Understanding the Physiological Aspects to Improving Feed Efficiency in Dairy Cows

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The Basics of Feed Efficiency

Information about this topic was published by the author in the 2014 Proceedinsgs of the TriState Dairy Nutrition Conference (VandeHaar, 2014) and in 2 recent reviews (Spurlock and VandeHaar, 2013; VandeHaar et al., 2016). In this paper, I will briefly discuss some of our group's most recent findings and other relevant work for understanding the physiology behind feed efficiency. Parts of this paper rely heavily and use direct quotes from the most recent paper (VandeHaar et al., 2016), published in the Journal of Dairy Science.

We generally define feed efficiency as the energy captured in milk and body tissues per unit of feed energy. Feed efficiency is best considered on a whole farm level and thus should account for feed wastage and the salability of products, as well as the economic value of feed and milk components. However, in a discussion of physiological factors, it is logical to more reasonable to consider efficiency on an individual cow basis. The questions then become: "Why are some cows and diets more efficient that others?" and "Can we accurately identify and reliably take advantage of these differences?"

The modern dairy cow is already amazingly efficient. Milk synthesis is an efficient process compared to muscle deposition, and the level of milk production is a major determinant of feed efficiency because more milk per cow dilutes out the feed associated with meeting the maintenance requirement of the cow. Body weight is also important because it is a major determinant of a cow's maintenance requirement and a driver of intake. Cows differ genetically from each other in their innate physiology associated with maintenance needs, milk production capacity, metabolism, and nutrient partitioning functions. Diet composition and management also influence feed efficiency because they determine the energy density of a diet, its losses as feces, methane, urine, and heat, and the cow's ad libitum intake, milk production, and body weight change. In addition, the portion of a cow's life spent as a heifer or dry cow will alter lifetime feed efficiency.

Feed energy can be considered several ways. The total energy of a feed is its Gross Energy (**GE**). Some GE is lost as the chemical energy in feces, urine, and gasses, and the remainder is Metabolizable Energy (**ME**). Some ME is lost as heat associated with processing food to Net Energy (**NE**), which is the chemical energy of products like milk and body tissues and that needed for maintenance. The major factors affecting feed efficiency can be divided into: 1) those that alter maintenance and the portion of NE that is captured in milk or body tissues instead of used for maintenance, and 2) those that alter the conversion of GE to NE. Cows that

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eat and produce more generally capture a greater fraction of NE in products. Cows also vary in converting GE to NE. How we breed, feed, and manage cattle can affect both of these.

Diluting Maintenance to Capture NE More Efficiently

Nutritionists have long considered the maintenance requirement of an animal to be proportional its "metabolic body weight" (**MBW**), defined as BW to the 0.75 power. In the Dairy NRC (2001), the average daily maintenance requirement for dairy cows is described by the formula, 0.08 Mcal of NE_L x MBW. Thus, the typical Holstein cow has a maintenance requirement of ~10 Mcal of NE_L/day (equivalent to ~25 Mcal of GE and ~6 kg of feed). This feed is used for life-sustaining functions, such as circulation and respiration when she is not producing milk, growing, working, or pregnant and she is in her thermoneutral zone. Thirty years ago, Baldwin and coworkers (1985) divided whole-body maintenance energy expenditure into 3 major classes: 40 to 50% is work functions (liver, heart, kidney, nerve, and lung work), 15 to 25% is cell component synthesis (primarily protein and membrane lipids), and 25 to 35% is membrane transport (mostly associated with membrane potential maintenance and Na^+, K^+-ATPase). They suggested that considerable animal variation in maintenance energy requirement seems to exist and could be used to increase efficiency. More recently, McNamara (2015) used simulations of reported variations in 2 basal maintenance functions, ion pumping and protein turnover, and found that the maintenance requirements could vary by 20% among cows producing similar levels of milk. For a cow weighing 700 kg (~1600 lb), this is ~2 Mcal of NE_L. To put in context, 40 kg of milk is ~30 Mcal of NE_L, so cows that need 20% less for maintenance, need 5% less feed (2 to 3 lb, 30 to 40¢) per day.

However, recent evidence suggests that the maintenance requirement per unit of metabolic BW (MBW, $BW^{0.75}$) has increased over time for dairy cattle and now is perhaps 0.1 x MBW or even higher (Moraes et al., 2015). Apparently, we have selected dairy cattle that require more feed per unit of MBW just to survive. Reasons for the higher maintenance requirement are not clear but likely are associated with increased digestive and metabolic activity. Statistical models assign this heat to maintenance, but in my view, it should instead be assigned to the extra heat production associated with feeding and lactation. All the same, a savings in maintenance costs could well be worth our attention.

The body size of dairy cattle has increased in the past 50 years, and most top sires in the AI industry were and still are larger than breed average (Hansen, 2000). This change is not consistent with the goal of increasing feed efficiency. We might expect that higher producing cows would weigh more because some of the hormones that control lactation, such as somatotropin, also control growth, and bigger cows might have greater capacity to eat and produce milk. At one time, a genetic correlation between BW and milk production might have existed (Freeman, 1975). However, our latest analysis on 5000 Holstein cows in mid-lactation demonstrated no genetic correlation between BW and milk energy output (VandeHaar et al., 2014); moreover, BW was genetically correlated negatively with gross feed efficiency. In a smaller subset of that data, Manzanilla-Pech et al. (2016) found that milk energy output was not positively correlated with BW, stature, chest width, or body depth. Already 40 years ago, Freeman (1975) pointed out that, "Heavier weight per se is not necessarily desirable, particularly when it is negatively correlated, phenotypically and genetically, with efficiency." It is ridiculous that parts of our industry continue to favor larger cows, despite the fact that the data show that they are less efficient and are not more profitable. In my opinion, based on these data, breeding for more milk is a more important priority to improve efficiency than is breeding for smaller BW, but smaller BW can be a means to improve efficiency with no concomitant negative consequence for milk production, and the best way to improve efficiency is to use a linear index that favors greater milk production and smaller BW together.

Considerations in Converting Feed GE to NE More Efficiently

The importance of diet in the conversion of GE to NE has been reviewed (Smith, 1988; VandeHaar, 1998; Arriola Apelo et al., 2014). Clearly, diet directly impacts feed efficiency. If a cow eats to her energy requirements, then less feed is needed as diets are more energy-dense. Hence, feeding: 1) more starch and less fiber, 2) fiber with greater digestibility, or 3) supplemental fat all would be expected to improve the conversion of GE to NE. Such changes can be predicted, albeit inaccurately, using nutrition models, such as NRC (2001). Diet composition also alters a cow's appetite and partitioning of nutrients (Allen and Piantoni, 2014). Thus, because feed intake alters the dilution of maintenance, the effect of diet on efficiency is not always easy to predict. However, feed efficiency is not very important in making decisions about diet composition. If attaining the highest feed efficiency was the goal in making feeding decisions, all dairy cattle would be fed diets high in grains and fats with minimal forage and byproduct feeds. One of the values of the ruminant system is its ability to obtain energy from fibrous feeds, such as forages and high-fiber byproducts. To enhance sustainability and justify the dairy industry as a contributor to food security for humans, the use of grains and fats in dairy diets should be limited to those times when they can be used to optimize production and health, and forages and byproduct feeds high in fiber should be fed to dairy cattle when possible. For the purposes of animal selection, however, gross feed efficiency is highly correlated with milk per acre and profitability per cow.

Feed intake, and thus feed efficiency, can be predicted with reasonable accuracy across a wide range of production levels and body weights (Berry and Crowley, 2013). Higher production per unit BW improves efficiency because of the dilution of maintenance. However, based on our data, feed efficiency varies considerably within a production level. One way to examine this variation is residual feed intake (**RFI**), a measure of efficiency that is independent of production level and can be considered "unjustified feed intake". Cows that eat less than expected based on production relative to BW and BW change have a negative RFI and are desirable. Using 5000 cows from North America, the Netherlands, and Scotland, we recently showed that RFI has a heritability of 0.17 (Tempelman et al., 2015). RFI has little value for nutritionists, but it has potential in our search for more efficient animals in selection.

For RFI to be effective in the search for a more efficient cow, it must be a repeatable trait across climate conditions, diets, lactation stage and number, and stage of life. Data to date suggest that it is. Potts et al. (2015) fed 109 cows diets with ~14 or 30% starch in a cross-over design and found the correlation for RFI of a cow when fed a high starch diet with her RFI when fed a low starch diet to be 0.7. Preliminary data from our lab suggest it also is repeatable across diets with varying forage content (Mangual et al., unpublished). Finally, RFI is repeatable across lactations, stages within a lactation, and stages of life (Connor et al., 2013; MacDonald et al., 2014; Tempelman et al., 2015).

Traditional selection cannot be used for RFI, because phenotypes of daughters on commercial farms are not known. However, the advent of genomic selection enables selection for new traits like feed efficiency. An excellent review on the methodology of genomic selection, especially for nongeneticists, is Eggen (2012). The use of genomics in selection against RFI or DMI is already beginning in Australia (Pryce et al., 2015) and the Netherlands (Veerkamp et al., 2014) and will likely occur in North America in the near future. It is important to note that RFI is only part of feed efficiency. Selection for efficiency must also consider the optimal levels of milk production relative to BW to dilute out maintenance. The approach used by Pryce et al. (2015) seems reasonable, with an index to select against body size and against RFI, while also selecting for milk yield and composition.

Biological Basis for Residual Feed Intake

RFI is essentially the differences in feed intake among animals that cannot be explained by diets, environment, milk production, BW, and BW change, or in other words, our best nutrition models. Differences in efficiency among cows in milk production relative to BW are accounted for in our models. RFI is associated mostly with the conversion of GE to NE, and thus is due to differences amongst cows in digestibility, methane production, urinary energy losses, and metabolic pathways involved in processing nutrients and determining how much heat is produced above the animal's basal heat production for maintenance. Based on limited data in beef cattle, Herd and Arthur (2009) estimated that the contribution of various biological processes to RFI was 10% digestion, 37% tissue metabolism, 9% heat increment of feeding, 10% activity, 5% body composition, 2% feeding patterns, and 27% unknown; interestingly, these contributions are reasonably similar to the energy flows found in typical nonlactating cattle. Given that measurement error is part of RFI, this unknown contribution could be error and the true biological RFI among cows is smaller than the measured RFI.

After accounting for the 27% unknown in Herd and Arthur (2009) estimates, differences in digestive efficiency might be expected to contribute 10 to 20% of the differences in RFI among cows. Recent data from our project upholds this. Based on data of 110 lactating cows fed 2 diets, we found that digestibility accounted for up to 33% of the variation in the ability of cows to extract NE from feed (Potts et al., 2015). In addition, the ruminal microbiome may play a role in feed efficiency and differences in the microbiome likely affect digestive efficiency, methanogenesis, and the heat of fermentation. However, it seems likely that the cow and what she is fed control the microbiome, not the other way around. Whether changes in the microbiome will someday be part of our decision-making in feeding and breeding is not clear to me, but differences in digestive ability (including microbial fermentation of course) surely will be an important consideration for productivity and methanogenesis, and likely efficiency.

Multiple postdigestion processes likely are involved in variation in RFI. In beef cattle, divergent RFI phenotypes have been associated with differences in mitochondrial function, muscle protein breakdown, cortisol levels, and feeding behavior (Castro et al., 2007; Bingham et al., 2009; Kelly et al., 2010; Kolath et al., 2006; Montanholi et al., 2010). Less work has been done in dairy cattle, but genomic analyses are beginning to give insight on the physiological basis for differences in efficiency amongst cows. Davis et al. (2014) developed genomically estimated breeding values (**GEBV**) for RFI in growing Holstein heifers and detected differences in RFI of lactating based on the heifer GEBV. Their data suggest that differences in efficiency are controlled by the digestive and metabolic factors that are important for both growth and lactation, such as mitochondrial function. In an analysis of 2900 Holstein cows, Spurlock et al. (2014) showed that 61,000 single nucleotide polymorphisms (**SNP**) accounted for 14% of the variance in RFI, with the top 10 SNP accounting for 7% of the genetic variance. Six of the 8 chromosomes harboring major quantitative trait locus (**QTL**) influencing RFI did not influence DMI, milk energy output, or BW, indicating the possibility that genes important for digestive or central metabolic functions might be involved. Verbyla et al. (2010) examined SNP that might account for differences in energy balance (which in their model was very similar to RFI) and found differences in a transcription factor (COUP-TFII) that plays an essential role in regulating adipogenesis, glucose homeostasis, and energy metabolism. Continued advancements in the science of nutritional and genetical genomics will help us to integrate our understanding of basic biology with more empirical data. Someday, we may be able to select for specific metabolic traits or to select genotypes to match environments.

Conclusion and Implications

Feed efficiency, or the efficiency of converting feed to milk, matters on farms because it has a major influence on farm profitability and environmental stewardship in the dairy industry. Dairy feed efficiency in North America has doubled in the past 50 years, largely as a byproduct of selecting and managing cows for increased productivity. Increasing productivity results in a greater percentage of total feed intake being used for milk instead of cow maintenance. In the future, we can continue to increase efficiency by striving for greater productivity relative to body size across the life of the cow and by directly setting product per unit feed as a goal. Mechanisms responsible for greater efficiency include improved digestibility and decreased metabolic work associated with maintenance and lactation functions, but we still have much to learn about why some cows are more efficient that others. Regardless, the science of genomics will enable us to select for more efficient genotypes for the future. Understanding the physiology will help us to optimize selection for the needs of the future.

Our decisions in sire selection determines what type of animal we must feed and manage in the future. Too often, we select for large cows just because we like large cows and think they will produce more milk, but the genetic correlation of cow size and productivity is zero within the Holstein breed. There can be absolutely no justification for favoring large cows, and it is time for all of us to quit showing them favoritism - they are making our industry less efficient! Someday, we will also be able to select cows against feed intake. In the meantime, it is reasonable to continue selecting for greater milk production, but we should also select for modest reductions in body size.

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