feed conversion ratio (FCR) for a range of studies in growing animals across different breeds and countries[1]

ADG	BW	FI	RFI	FCR	Breeds[2]	Country	Animals, n	Reference
0.35 (0.11)		0.62 (0.12)	0.62 (0.14)	0.42 (0.13)	AN, HE, Polled HE, SH	Australia	760	Archer et al. (1997)
0.41 (0.08)	0.68 (0.08)	0.59 (0.07)	0.44 (0.07)	0.31 (0.09)	AN, HE, SH	Australia	966	Arthur et al. (1997)
0.28 (0.04)	0.40 (0.02)	0.39 (0.03)	0.39 (0.03)	0.29 (0.04)	AN	Australia	1,180	Arthur et al. (2001a)
0.34 (0.04)	0.37 (0.04)	0.48 (0.04)	0.39 (0.04)	0.46 (0.04)	CH	France	792	Arthur et al. (2001c)
0.41 (0.06)	0.46 (0.05)	0.48 (0.06)	0.43 (0.04)	0.31 (0.06)	CH	France	397	Arthur et al. (2001c)
0.34 (0.12)	0.47 (0.16)	0.49 (0.15)	0.24 (0.11)		Brahman	Australia	1,007	Barwick et al. (2009)
0.20 (0.10)	0.39 (0.13)	0.51 (0.14)	0.38 (0.12)		Tropical Composite	Australia	1,209	Barwick et al. (2009)
0.48 (0.21)	0.39 (0.19)	0.37 (0.19)		0.19 (0.16)	Bonsmara	South Africa	298	Bergh et al. (1992)
0.48 (0.21)		0.06 (0.12)		0.46 (0.20)	FRXHE	United Kingdom	327	Bishop et al. (1992)
	0.57 (0.10)	0.30 (0.08)	0.26 (0.10)	0.30 (0.12)	BA	France	678	Bouquet et al. (2010)
	0.30 (0.08)	0.48 (0.14)	0.45 (0.18)	0.23 (0.15)	LI	France	708	Bouquet et al. (2010)
0.36 (0.11)				0.14 (0.07)	AN	United States	393	Brown et al. (1988)
0.33 (0.11)				0.13 (0.08)	HE	United States	340	Brown et al. (1988)
			0.30 (0.06)		CH-sired steers	Canada	281	Crews et al. (2003)
			0.26 (0.07)		CH-sired steers	Canada	274	Crews et al. (2003)
0.30 (0.06)	0.69 (0.07)	0.49 (0.07)	0.45 (0.07)	0.30 (0.06)	AN, CH, HE, SI, LI	Ireland	2,605	Crowley et al. (2010)
0.06 (0.08)		0.30 (0.15)	0.19 (0.12)	0.07 (0.09)	ANX, CHX	Canada	402	Durunna et al. (2011b)
0.17 (0.28)		0.43 (0.14)	0.36 (0.13)	0.26 (0.12)	ANX, CHX	Canada	419	Durunna et al. (2011b)
		0.21 (0.07)	0.14 (0.06)	0.18 (0.07)	AN, BR, BA	United States	1,129	Elzo et al. (2010)
0.43 (0.24)	0.45 (0.22)	0.27 (0.15)	0.23 (0.12)	0.35 (0.22)	AN	Canada	263	Fan et al. (1995)
0.16 (0.15)	0.43 (0.22)	0.18 (0.10)	0.07 (0.13)	0.08 (0.09)	HE	Canada	271	Fan et al. (1995)
0.55 (na)	0.51 (na)	0.58 (na)		0.16 (na)	BB	France	1,442	Gengler et al. (1995)
0.25 (na)		0.24 (na)		0.14 (na)	HE	United States	486	Glaze and Schalles (1995)
0.38 (0.10)	0.42 (0.10)	0.31 (0.08)	0.16 (0.08)	0.17 (0.09)	HE	United Kingdom	540	Herd and Bishop (2000)
0.20 (0.10)	0.47 (0.10)	0.34 (0.11)	0.24 (0.11)	0.15 (0.04)	Japanese Black (Wagyu)	Japan	740	Hoque et al. (2006)
		0.36 (0.09)	0.49 (0.09)	0.38 (0.07)	Japanese Black (Wagyu)	Japan	514	Hoque et al. (2009)
		0.70 (0.11)	0.22 (0.07)	0.11 (0.05)	Japanese Black (Wagyu)	Japan	863	Inoue et al. (2011)
0.37 (na)		0.26 (na)		0.27 (na)	HO, BS	Denmark	630	Jensen et al. (1991)
		0.28 (0.11)			HO, BS	Denmark	650	Jensen et al. (1992)
0.21 (0.12)	0.35 (0.15)	0.48 (0.14)	0.47 (0.13)	0.29 (0.12)	Brangus	United States	468	Lancaster et al. (2009)
0.65 (0.13)		0.64 (0.12)	0.28 (0.11)		AN, HE, SH	United States	1,324	Koch et al. (1963)
0.30 (0.11)	0.77 (0.09)	0.56 (0.11)	0.22 (0.11)	0.18 (0.08)	HO, HO × Dutch	Netherlands	417	Korver et al. (1991)
0.26 (0.04)	0.33 (0.03)	0.36 (0.05)			AN	United States	4,215 to 18,169	MacNeil et al. (2011)
				0.33 (0.10)	HE	United Kingdom	452	Mrode et al. (1990)
			0.18 (0.14)		AN, CH, composite	Canada	387	Mujibi et al. (2010)
0.28 (0.11)		0.41 (0.12)	0.29 (0.12)		AN, CH, composite	Canada	721	Mujibi et al. (2011)
0.59 (0.17)	0.32 (0.14)	0.54 (0.15)	0.21 (0.12)	0.41 (0.15)	AN, CH, composite	Canada	464	Nkrumah et al. (2007b)
0.26 (na)	0.39 (na)	0.33 (na)	0.29 (na)	0.14 (na)	Japanese Black (Wagyu)	Japan	1,304	Okanishi et al. (2008)
0.23 (0.06)	0.41 (0.07)	0.27 (0.06)	0.18 (0.06)	0.06 (0.04)	Tropically adapted, temperate	Australia	1,481	Robinson and Oddy (2004)
0.09 (na)		0.14 (na)	0.14 (na)		AN	United States	698	Rolf et al. (2010)
0.26 (0.10)	0.35 (0.12)	0.40 (0.02)	0.52 (0.14)	0.27 (0.10)	Multibreed	United States	1,141	Rolfe et al. (2011)
0.35 (0.03)	0.35 (0.02)	0.44 (0.06)	0.38 (0.07)	0.37 (0.06)	CH, LI, AN, SI, HE, BA	Canada	2,284	Schenkel et al. (2004)
0.27 (0.12)	0.88 (0.11)	0.46 (0.14)	0.19 (0.12)	0.37 (0.14)	HO	Netherlands	360	Van Arendonk et al. (1991)
0.37 (na)			0.31 (na)	0.34 (na)	Bonsmara	South Africa	6,738	Van der Westhuizen et al. (2004)
0.22 (0.10)	0.32 (0.12)	0.17 (0.10)	0.27 (0.12)		HO	Australia	903	Williams et al. (2011)

[1]na = not available.

[2]AN = Angus; BA = Brangus; BB = Belgian Blue; BR = Brahman; BS = Brown Swiss; CH = Charolais; CHX=Charolais crossbred; FRXHE = Friesian-Hereford crossbreds; HE = Hereford; HO = Holstein; LI = Limousin; SH = Shorthorn; SI = Simmental.

ciations. Vallimont et al. (2011) reported a strong positive genetic correlation (0.87) between feed conversion efficiency (i.e., 305-d fat-corrected milk yield divided by 305-d DMI) and milk yield in 970 U.S. dairy cattle; they also reported strong negative genetic correlations with BW (−0.66) and BCS (−0.70). These trends were substantiated by phenotypic differences in Irish Holstein-Friesian grazing dairy cows stratified on feed conversion

Table 2. Heritability estimates (SE in parentheses) for BW, feed intake (FI), residual feed intake (RFI), and feed conversion ratio (FCR) for a range of studies in lactating or dry mature animals across different breeds and countries[1]

BW	FI	RFI	FCR	Breeds[2]	Country	Animals, *n*	Reference
0.71 (na[1])	0.28 (na)	0.23 (na)	0.26 (na)	AN, HE, Polled HE, SH	Australia	751	Archer et al. (2002)
0.29 (0.09)	0.02 (0.02)	0.23 (0.11)	0.18 (0.15)	HE	Canada	295	Fan et al. (1996a)
0.40 (0.04)	0.11 (0.02)	0.03 (0.01)	0.11 (0.06)	HE, multibreed	Canada	1,174	Fan et al. (1996a)
0.20 (0.12)	0.03 (0.01)	0.03 (0.02)	0.11 (0.10)	HE	Canada	206	Fan et al. (1996b)
0.44 (0.17)	0.16 (0.02)	0.22 (0.04)	0.05 (0.01)	HE, multibreed	Canada	729	Fan et al. (1996b)
		0.05 to 0.38		Holstein-Friesian	Ireland	463	Lopez-Villalobos et al. (2008)
	0.16 (na)			HO	United States	247	Ngwerume and Mao (1992)
0.43 to 0.72	0.18 to 0.63		0.32 (0.13)	HO	United States	402	Spurlock et al. (2012)
0.65 (0.01)		0.04 (0.05)		Norwegian	Norway	353	Svendsen et al. (1993)
0.65 (0.02)		0.00 (0.03)		Norwegian	Norway	353	Svendsen et al. (1993)
0.71 (na)		0.38 (na)		HO	Netherlands	204	Veerkamp et al. (1995)
0.59 (0.09)	0.16 (0.07)	0.01 (0.05)	0.14 (0.06)	HO	United States	970	Vallimont et al. (2011)

[1]na = not available.

[2]AN = Angus; HE = Hereford; HO = Holstein; SH = Shorthorn.

efficiency (Coleman et al., 2010) defined similarly to that used by Vallimont et al. (2011).

Gaps in Knowledge on Variance Components for Feed Efficiency

Genotype-by-environment interactions can result in reranking or rescaling of animals for genetic merit in different environments, and the likelihood of a G×E interaction is a function of the extent of the difference between environments and between genotypes of animals. Knowledge of G×E interactions is particularly relevant for feed efficiency variables where the phenotypes used to rank selection candidates are generally generated in a system of production or diet different to what may be undertaken commercially. It is also important to note that with index traits (i.e., traits that are a mathematical combination of other traits) such as RFI, RG, and RIG, genetic correlations of unity between the same component traits across environments can still result in reranking of animals for the index trait if the genetic variance of the component traits in the environments differs (Namkoong, 1985).

Until recently, few have attempted to quantify the extent of G×E interaction for feed efficiency in growing (Durunna et al. (2011a,b, 2012) and lactating (Coleman et al., 2010; Prendiville et al., 2011) animals. Recent research from Canada evaluated the change in animal ranking for RFI, FCR, and KR in beef steers (Durunna et al., 2011a) and heifers (Durunna et al., 2012) across time and/or diet. Irrespective of sex, reranking among

Table 3. Genetic (below the diagonal; SE in parentheses) and phenotypic (above the diagonal) between feed intake (FI), ADG, BW, feed conversion ratio (FCR), residual feed intake (RFI), residual BW gain (RG), relative growth rate (RGR), Kleiber ratio (KR), and residual intake and gain (RIG) across a range of studies in growing animals[1]

Trait	FI	ADG	BW	FCR	RFI	RG	RGR	KR	RIG
FI		0.42 [−0.67 to 0.76]	0.40 [0.72 to 0.56]	0.23 [−0.29 to 0.98]	0.66 [0.43 to 0.88]	0.00 [0.00 to 0.00]	0.05 [−0.03 to 0.13]	0.19 [0.09 to 0.32]	−0.34[1]
ADG	0.78 (0.02)[12] [−0.72 to 0.90]		0.45 [0.18 to 0.77]	−0.52 [−0.91 to 0.65]	0.00 [-0.06 to 0.04]	0.70 [0.70 to 0.70]	0.74 [0.68 to 0.80]	0.85 [0.83 to 0.88]	0.41[1]
WT	0.75 (0.02)[9] [0.36 to 0.99]	0.68 (0.03)[8] [0.06 to 0.86]		−0.01 [−0.67 to 0.35]	−0.01 [−0.26 to 0.16]	0.00 [0.00 to 0.00]	−0.35 [−0.35 to −0.35]	0.08 [−0.20 to 0.37]	0.00[1]
FCR	0.39 (0.04)[13] [−0.57 to 0.90]	−0.62 (0.04)[11] [−0.89 to 0.75]	−0.03 (0.04)[11] [−0.62 to 0.88]		0.39 [−0.62 to 0.76]	−0.71 [−0.71 to −0.71]	−0.35 [−0.76 to 0.73]	−0.74 [−0.80 to −0.67]	−0.66[1]
RFI	0.72 (0.02)[18] [−0.34 to 0.85]	0.02 (0.05)[13] [−0.15 to 0.53]	−0.01 (0.04)[14] [−0.40 to 0.33]	0.75 (0.02)[13] [−0.21 to 0.93]		−0.40 [-0.40 to 0.00]	−0.01 [−0.03 to 0.02]	−0.01 [−0.04 to 0.01]	−0.85[1]
RG	−0.03 (0.13)[1] [−0.03 to 0.00]	0.82 (0.05)[1] [0.82 to 0.82]	0.07 (0.12)[1] [0.07 to 0.07]	−0.89 (0.03)[1] [−0.89 to −0.89]	−0.46 (0.11)[1] [−0.46 to −0.46]		0.65 [0.65 to 0.65]	0.72 [0.72 to 0.72]	0.85[1]
RGR	−0.18 (0.06)[2] [−0.21 to 0.00]	0.77 (0.06)[3] [0.56 to 0.86]	−0.54 (0.09)[1] [−0.54 to 0.00]	−0.66 (0.07)[1] [−0.84 to −0.56]	−0.01 (0.07)[2] [−0.13 to 0.21]	0.61 (0.08)[1] [0.61 to 0.61]		0.86 [0.74 to 0.97]	0.36[1]
KR	−0.04 (0.03)[4] [−0.15 to 0.55]	0.80 (0.03)[3] [−0.34 to 0.91]	−0.09 (0.08)[3] [−0.34 to 0.39]	−0.78 (0.06)[1] [−0.81 to −0.74]	−0.19 (0.07)[3] [−0.40 to 0.15]	0.76 (0.06)[1] [0.76 to 0.76]	0.97 (0.01)[2] [0.96 to 0.97]		0.41[1]
RIG	−0.35 (0.10)[1]	0.47 (0.10)[1]	0.11 (0.10)[1]	−0.80 (0.05)[1]	−0.87 (0.03)[1]	0.83 (0.04)[1]	0.26 (0.12)[1]	0.37 (0.11)[1]	

[1]The range in genetic correlations is summarized in square brackets. The superscript beside the genetic correlation is the number of studies included in the meta-analysis.

the same animals tended to occur between two test periods, close together in the lifetime of the animals, yet based on the same diet. Results indicate that 1) age may be the main factor influencing reranking, although this is unlikely given the similarity in ages, or 2) RFI contains a large element of statistical error as well as true differences in feed efficiency (in this study at least); the same logic holds for the other feed efficiency traits. Also, as previously alluded to, variance of the component traits across environments can result in reranking of index traits such as RFI; variances for DMI, ADG, and BW were generally greater in the second period of the study reported by Durunna et al. (2011a). Durunna et al. (2011b) reported genetic correlations between RFI in animals fed a grower and later a finisher diet and between the DMI and ADG in both diets. The genetic correlations for ADG expressed in both environments was 0.80 ± 0.79, whereas the genetic correlation for DMI was 0.78 ± 0.27, which are close to the threshold of 0.80 suggested by Robertson (1959) to indicate the presence of G×E interactions. The genetic correlation between RFI in the 2 environments was 0.50 ± 0.48, and although associated with a large SE, it indicates the presence of G×E interactions for the index trait.

Herd et al. (2006) documented a moderate repeatability of RFI (0.39) between postweaning and mature stages of life in Angus females, whereas Archer et al. (2002) documented a phenotypic correlation of 0.40 between RFI in postweaning animals and mature cows. In the same study, Archer et al. (2002) estimated a genetic correlation close to unity (0.98; no SE were quoted) between postweaning RFI and cow RFI measured on the same 751 animals; postweaning feed intake had a genetic correlation of 0.69 with cow feed intake. Animals were fed the same diet at both ages, and cow feed intake was measured in the second parity, after weaning of the calf and while not in calf. Albeit with relatively large SE, Crews et al. (2003) reported a genetic correlation of 0.55 ± 0.30 between RFI of animals in the growing and finishing periods, indicating considerable reranking of animals for genetic merit on RFI, although the correlation was not >2 SE from unity.

An additional gap in knowledge is the influence of nonadditive genetic variation (i.e., dominance, epistasis) to phenotypic differences in feed efficiency among animals. Such effects include heterosis and recombination effects as well as cytoplasmic effects. Finally, it is unclear if genetic evaluations for feed efficiency account for possible heterogeneity of variances across contemporary groups; MacNeil et al. (2011) standardized feed intake data within test group. Because few animals are generally performance tested annually, usually, data from many years are included in national genetic evaluations. Diets or other management criteria may, however, change over time (Crowley et al., 2010), thereby contributing to possible heterogeneity of variances over time that could impact genetic evaluations if not appropriately accounted for.

GENETIC CORRELATIONS OF FEED EFFICIENCY WITH OTHER PERFORMANCE TRAITS

A meta-analysis of the genetic correlations between feed efficiency traits and a range of performance traits was undertaken with the mean genetic correlation across studies estimated using the earlier described approach (Koots et al., 1994b). Correlations with RFI included in the meta-analysis were based on RFI calculated from regressing feed intake on ADG and BW.

Male and Female Fertility

Relative to most other performance traits, few studies have attempted to quantify the impact of selection for feed efficiency on reproductive performance. Koots et al. (1994b), in a review of the literature in beef cattle, reported a genetic correlation of 0.04 between FCR and scrotal circumference. In their review, they did not have estimates of genetic correlations with RFI or any other measure of feed efficiency, and no correlations between FCR and female reproduction were reported. Although associated with relatively large SE, Crowley et al. (2011a) reported unfavorable genetic correlations between 3 different measures of feed efficiency (i.e., FCR, RFI, and RG) in performance-tested bulls and age at first calving in beef cows (-0.55 ± 0.14, -0.29 ± 0.14, and 0.36 ± 0.15, respectively). In the same study, the genetic correlations of these feed efficiency traits with calving interval (0.07, 0.01, and −0.01, respectively) and calving to first service interval (0.21, −0.03, and −0.15, respectively) were not different from zero.

Basarab et al. (2011) reported no difference in average calving dates among beef heifers divergent for RFI measured at approximately 9 mo of age. However, no account was taken of right-censored data with a decreased calving rate in the low-RFI heifers; there was an 11% difference in calving rate between divergent groups when RFI was defined with just ADG and BW included in the multiple regression model for RFI. This difference was negated by including ultrasound fat in the multiple regression model to generate RFI. This may be another reason, apart from accounting for differences in composition of growth, to include ultrasound fat in the derivation of RFI, that is, to avoid indirect selection of later maturing animals in a scenario where RFI is a selection criterion. Arthur et al. (2005), after a divergent selection experiment, documented a 5-d later calving date in low-

RFI cows compared with high-RFI cows, and similarly, Basarab et al. (2007) reported that cows producing low-RFI progeny calved 5 to 6 d later than cows producing medium- to high-RFI progeny.

Antagonistic genetic correlations can be (somewhat) negated through balanced breeding objectives including all traits affecting profitability appropriately weighted. However, the low heritability of traditional fertility traits (Veerkamp and Beerda, 2007) and the sometimes lack of available phenotypic data, especially in beef range production systems, may result in low accuracy of selection for fertility traits. Therefore, unfavorable responses to selection in fertility may materialize if RFI is also included in the breeding objective with accurate estimates of genetic merit. Reducing fertility may negate any gains in daily feed efficiency by reducing the feed efficiency of the entire production system. The impact of selection on feed efficiency on fertility and survival merits further investigation.

Carcass Traits

Although lacking consistency across all studies, there is a general tendency for RFI to be negatively correlated with carcass conformation in beef cattle (Table 4); better RFI animals have improved carcass conformation. This is substantiated by genetic correlations reported between RFI and muscularity, scored in live animals, which showed that genetically superior RFI animals had, on average, superior genetic merit for muscularity (Bouquet et al., 2010; Crowley et al., 2011b). The genetic correlation between muscle score measured subjectively on live animals and RFI varied from −0.44 to −0.22 (Bouquet et al., 2010; Crowley et al., 2011b). Genetic correlations between carcass conformation

and FCR were also generally negative and the genetic correlations between live muscularity score and FCR (Crowley et al., 2011b) and RG (Crowley et al., 2011b) were similar in magnitude to the genetic correlations between live muscularity score and RFI. Furthermore, the genetic correlations estimated between RFI and body lean in beef cattle, although variable across studies, were, on average, negative (Table 4).

Although lacking consistency across studies, which may partly be explained by relatively large SE in some instances, in general, there was a positive genetic association of both RFI and FCR with body fat in beef animals, either in live animals or carcasses (Arthur et al., 2001a; Robinson and Oddy, 2004; Barwick et al., 2009; Bouquet et al., 2010; Crowley et al., 2011b). Residual feed intake used in the meta-analysis was not adjusted for differences in body composition. The associations, however, may be influenced by the breed, the age of the animal when tested, and G×E interactions. Similarly, Veerkamp et al. (1995) reported positive genetic correlations (0.26 to 0.36) between RFI in lactating animals and subjectively scored BCS. Inoue et al. (2011) reported a positive genetic correlation between RFI and beef marbling score. Robinson and Oddy (2004) also reported a positive genetic correlation (0.22 ± 0.17) between RFI and intramuscular fat in cattle and a strong positive genetic correlation (0.72 ± 0.17) between RFI and P8 rump subcutaneous fat depth measured by ultrasound on live animals. Similar genetic correlations were reported between FCR and the different measures of fat in the animal (Robinson and Oddy, 2004). Robinson and Oddy (2004) estimated the genetic covariance between RFI and the fat traits using either age or carcass weight as a covariate in the model, and the correlations did not change substantially, indicating that selection for

Table 4. Genetic correlations (SE in parentheses) between feed intake (FI), ADG, BW, feed conversion ratio (FCR), residual feed intake (RFI), residual gain (RG), relative growth rate (RGR), Kleiber ratio (KR), and a range of other performance traits across a range of studies in growing animals[1]

Trait	FI	ADG	BW	FCR	RFI	RG	RGR	KR
Lean	0.34 (0.05)[9]	0.15 (0.09)[6]	0.36 (0.08)[5]	−0.47 (0.05)[8]	−0.18 (0.05)[14]	0.03 (0.28)	0.80 (0.10) [2]	0.81 (0.10)[2]
	[0.03 to 0.44]	[−0.09 to 0.45]	[0.04 to 0.50]	[−0.72 to 0.54]	[−0.52 to 0.52]		[−0.23 to 0.87]	[−0.18 to 0.87]
Fat	0.28 (0.04)[10]	0.09 (0.06)[7]	0.21 (0.07)[5]	0.08 (0.05)[6]	0.20 (0.04)[12]	−0.44 (0.20)	−0.18 (0.22)[1]	−0.29 (0.22)[1]
	[−0.35 to 0.61]	[−0.54 to 0.4]	[−0.26 to 0.41]	[−0.29 to 0.49]	[−0.79 to 0.48]		[−0.18 to −0.18]	[−0.29 to −0.29]
Carcass conformation	0.29 (0.07)[5]	0.73 (0.08)[2]	0.18 (0.06)[3]	−0.47 (0.06)[6]	−0.30 (0.05)[7]	0.35 (0.14)	0.35 (0.10)[2]	−0.35 (0.09)[2]
	[−0.23 to 0.67]	[0.14 to 0.85]	[−0.05 to 0.33]	[−0.60 to −0.02]	[−0.56 to 0.29]		[0.15 to 0.53]	[−0.62 to 0.21]
Carcass fat	0.35 (0.07)[5]	0.12 (0.13)[2]	0.14 (0.07)[3]	−0.23 (0.07)[6]	0.06 (0.06)[7]	−0.10 (0.15)	−0.19 (0.09)[2]	−0.38 (0.08)[2]
	[0.07 to 0.63]	[−0.26 to 0.39]	[−0.17 to 0.32]	[−0.61 to 0.11]	[−0.37 to 0.33]		[−0.35 to 0.07]	[−0.51 to 0.07]
Carcass weight	0.72 (0.05)[5]	0.22 (0.13)[1]	0.72 (0.06)[3]	−0.44 (0.06)[6]	−0.11 (0.06)[8]	0.32 (0.13)	0.17 (0.07)[2]	0.06 (0.08)[2]
	[0.00 to 0.87]	[0.22 to 0.22]	[0.08 to 0.91]	[−0.69 to −0.26]	[−0.60 to 0.26]		[0.16 to 0.18]	[−0.03 to 0.20]
Mature weight	0.28 (0.32)[1]	0.63 (0.33)[1]	0.35 (0.29)[1]	−0.62 (0.36)[1]	−0.23 (0.31)[1]	0.67 (0.34)	0.32 (0.35)[1]	0.54 (0.34)[1]
	[0.28 to 0.69]	[0.63 to 0.91]	[0.35 to 0.82]	[−0.62 to −0.54]	[−0.23 to −0.22]		[0.32 to 0.32]	[0.54 to 0.54]
Milk	0.32 (0.22)[1]	0.52 (0.17)[1]			0.03 (0.21)[1]	0.57 (0.25)	0.50 (0.26)[1]	0.57 (0.26)[1]
	[0.32 to 0.32]	[0.52 to 0.52]			[0.03 to 0.03]		[0.50 to 0.5]	[0.57 to 0.57]

[1]The range in genetic correlations is summarized in square brackets. The superscript beside the genetic correlation is the number of studies included in the meta-analysis.

reduced RFI alone will, on average, decrease both sub-cutaneous and intramuscular fatness at both a constant weight and constant age.

Few studies have estimated genetic correlations between feed efficiency and meat quality measures. Inoue et al. (2011) quantified the genetic correlations between both FCR and RFI with meat fatty acid composition in Japanese Black steers. The genetic correlations between RFI and the different fatty acids evaluated were all close to zero. The genetic correlations with FCR were stronger but still weak, varying from −0.38 (sum of C18:0 and C18:1) to 0.43 (C14:1); the standard errors of the correlations were approximately 0.20.

Animal Size

Across most, but not all, studies, selection on FCR alone, with no cognizance of other traits, will increase animal size or BW (Table 3). The increase in animal size from selection solely on FCR exists irrespective of whether the measure of size was test period metabolic BW (Hoque et al., 2006; Bouquet et al., 2010), cow BW (Crowley et al., 2011a), carcass weight (Bouquet et al., 2010; Crowley et al., 2011b), or linear type traits on live animals describing the skeletal conformation of an animal (Bouquet et al., 2010). Because of the mathematical properties of least squares linear regression, the residual from the multiple regression model is independent of the independent variables in the model. This was subsequently implied to result in genetic independence from mature BW. However, genetic independence between RFI and the regressor variables is not implied if RFI is defined phenotypically (Kennedy et al., 1993), and BW measured during test may not be genetically the same trait as mature BW. Crowley et al. (2011a), using Irish data, reported a weak genetic correlation (0.35 ± 0.29) between midtest metabolic BW of performance-tested beef bulls (n = 2,605) and commercial beef cows (n = 7,961). All else being equal, superior RFI animals are likely to be gaining more protein per unit ADG than fat, assuming body composition is not included in the definition of RFI, because the energy requirement of gaining 1 unit of protein is less than the energy requirement of gaining 1 unit of fat (SCA, 1990). Therefore, for animals of similar age, there may be a tendency for RFI, defined without a body composition measure, to be selecting for later maturing animals and therefore possibly animals with a greater mature BW.

Environmental Load

To our knowledge, no study has attempted to estimate the genetic covariance between feed efficiency and methane emissions, most likely because of the large cost of collecting methane emission and feed efficiency data on a sufficiently sized population to estimate precise genetic correlations. Nonetheless, a favorable association between feed efficiency and methane production is expected given that methane production represents a source of energy loss (Johnson and Johnson, 1995) and therefore inefficiency. The existence of genetic variation in daily methane emissions is also not known; using genetic variance of methane intensity (i.e., methane per unit feed intake) should be interpreted with caution because the perceived genetic variance in methane intensity may actually be due to genetic variation in feed intake. Of importance is knowledge of whether or not genetic variation in "residual methane production" exists. Residual methane production could be derived using mathematical principles similar to the derivation of RFI by regressing daily methane emissions on traits such as DMI, production (i.e., growth rate or milk output), maintenance, and possibly body tissue change.

Hegarty et al. (2007) reported no association between RFI calculated during a 70-d intake period and methane emissions per day in 76 Angus steers; methane was measured using the sulfur hexafloride method. However, they found that mean DMI of the population was less during the period of methane measurement relative to the rest of the test period, and therefore, they calculated RFI across the 15 d in which methane emissions were measured. Body weight was measured every 2 d during the methane measurement period, but it was not clear from the study how often BW was measured during the 15-d period or how many BW records were used in the calculation of ADG during the period. Using the new RFI variable (**RFI$_{15}$**), they reported a positive association (P = 0.002) between RFI and daily rate of methane production (Hegarty et al., 2007); the correlation between RFI and daily rate of methane production was 0.35. Nonetheless, this shows that the impact of the methane measurement period on methane production was not consistent across all animals. The impact was greater in the low-RFI animals compared with the high-RFI animals. Hegarty et al. (2007) also reported no association between estimated breeding value for RFI (estimated from the long-term experiment; Arthur et al., 2001b) and rate of methane production; however, when they adjusted for the discrepancies between RFI measured in the 15-d period before methane measurement and RFI measured during the entire 70-d test, an association did exist, but no statistical significance was attributed to the value. Hegarty et al. (2007) reported a difference (P = 0.01) in daily methane production between the 10 highest and 10 lowest RFI animals (measured during the 15-d period), but no difference existed in methane emissions per kilogram ADG (P = 0.09) or per kilogram DMI (P = 0.37). The lack of a difference in methane emissions per kilogram DMI in-

dicates that the differences in daily methane emissions between animals divergent in RFI are due primarily to their differences in DMI.

Similar to the calculated phenotypic correlation of 0.35 between RFI (calculated over a 15-d period and not the entire 70-d test period) and daily methane production from the results provided by Hegarty et al. (2007) in 76 Australian Angus cattle, Nkrumah et al. (2006) reported a phenotypic correlation of 0.44 ($P < 0.05$) between RFI and daily methane production in 27 Canadian Continental × British hybrid beef steers sired by Angus or Charolais bulls. Nkrumah et al. (2006) measured methane using an indirect calorimetry system (measured over two 16-h periods, 3 d apart). However, Nkrumah et al. (2006) reported significant differences ($P = 0.04$) among animals divergent for RFI for methane production as a percentage of gross energy intake with quoted values of 4.28%, 4.25%, and 3.19% for high-RFI, medium-RFI, and low-RFI animals, respectively.

The well-established phenotypic and genetic associations between RFI and DMI (Table 3) can have implications for potentially less manure production and, all else being equal, potentially less nitrous oxide release into the atmosphere; the possibly reduced protein turnover of superior RFI may contribute to less nitrogen excretion. Although not statistically significant (the study included 27 animals divided into three RFI-divergent groups), fecal DM production was 15.5% and 8.1% greater in high- and medium-RFI growing beef animals compared with low-RFI growing beef animals (Nkrumah et al., 2006). The correlation between RFI and daily fecal DM output was 0.33 ($P < 0.10$), but this was similar to the correlation (0.32) between DMI and daily fecal DM output. Assuming a phenotypic correlation of 0.66 between RFI and feed intake (Table 3), the correlation between RFI and daily fecal output after accounting for differences in intake is 0.17, indicating less DM fecal output in superior RFI animals even after accounting for the fact that lower-RFI animals, on average, eat less.

Milk Yield

Little is known about the impact of selection on feed efficiency in growing animals on the milk yield of the mature herd. Crowley et al. (2011a) found zero genetic correlation between RFI and maternal weaning weight, a proxy for milk yield in beef cows, but they documented a negative genetic correlation of −0.61 ± 0.25 between FCR and maternal weaning weight. Crowley et al. (2011a) reported positive genetic correlations (i.e., 0.50 to 0.57) of KR, RG, and RGR with maternal weaning weight in beef cows. Furthermore, Arthur et al. (2005) reported no difference in milk yield, on average, 60 d postcalving in 122 Angus cows divergently selected for

1.5 generations for postweaning RFI. Strong positive genetic and phenotypic correlations in dairy cattle have been reported between milk yield and feed efficiency, defined as the ratio of milk production to feed intake (Vallimont et al., 2011); this, however, is expected given the statistical part-whole relationship between the 2 traits. Phenotypic correlations between milk production, BW, and RFI assessed in lactating dairy cattle, however, are near zero (Veerkamp et al., 1995), but this is because traits reflecting milk production were included in the multiple regression model defining RFI. Selection for improved FCR in growing bulls is expected to improve 305-d fat-corrected milk in first-parity dairy cows (Nieuwhof et al., 1992).

Animal Health

There is a paucity of information on the relationship between feed efficiency and animal health, most likely because of the lack of sufficiently large quantities of information on animal health. Waasmuth et al. (2000), using Danish Jersey, Danish Red, and Danish Friesian dairy cattle, estimated genetic correlations between FCR in growing bulls and health traits in lactating animals. Many of the genetic correlations were not different from zero, the large SE partially attributable to the low heritability of the health traits. However, negative genetic correlations existed between FCR in bulls and mastitis (−0.79 to −0.15) in Danish Friesian and Jersey cows, as well as with ketosis in Danish Jersey cows (−0.37). Such possible relationships need further quantification in other populations.

Gaps in Knowledge

Although some studies in beef cattle have reported genetic correlations between feed efficiency traits and cow performance (Crowley et al., 2011a), few studies exist, and they have generally been limited in size and therefore are prone to have large associated sampling variation. Similar conclusions are evident for dairy cattle. Greater information on these associations is required.

Many traits are a function of a combination of "subtraits," and differing effects of selection for feed efficiency on the individual subtraits may not actually be observed in any differences in the phenotype itself. For example, the fertility trait calving interval is a combination of calving to first ovulation interval, expression of estrus, conception rate, ability to establish pregnancy, number of services, and gestation length. Favorable effects of selection on feed efficiency on calving to first ovulation interval and unfavorable effects on pregnancy rate may actually result in no difference in calving interval, yet the cost associated with

a greater number of required services increases. Other examples of potentially important correlated traits not generally measured are immunological status and, in grazing systems of production, the robustness of the animal to withstand any short-term reduction in either feed supply or feed quality. The latter may require altering the partitioning of energy in the animal away from production, but this repartitioning of energy away from production may not differ in animals differing in feed efficiency. Greater knowledge on the impact of selection for feed efficiency on health and disease resistance or resilience needs to be urgently quantified.

FEED EFFICIENCY IN BREEDING PROGRAMS

There is considerable commentary in the scientific literature suggesting that feed efficiency (usually RFI) should be explicitly included in the selection index or breeding goal (Van der Werf, 2004). There is no doubt that RFI has an economic weight; this is the economic value of feed intake. It is important to note that the cited "inventors" of RFI, Koch et al. (1963), suggested the use of the RFI trait when selection index methodology (Hazel, 1943) was not widely accepted as optimal. Residual feed intake is merely a selection index and can be derived using restriction index methodology (Eisen, 1977). However, restricted selection indexes will never improve the efficiency of an index unless the index weighting on the constrained trait in the unrestricted selection index is zero (Mrode, 2005). Gibson and Kennedy (1990) reported that restricted indexes cause severe losses in genetic gain and stated that restriction indexes should not be used when the goal is to improve economic merit. This may not, however, be the case if traits with nonmarket values are included in the overall breeding goal. Nonmarket goods are goods that are generally not transacted in conventional markets but, nonetheless, have public good characteristics.

Van der Werf (2004) showed that, in growing animals, including all component traits of RFI in a breeding objective or selection index is mathematically equivalent to including RFI assuming no fixed effects are included in the genetic evaluation model. Therefore, there is no additional benefit of including RFI (or any measure of feed efficiency) in a breeding goal or selection index that already includes the individual feed and production traits. Also, feed intake in a breeding goal may be an easier concept to understand by the end user compared with RFI; one option may be simply to refer to RFI as (corrected) feed intake.

Publication of breeding values for RFI (or other measures of feed efficiency) can also, however, have merit. For example, some producers may wish to apply independent culling levels for certain traits in combination with multitrait index selection despite this being suboptimal. Information nonetheless could be provided to facilitate this type of breeding strategy; producers may be reluctant to apply independent culling levels to feed intake or even accept a breeding goal that includes feed intake because of the perception that it may lead to slower-growing animals or cows that are unable to consume sufficient feed to achieve good performance (e.g., reproduction and lactation). Moreover, subindexes of traits are commonly used in breeding goals, and therefore, a subindex for feed efficiency including a residual trait (e.g., RFI, RG, RIG) may have some merit. How this subindex is marketed, however, should be undertaken with caution. If derived using genetic regression, the residual traits are genetically independent of the energy sinks but only within the population used to estimate the genetic parameters. Because genetic parameters are population specific, independence between the residual trait and the independent variable in the selection index may not be guaranteed among, for example, the elite animals. Therefore, an inappropriate recommendation may be to first screen animals on the feed efficiency traits (e.g., RFI) because of its (falsely) perceived independence from the energy sinks and subsequently select on the entire breeding goal. Irrespective, nonetheless, of whether feed intake or feed efficiency directly is included in a national breeding goal, care should be taken in how the information is used by the producer.

Furthermore, if RFI is included in a breeding goal, then the mean intake associated with a unit change in the energy sinks included in the RFI model need to be applied to the economic weight of the individual energy sink traits. For example, if RFI is calculated as the residuals from a least squares regression of feed intake on BW, then the economic value on BW will be the revenue attainable from the greater BW (as well as any non-feed-associated costs such as opportunity costs) plus the regression coefficient from the RFI regression model times the cost of feed times BW. If projected feed prices are high, then the economic weight on BW (or carcass weight) will be low or even negative, and this will likely result in poor acceptance by industry; the latter may be particularly true in countries where beef production is financially subsidized because the cost of production may be greater than the revenue attainable. Modifying breeding goals that include RFI (as opposed to feed intake directly as a goal trait) to customize for individual farming systems (e.g., rangeland farming where the economic value of feed intake may be less than for higher-energy density diets) will also be more difficult and less transparent. Moreover, Wulfhorst et al. (2010) concluded that RFI is a difficult concept, and therefore, including feed intake directly in breeding objectives may avoid confusion among the end users. Nevertheless, irrespective

of whether RFI or feed intake is directly included in a breeding objective as a goal trait in itself, the dilemma persists that to achieve very high accuracy of selection on individual animals, feed intake information is still required on a large number of animals to include either RFI (or other measures of feed efficiency based on feed intake) or feed intake in the breeding goal. The question is, what is the marginal economic benefit of measuring feed intake to capture feed efficiency in a breeding goal?

Selection index methodology (Hazel, 1943) can be used to indirectly select for a given trait by exploiting known genetic correlations with other heritable traits, where routine access to data is obtainable. We developed selection indexes to predict feed intake separately for growing and mature animals. In growing animals the genetic correlations used in the selection indexes were the mean genetic correlations from the meta-analysis of genetic correlations presented in Tables 2 and 3. Four selection indexes were evaluated: 1) ADG + BW, 2) ADG + BW + fat, 3) ADG + BW + fat + loin development as a measure of muscularity, which is known to be genetically correlated with RFI (Crowley et al., 2011b) and therefore the residual in the selection index that also includes ADG + BW, and 4) ADG + BW + fat + loin development + height at withers, which is genetically correlated with feed intake but weakly correlated with the other traits in the selection index (Crowley et al., 2011b). Only the correlation matrix for index 4 was not positive definite and required bending so that all eigenvalues were positive; only 4 of the 15 correlations changed, and all 4 changed by just 0.001. The proportion of variation in feed intake explained by the aforementioned 4 indexes was 0.70, 0.72, 0.90, and 0.99, respectively. Therefore, very high accuracy of selection on feed intake is achievable even with only a few predictor traits. However, 1) these calculations assume very large progeny group sizes with information on the predictor traits, 2) genetic parameters are likely to be population specific, and therefore, the analysis needs to be undertaken within the population where it will be used, and 3) sampling errors in the correlations may misrepresent the true genetic interrelationships. If paternal progeny group size was only 100, then the respective reliability (i.e., squared accuracy) for the different indexes would be 0.64, 0.65, 0.81, and 0.85, whereas the reliability of selection for feed intake with only feed intake information on 100 progeny would be 0.92 using the heritability estimates from the meta-analysis and the variance components from Crowley et al. (2010) and Mc Hugh et al. (2011). Nevertheless, this analysis shows that traits that can be measured routinely can actually provide very accurate predictions of genetic merit for feed intake and therefore feed efficiency. Other traits such as activity (Robinson and Oddy, 2004), where recording can also be automated, could further improve the accuracy of predic-

tions. The remaining unexplained variation in feed intake is RFI; however, as prediction models improve, the biological variation in RFI will diminish.

Using estimated genetic correlations between feed intake and milk yield, BW, BCS, and stature and chest width type traits of lactating Holstein-Friesian dairy cows in the United Kingdom (Veerkamp and Brotherstone, 1997) and a correlation of 0.37 between stature and chest width estimated in lactating Irish Holstein-Friesian primiparous cows (Berry et al., 2004), 3 selection indexes were also generated to predict mature cow feed intake. The 3 selection indexes were 1) milk yield + BW, 2) milk yield + BW + chest width, and 3) milk yield + BW + chest width + stature. The proportion of genetic variation in feed intake explained by the three indexes was 1) 0.45, 2) 0.51, and 3) 0.89. Type traits are routinely recorded in dairy cattle breeding programs and can also be used to predict BW (Banos and Coffey, 2012). Therefore, good accuracy of selection for mature cow feed intake is possible using routinely available traits.

Gaps in Knowledge

Although research is ongoing on methods to collect actual feed intake at a low cost, the ability to predict feed intake at a genetic level, using more easily collected information, should also be investigated. Here we presented examples using a selection of traits and genetic parameters taken from the literature. Because genetic parameters are population specific and not all traits are measured in all breeding programs, the calculations should be undertaken in different populations. The proportion of genetic variance in feed intake explained by the traits in the selection index can easily be calculated as

$$C'V^{-1}C,$$

where C is the vector of genetic correlations between the predictor traits and feed intake and V is the matrix of genetic correlations among the predictor traits.

Where unexplained genetic variation in feed intake exists after using all potential predictor traits available, the usefulness of other potential predictor traits should also be investigated. One such example trait may be a measure of animal capacity, either subjectively scored as undertaken in many linear type classification systems in dairying (Berry et al., 2004) or by objective measurement of girth, as well as other skeletal measures (Berry et al., 2005). Other biologically plausible phenotypic tools already available, such as measurements from pedometers for grazing animals, can be used to predict the quantity of time spent grazing. Current technologies can also be easily modified to aid in the estimation of genetic merit for feed intake. For example, electronic identifica-

tion of animals during milking can easily be modified and placed near the feed bunker to quantify the time each animal spends eating or the number of feed events; differences in feeding activity are phenotypically associated with differences in feed intake (Basarab et al., 2011; Durunna et al., 2012). Whether or not to invest in the collection of such phenotypic information will be dictated by the marginal response in genetic gain (ignoring any benefits to management decisions) in the overall breeding goal from measuring such traits.

Well-designed selection experiments are key to understanding the implications of selection for feed efficiency. The "saved" energy in more efficient animals is likely to have implications for the animal, and this can be best identified by aggressive selection for the phenotype under investigation and evaluating the impact in contrasting production systems. This is particularly important if estimates of genetic merit for feed efficiency are derived in a production system different from where most of the germplasm will be used (i.e., performance testing on a high-energy diet where progeny will produce on extensive production systems). To our knowledge, estimates of predicted feed efficiency performance in animals are solely based on additive genetic merit. Although the contribution of nonadditive genetic variation to differences in feed efficiency is not known, heterosis and recombination losses contribute to phenotypic variation. Many animals are crossbred, and therefore, an index that combines additive and nonadditive genetic merits, including systematic environmental effects that were removed in the genetic evaluation statistical model but that will influence the performance of the animals (e.g., dam parity), could be generated for individual animals, and these animals could be grouped and possibly managed differently. This is particularly true if the already observed G×E interactions for feed efficiency (Durunna et al., 2011b) result in management protocols for animals differing in feed efficiency. Feedlot animals will not be used for breeding, so differentiation of additive and nonadditive genetic variation is not important, but predicted performance is important for the producer.

SUMMARY AND CONCLUSIONS

There is no denying the large task faced by animal scientists of feeding an ever-increasing world population while taking cognizance of the environmental footprint of such endeavors. Improved feed efficiency over a given time period is crucial in achieving this goal. The marginal cost:benefit of measuring individual animal feed intake should be quantified for animal breeding programs. Nonetheless, populations segregated for feed efficiency variables, such as RFI or RG, can provide a very useful research resource to understanding the biological mecha-

nisms governing differences in animals for the trait under investigation. Large gaps in knowledge have been identified, and further research is required to fill these gaps.

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