Breeding Dairy Cattle for Improved Feed Efficiency: An Overview

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Abstract

The economic importance of selecting for improved feed efficiency has been clearly recognized by cattle producers. It has the potential to reduce costs considerably, minimize environmental impacts (e.g. reduce nutrient loss in manure and methane intensity) and improve the cattle industry profitability. Feed efficiency is a complex trait that describes units of product output per unit of feed input, with the units generally being mass, energy, protein, or economic value. The objective of this paper is to present, using layman's terms, a summarized overview of genetic selection for improved feed efficiency and international initiatives to implement genomic selection for feed efficiency, with a focus on dairy cattle. Various studies have indicated that feed efficiency, assessed based on alternative indicators, is heritable and genomic selection can be successfully implemented. However, selection based on genomic information still requires genotyping of selection candidates, as well as continued collection of phenotypic and genotypic records from genetically-representative individual animals (i.e. training population). Initiatives around the world have worked collaboratively to develop research and gather datasets for successful implementation of joint genomic evaluations.

Introduction

The global human population is expected to reach 9.8 billion people by 2050 (FAOSTAT, 2019), and consequently, a substantial increase in food demand is expected. In addition, the projected reduction in poverty and expansion of the middle class will reflect in a greater demand for larger amounts of high-quality meat and dairy products, produced under exemplary welfare conditions and leaving reduced environmental footprints. Therefore, there is an urgent need to develop strategies to optimize the efficiency of food production. The current worldwide cattle population has more than 1.5 billion animals, with over 105 million being raised in Canada and the United States (FAOSTAT, 2019). Feeding is currently one of the largest expenses in cattle production (Ho et al., 2013; Connor, 2015), and therefore, even a small improvement in nutrient utilization (i.e. better digestibility and/or greater nutrient absorption) can have major economic and environmental impacts worldwide. Among them, reductions in feeding costs will positively impact not only the farmer's profitability, but also the final prices of meat and dairy products available to consumers.

In order to optimize animal nutrition practices, there have been significant investments in research over the past decades. Consequently, the science of animal nutrition has evolved rapidly and resulted in major contributions

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to a better understanding of the nutritional physiology of cattle and its nutrient requirements, which has brought as outcome advances in diet formulation, supplementation, and techniques for food processing and storage (Eastridge, 2010; Coffey et al., 2016; Ondarza and Tricarico, 2017; Tedeschi et al., 2017). Despite the clear effectiveness of all these developments, the need for a more permanent and cumulative solution has been envisioned through genetic selection for a long time in various livestock species, including cattle (e.g., Stone et al., 1960; Koch et al., 1963; Freeman, 1967; Herd et al., 2003).

The economic importance of selecting for improved feed efficiency has been clearly recognized by cattle producers. Selecting animals for feed efficiency has the potential to reduce costs considerably, minimize environmental impacts (e.g. reduce nutrient loss in manure and methane intensity) and improve the cattle industry profitability (Richardson and Herd, 2004; Basarab et al., 2013). However, the inclusion of feed efficiency in selection indexes used in commercial breeding programs has been delayed for various reasons, among them: 1) the limited amount of phenotypic records for feed efficiency (and related variables) in commercial herds; 2) the differences in measurement protocols and data sources (e.g. different breeds, lactation stages, parity, diet, etc.); and 3) unclear definition of the breeding goal (based on indicator traits) (Berry and Crowley, 2013; Pryce et al., 2014; Connor, 2015; Hurley et al., 2016).

With the more recent advancements in genomic methods and technologies, selection for feed efficiency in cattle has become more feasible, as genomics can be used as a tool to transfer the knowledge generated in research farms to genetically-connected commercial populations (Connor, 2015). However, selection based on genomic information still requires genotyping of selection candidates, as well as continued collection of phenotypic and genotypic records from genetically-representative individual animals (i.e., training population). The objective of this paper is to present, using layman's terms, a summarized overview of genetic selection for improved feed efficiency and international initiatives to implement genomic selection for feed efficiency, with a focus on dairy cattle.

Definitions of Feed Efficiency and Indicator Traits

Dairy cattle breeding programs have been successful on improving traits of interest to the industry (as reviewed by Miglior et al., 2017). The first step to promote genetic progress in the right direction in any breeding program is to clearly define the breeding goals. In the case of feed efficiency, it has been broadly defined as animals that eat less with no compromise in performance or that produce more consuming the same amount of feed. In other words, feed efficiency describes units of product output per unit of feed input, with the units generally being mass, energy, protein, or economic value (Vandehaar et al., 2016). It is also of interest of cattle breeders to select animals that do not compromise other vital functions (e.g., reproduction, health, etc.) in order to achieve a greater feed efficiency.

Feed efficiency is a very complex trait, as feed intake and nutrient utilization are associated with various biological and physiological mechanisms that can be altered by the environment (e.g., diet composition, nutritional management practices) and other genetic effects (e.g., breed). For instance, variability in feed efficiency can arise due to variations in feed intake levels, digestion of feed (and the associated energy costs) and absorption of nutrients, metabolism (anabolism and catabolism associated with body composition), physiological stage, health

status, rumen microbial metabolism, activity, and thermoregulation (Herd et al., 2004; Herd and Arthur, 2007; Patience et al., 2015; Li et al., 2016).

Over time, a large number of indicator traits have been proposed and utilized to assess feed efficiency (Koch et al., 1963; Berry and Crowley, 2013; Pryce et al., 2014; Connor, 2015; Hurley et al., 2016; Ondarza and Tricarico, 2017). In 1963, Koch et al. suggested the use of "residual feed intake (**RFI**)" as an indicator of feed efficiency. In brief, RFI measures, through a regression model, the difference (residual) between the observed feed intake and expected feed intake (based on feeding requirements assessed according to metabolic body weight (**BW**) and level or quantity of product outcome). Additional energy sinks, such as energy required for certain activities and reproduction, can also be included in the calculations (Berry and Crowley, 2013; Pryce et al., 2014). RFI has been widely used in beef cattle (Berry and Crowley, 2013); however, more recently, it has also started to be studied in dairy cattle (Waghorn et al., 2012). In the case of dairy cattle, RFI is calculated by regressing dry matter intake (**DMI**) on various energy sinks of the animal, including parameters representative of milk yield and composition, metabolic BW, changes in BW and/or body condition score, and lactation stage (Connor, 2015; Byskov et al., 2017).

As described in Pryce et al. (2015), the practicality and costs of collecting individual feed intake on a large number of animals motivated the implementation of selection for improved feed efficiency based on indirect traits, such as production levels, BW (or predicted BW) and/or conformation traits. Some national breeding programs (e.g., Australia, New Zealand and USA) have incorporated this indirect measure of feed efficiency into their selection indexes (VanRaden et al., 2007; Veerkamp et al., 2013; Pryce et al., 2014; Pryce et al., 2015). One of the limitations with this approach is that the true variation in feed efficiency remains uncaptured (Pryce et al., 2015). Gibson (1986) presented a correlation between RFI and predicted feed efficiency (derived from BW and production) of 0.84, indicating the relevance to actually measure feed intake (as discussed in Pryce et al., 2014).

In the 1990's, there was a great interest from the industry to include feed efficiency as part of the dairy breeding objectives, which motivated various organizations to collect individual feed intake records for research and genetic evaluations, as described in various studies, such as Van Arendonk et al. (1991) and Veerkamp et al. (1994). The majority of these pioneer studies investigating feed efficiency in dairy cattle focused on individual feed intake recorded in lactating cows. In this context, Veerkamp et al. (2014) suggested selecting for reduced DMI predicted using actual DMI records in addition to selected yield and type traits.

Another group of indicators of feed efficiency are based on nutrient usage, such as energy and nitrogen efficiency, unfolding nutrient partitioning between milk production and other nutrient uses (Ondarza and Tricarico, 2017). Energy conversion efficiency is calculated as milk energy output divided by metabolizable energy intake. Similar to feed efficiency based on DMI, it does not account for mobilization of body reserves. To account for body reserve changes, "residual energy intake" has also been proposed as actual metabolizable energy intake minus the predicted energy requirement of the cow based on production, BW, changes in BW and/or body condition score, and gestational energy needs (Mantysaari et al., 2012).

As the costs to measure feed intake in individual cows are still high, alternatives have been investigated. A very promising option is to use predictor traits that can be measured in a large number of animals from an easily acquired sample, such as milk, blood, sensors, and automated recording systems. Some examples include: infrared thermography (Montanholi et al., 2010), plasma concentrations of IGF-1 (Moore et al., 2005), milk mid-infrared (**MIR**) spectrometry (O'Donovan et al., 2014; Wallen et al., 2018), and fatty acid composition (Kelly et al., 2010). Currently, the majority of Dairy Herd Improvement (**DHI/DHIA**) milk laboratories routinely quantify major milk components, such as fat or protein, using MIR spectrometry due to its efficiency and low cost compared to traditional chemical analysis. Thus, the MIR spectrometry may yield very useful source of information for genetic selection to improve feed efficiency.

Genetic Architecture of Feed Efficiency

Before including a trait in a genetic selection index, it is important to evaluate its heritability (h^2) in the population of interest, as well as its genetic correlation with other economically important traits. These genetic parameters give insights into the rate of genetic progress that can be achieved per generation and contribute to better designing the genetic evaluation systems. Studies in the literature have indicated that feed efficiency, assessed in different ways using indicator traits, is moderately heritable (Table 1). For example, Williams et al. (2011) reported that significant variation in RFI exists in dairy heifers and this could be an alternative to indirectly selecting dairy cows for improved feed efficiency, as it is easier to record feed intake in heifers (similar systems compared to beef cattle). Spurlock et al. (2012) estimated genetic parameters and made recommendations regarding traits

related to energy balance, including DMI, BW, body condition score, energy-corrected milk production, and gross feed efficiency.

The h^2 estimates presented in Table 1 indicate that feed efficiency, measured using the different indicator traits, has a moderate genetic component, and therefore, can be improved through genetic selection. The wide range of h^2 estimates reported in the literature are likely related to the different populations used in each study, as genetic parameters (such as h^2 estimates) are population-specific. Thus, this suggests the importance of (re-)estimating specific genetic parameters for each population.

It is important to note that selection for improved feed efficiency might also impact other economically important traits, due to genetic correlations. Genetic correlations published for different indicator traits of feed efficiency and some production traits are summarized in Table 2.

Genomic Selection

As previously outlined, the costs and practicality of measuring individual feed intake (and related traits, such as BW) in a large number of animals with pedigree information has limited the implementation of genetic selection for feed efficiency. More recently, genomic selection has become widely available in the dairy cattle industry and has enabled selection of breeding candidates based on their predicted genetic merit for feed efficiency. This is because animals from research herds can be used as a training population to estimate the marker effects, which are then used to predict the breeding values for selection candidates based on their own genotype (Veerkamp et al., 2015). In brief, genomic selection refers to the use of genome-wide genetic markers to predict breeding values of selection candidates (Meuwissen et al., 2001).

In 2014, Gonzalez-Recio et al. described the implementation of heifer feed efficiency in the Australian selection index, using genomic selection and its impact in the industry. In 2015, the same research group (Pryce et al., 2015) defined and described the implementation of genetic evaluation for feed saved, as a new indicator of feed efficiency in dairy cows. "Feed saved" combines RFI with mature BW estimated using estimated breeding values (**EBV**) for predicting maintenance costs, so that feed requirements are quantified in a single breeding value. Since April 2015, feed saved has been included as part of the Australian national selection index.

The success of the use of genomics to select for improved feed efficiency can be measured based on the accuracy of genomic predictions, which depends on various factors, including trait heritability, size of the training population (number of individuals with both genotypes and phenotypic records), linkage disequilibrium, SNP chip panel used for genotyping, and effective population size. Among those factors, the number of animals used in the training population is still the main limiting factor to implement genomic selection for feed efficiency in the dairy industry (Berry and Crowley, 2013). Some alternatives have been investigated to increase the training population for feed efficiency, including the use of data from nutrition studies (Veerkamp et al., 2014; Tempelman et al., 2015) and combining data from different countries (de Haas et al., 2012; Pryce et al., 2012; Banos and Coffey, 2012; Berry et al., 2014; Tempelman et al., 2015) or breeds (Khansefid et al., 2014). It is worth noting that in the last few years, a collaboration group named "The global Dry Matter Initiative (**gDMI**)" has been created to combine feed intake records, which includes 10 research herds from 9 countries (de Haas et al., 2015). Other contributions to international

genetic evaluations for feed intake in dairy cattle are presented in Berry et al. (2014). There are also other initiatives to combine data from all over the world for genomic predictions for feed efficiency, such as the Efficient Dairy Genome Project (http://genomedairy.ualberta.ca/), which will be mentioned in more details later.

In general, genomic predictions for feed efficiency have been performed based mainly on DMI and RFI, which is probably related to the greater availability of phenotypic records for these indicator traits. Some accuracies of genomic predictions for DMI and RFI that have been reported in the literature are summarized in Table 3. These results indicate that there is still room for improving the prediction of genomic breeding values. The refining of the statistical models used, as well as an increase in the training populations, will likely contribute to improve the observed accuracies.

Data Collection and International Efforts for Data Gathering

To genetically select animals for improved feed efficiency, at least pedigree information and individual phenotypic records associated with feed intake and production traits are required. The simplest way to record DMI is based on the amount of feed offered and refused by each cow per day, with the associated DM percentage. Other important variables to be recorded are milk production and composition, lactation stage, water intake, diet composition, BW and body condition score over the course of lactation, health/disease events, and reproductive performance traits. It is important to notice that even if not all these variables are used in the genetic/genomic evaluations, they might be useful in the future for research and also selection purposes. Furthermore, the costs to record these additional traits are low compared to the cost of individual feed intake recording (Veerkamp et al., 2015).

There are various automated systems available for feed intake recording, including Calan Broadbent (American Calan Inc. Northwood, NH), Gallagher Animal Management Systems (Hamilton, New Zealand), GrowSafe 4000 System (GrowSafe Systems, Ltd., Airdrie, AB, Canada), and the RIC system (i.e. Insentec; Hokofarm Group B.V., Marknesse, The Netherlands). These systems are mostly based on radio-frequency identification to track and record individual feed intake, as well as feeding behavior (e.g. number of visits per day and intake duration). As discussed by Connor (2015), the use of these systems in dairy cattle has been limited to research herds or growing heifers. The use of automated feed monitoring systems in larger groups of lactating cows is greatly hindered by the limited feeding capacity of the automated feed bunks, meaning that significantly fewer cows can be fed from a single bunk relative to growing cattle to accommodate substantially greater intakes of lactating cows (Connor, 2015).

It is well-established that the success and long-term sustainability of any livestock breeding program is largely dependent on the amount and quality of pedigree, phenotypic and genotypic data available for genetic and genomic evaluations. As feed efficiency is difficult and expensive to measure, a global effort to enlarge the training population for genomic evaluations is crucial and has the potential to greatly benefit all groups involved in the project. In addition to the gDMI Project mentioned before, the Efficient Dairy Genome Project (EDGP, www.genomedairy.ualberta.ca) is a large international research project led by Canadian institutions aiming to develop strategic research, tools, and the whole infrastructure to implement genetic and genomic evaluations for improved feed efficiency and reduced methane emissions in dairy cattle.

The EDGP database was developed in 2017 to allow data sharing among the international collaborators. Currently, the database contains records on feed intake of 5,289 cows and methane emissions on 1,337 cows from 8 research herds in 6 countries (Australia, Canada, Denmark, Switzerland, United Kingdom and United States). An international genetic evaluation seems possible due to the high level of relatedness of the Holstein population, the most common dairy breed with records for feed efficiency. Moreover, all collaborators are members of the International Committee for Animal Recording (ICAR, www.icar.org/), providing standardized information on production records.

Conclusions

Feed efficiency, assessed based on different indicators, is a heritable trait and can be improved through genetic and genomic selection. There is still a need to refine the breeding goal and identify indicator traits that can be easily and cheaply measured. Various groups around the world are collaboratively working to refine the methods used in the evaluations, as well as enlarging the datasets used for genomic evaluations.

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References

Banos, G., M.P. and Coffey. 2012. Technical note: Prediction of live weight from linear conformation traits in dairy cattle. J. Dairy Sci. 95, 2170–2175.

Basarab, J.A., K.A. Beauchemin, V.S. Baron, K. H. Ominski, L.L. Guan, S.P. Miller, and J.J. Crowley. 2013. Reducing GHG emissions through genetic improvement for feed efficiency: Effects on economically important traits and enteric methane production. Animal. doi:10.1017/S1751731113000888.

Berry, D.P., and J. J. Crowley. 2013. Cell biology symposium: Genetics of feed efficiency in dairy and beef cattle. J. Anim. Sci. doi:10.2527/jas.2012-5862.

Berry, D.P., M.P. Coffey, J.E. Pryce, Y. De Haas, P. Løvendahl, N. Krattenmacher, J.J. Crowley, Z. Wang, D. Spurlock, K. Weigel, and K. Macdonald. 2014. International genetic evaluations for feed intake in dairy cattle through the collation of data from multiple sources. J. Dairy Sci. 97(6):3894-3905.

Bilal, G., R.I. Cue, and J.F. Hayes. 2016. Genetic and phenotypic associations of type traits and body condition score with dry matter intake, milk yield, and number of breedings in first lactation Canadian Holstein cows. Can. J. Animal Sci. 96(3):434-447.

Bolormaa, S., J.E. Pryce, K. Kemper, K. Savin, B.J. Hayes, W. Barendse, A. Reverter, R.M. Herd, Y. Zhang, B. Tier, and M.E. Goddard. 2013. Prediction of genomic breeding values in beef cattle. J. Animal Sci. 91:3088–3104.

Byskov, M.V., A. Fogh, and P. Løvendahl. 2017. Genetic parameters of rumination time and feed efficiency traits in primiparous Holstein cows under research and commercial conditions. J. Dairy Sci. doi:10.3168/jds.2016-12511.

Coffey, D., K. Dawson, P. Ferket, and A. Connolly. 2016. Review of the feed industry from a historical perspective and implications for its future. J. Appl. Anim. Nutr. doi:10.1017/jan.2015.11.

Connor, E.E. 2015. Invited review: Improving feed efficiency in dairy production: Challenges and possibilities. Animal. doi:10.1017/S1751731114002997.

De Haas, Y., M.P.L. Calus, R.F. Veerkamp, E. Wall, M.P. Coffey, H.D. Daetwyler, B.J. Hayes, and J.E. Pryce. 2012. Improved accuracy of genomic prediction for dry matter intake of dairy cattle from combined European and Australian data sets. J. Dairy Sci. 95:6103–6112.

De Haas, Y., J.E. Pryce, M.P.L. Calus, E. Wall, D.P. Berry, P. Løvendahl, N. Krattenmacher, F. Miglior, K. Weigel, D. Spurlock, and K.A. Macdonald. 2015. Genomic prediction of dry matter intake in dairy cattle from an international data set consisting of research herds in Europe, North America, and Australasia. J. Dairy Sci. 98(9):6522-6534.

Eastridge, M.L. 2010. Major advances in applied dairy cattle nutrition. J. Dairy Sci. doi:10.3168/jds.s0022-0302(06)72199-3.

FAOSTAT, 2019. Food and Agriculture Organization of the United Nations. Food and Agriculture database. Access at: http://www.fao.org/faostat/en/#data/QL.

Freeman, A.E. 1967. Genetic aspects of the efficiency of nutrient utilization for milk production. J. Animal Sci. 26(5):976-983.
Gibson, M.P. 1986. Efficiency and performance of genetically high and low milk- producing British Friesian and Jersey cattle. Animal Prod. 42:161–182.

Gonzalez-Recio, O., J. Pryce, M. Haile-Mariam, and B. Hayes. 2014. Incorporating heifer feed efficiency in the Australian selection index using genomic selection. J. Dairy Sci. 97:3883–3893.

Herd, R.M., J.A. Archer, and P.F. Arthur. 2003. Reducing the cost of beef production through genetic improvement in residual feed intake: Opportunity and challenges to application. J. Anim. Sci. doi:10.2527/2003.8113_suppl_1E9x.

Herd, R. M., and P. F. Arthur. 2007. Physiological basis for residual feed intake. J. Anim. Sci. 87:E64–71. doi:10.2527/jas.2008-1345.

Herd, R.M., V.H. Oddy, and E.C. Richardson. 2004. Biological basis for variation in residual feed intake in beef cattle. 1. Review of potential mechanisms. Aust. J. Exp. Agric. doi:10.1071/ea02220.

Ho, C., B. Malcolm, and P. Doyle. 2013. Potential impacts of negative associative effects between concentrate supplements, pasture and conserved forage for milk production and dairy farm profit. Anim. Prod. Sci. 53:437–452.

Hurley, A.M.M., N. López-Villalobos, S. McParland, E. Kennedy, E. Lewis, M. O'Donovan, J.L.L. Burke, and D.P.P. Berry. 2016. Inter-relationships among alternative definitions of feed efficiency in grazing lactating dairy cows. J. Dairy Sci. doi:10.3168/jds.2015-9928.

Hurley, A.M., N. López-Villalobos, S. McParland, E. Lewis, E. Kennedy, M. O'Donovan, J.L. Burke, and D.P. Berry. 2017. Genetics of alternative definitions of feed efficiency in grazing lactating dairy cows. J. Dairy Sci. 100(7):5501-5514.

Jensen, J., W.D. Hohenboken, P. Madsen, and B.B. Andersen. 1995. Sire nutrition interactions and genetic parameters for energy intake, production and efficiency of nutrient utilization in young bulls, heifers and lactating cows. Acta Agric. Scand. A-Animal Sci. 45(2):81-91.

Kelly, A.K., M. McGee, D.H. Crews, A.G. Fahey, A.R. Wylie, and D.A. Kenny. 2010. Effect of divergence in residual feed intake on feeding behavior, blood metabolic variables, and body composition traits in growing beef heifers. J. Anim. Sci. doi:10.2527/jas.2009-2196.

Khansefid, M., J.E. Pryce, S. Bolormaa, S.P. Miller, Z. Wang, C. Li, and M.E. Goddard. 2014. Estimation of genomic breeding values for residual feed intake in a multibreed cattle population. J. Animal Sci. 92(8):3270-3283.

Koch, R.M., L.A. Swiger, D. Chambers, and K.E. Gregory. 1963. Efficiency of feed use in beef cattle. J. Anim. Sci. 22:486–494.

Köck, A., M. Ledinek, L. Gruber, F. Steininger, B. Fuerst-Waltl, and C. Egger-Danner. 2018. Genetic analysis of efficiency traits in Austrian dairy cattle and their relationships with body condition score and lameness. J. Dairy Sci. 101(1):445-455.

Korver, S., E.A.M. Van Eekelen, H. Vos, G.J. Nieuwhof, and J.A.M. Van Arendonk. 1991. Genetic parameters for feed intake and feed efficiency in growing dairy heifers. Livest. Prod. Sci. 29(1):49-59.

Li, F., M. Zhou, K. Ominski, and L.L. Guan. 2016. Does the rumen microbiome play a role in feed efficiency of beef cattle? J. Anim. Sci. doi:10.2527/jas.2016-0524.

Liinamo, A.E., P. Mäntysaari, and E.A. Mäntysaari. 2012. Genetic parameters for feed intake, production, and extent of negative energy balance in Nordic Red dairy cattle. J. Dairy Sci. 95(11):6788-6794.

Lu, Y., M.J. Vandehaar, D.M. Spurlock, K.A. Weigel, L.E. Armentano, E.E. Connor, M. Coffey, R.F. VeerKamp, Y. de Haas, C.R. Staples, Z. Wang, M.D. Hanizan, and R.J. Tempelman. 2018. Genome-wide association analyses based on a multiple-trait approach for modeling feed efficiency. J. Dairy Sci. 101(4):3140-3154.

Mantysaari, P., A.-E. Liinamo, and E.A. Mantysaari. 2012. Energy efficiency and its relationship with milk, body, and intake traits and energy status among primiparous Nordic Red dairy cattle. J. Dairy Sci. 95(6):3200-3211.

Meuwissen, T.H.E., B.J. Hayes, and M.E. Goddard. 2001. Prediction of total genetic value using genome-wide dense marker maps. Genetics 157:1819–29.

Miglior, F., A. Fleming, F. Malchiodi, L.F. Brito, P. Martin, and C.F. Baes. 2017. A 100-Year Review: Identification and genetic selection of economically important traits in dairy cattle. J. Dairy Sci. 100. doi:10.3168/jds.2017-12968.

Montanholi, Y.R., K.C. Swanson, R. Palme, F.S. Schenkel, B.W. McBride, D. Lu, and S.P. Miller. 2010. Assessing feed efficiency in beef steers through feeding behavior, infrared thermography and glucocorticoids. Animal. doi:10.1017/S1751731109991522.

Moore, K.L., D.J. Johnston, H.U. Graser, and R. Herd. 2005. Genetic and phenotypic relationships between insulin-like growth factor-I (IGF-I) and net feed intake, fat, and growth traits in Angus beef cattle. Aust. J. Agric. Res. doi:10.1071/AR04248.

Mujibi, F.D.N., J.D. Nkrumah, O.N. Durunna, P. Stothard, J. Mah, Z. Wang, J. Basarab, G. Plastow, D.H. Crews, Jr., and S.S. Moore. 2011. Accuracy of genomic breeding values for residual feed intake in beef cattle. J. Animal Sci. 89:3353–3361.

O'Donovan, M., D.P. Berry, E. Kennedy, S.G. Moore, E. Lewis, J.E. Pryce, B. McCarthy, S. McParland, and S.T. Butler. 2014. Mid-infrared spectrometry of milk as a predictor of energy intake and efficiency in lactating dairy cows. J. Dairy Sci. doi:10.3168/jds.2014-8214.

Ondarza, M.B.De, and J.M. Tricarico. 2017. Review: Advantages and limitations of dairy efficiency measures and the effects of nutrition and feeding management interventions. Prof. Anim. Sci. 33:393–400. doi:10.15232/pas.2017-01624.

Patience, J.F., M.C. Rossoni-serão, and N.A. Gutiérrez. 2015. A review of feed efficiency in swine: Biology and application. J. Anim. Sci. Biotechnol. 1–9. doi:10.1186/s40104-015-0031-2. Available from: http://dx.doi.org/10.1186/s40104-015-0031-2.

Pryce, J.E., J. Arias, P.J. Bowman, S.R. Davis, K.A. Macdonald, G.C. Waghorn, W.J. Wales, Y.J. Williams, R.J. Spelman, and B.J. Hayes. 2012. Accuracy of genomic predictions of residual feed in- take and 250-day body weight in growing heifers using 625,000 sin- gle nucleotide polymorphism markers. J. Dairy Sci. 95:2108–2119.

Pryce, J.E., G. Nieuwhof, W.J. Wales, M.P. Coffey, and B.J. Hayes. 2015. Hot topic : Definition and implementation of a breeding value for feed efficiency in dairy cows. J. Dairy Sci. 98:7340–7350.

Pryce, J.E., W.J. Wales, Y. De Haas, R.F. Veerkamp, and B.J. Hayes. 2014. Genomic selection for feed efficiency in dairy cattle. Animal. doi:10.1017/S1751731113001687.

Richardson, E.C., and R.M. Herd. 2004. Biological basis for variation in residual feed intake in beef cattle. 2. Synthesis of results following divergent selection. Aust. J. Exp. Agric. 44:431–440.

Shonka, B.N., S. Tao, G.E. Dahl, and D.M. Spurlock. 2015. Genetic regulation of prepartum dry matter intake in Holstein cows. J. Dairy Sci. 98(11):8195-8200.

Spurlock, D. M., J.C.M. Dekkers, R. Fernando, D.A. Koltes, and A. Wolc. 2012. Genetic parameters for energy balance, feed efficiency, and related traits in Holstein cattle. J. Dairy Sci. 95:5393–5402.

Stone, J.B., G.W. Trimberger, C.E. Henderson, J.T. Reid, K.L. Turk, and J.K. Loosli. 1960. Forage intake and efficiency of feed utilization in dairy cattle. J. Dairy Sci. 43(9):1275-1281.

Svendsen, M., P. Skipenes, and I.L. Mao. 1993. Genetic parameters in the feed conversion complex of primiparous cows in the first two trimesters. J. Animal Sci., 71(7):1721-1729.

Tedeschi, L.O., A.K. de Almeida, A.S. Atzori, J.P. Muir, M.A. Fonseca, and A. Cannas. 2017. A glimpse of the future in animal nutrition science. 1. Past and future challenges. Rev. Bras. Zootec. doi:10.1590/S1806-92902017000500011.

Tempelman, R.J., D. Spurlock, M. Coffey, R. Veerkamp, L. Armenta- no, K. Weigel, Y. de Haas, C. Staples, E. Connor, and Y. Lu. 2015. Heterogeneity in genetic and nongenetic variation and energy sink relationships for residual feed intake across research stations and countries. J. Dairy Sci. 98:2013–2026.

Tetens, J., G. Thaller, and N. Krattenmacher. 2014. Genetic and genomic dissection of dry matter intake at different lactation stages in primiparous Holstein cows. J. Dairy Sci. 97(1): 520-531.

Vallimont, J. E., C. D. Dechow, J. M. Daubert, M. W. Dekleva, J. W. Blum, C. M. Barlieb, W. Liu, G. A. Varga, A. J. Heinrichs, and C. R. Baumrucker. 2010. Genetic parameters of feed intake, production, body weight, body condition score, and selected type traits of Holstein cows in commercial tie-stall barns. J. Dairy Sci. 93:4892–4901.

Vallimont, J.E., C.D. Dechow, J.M. Daubert, M.W. Dekleva, J.W. Blum, C.M. Barlieb, W. Liu, G.A. Varga, A.J. Heinrichs, and C.R. Baumrucker. 2011. Short communication: Heritability of gross feed efficiency and associations with yield, intake, residual intake, body weight, and body condition score in 11 commercial Pennsylvania tie stalls. J. Dairy Sci. 94:2108–2113.

Van Arendonk, J.A. M., G.J. Nieuwhof, H. Vos, and S. Korver. 1991. Genetic aspects of feed intake and efficiency in lactating dairy heifers. Livest. Prod. Sci. doi:10.1016/0301-6226(91)90103-W.

Vandehaar, M.J., L.E. Armentano, K. Weigel, D.M. Spurlock, R.J. Tempelman, and R. Veerkamp. 2016. Harnessing the genetics of the modern dairy cow to continue improvements in feed efficiency. J. Dairy Sci. 4941–4954.

VanRaden, P.M., G.R. Wiggans, M.E. Tooker, J.H. Megonigal, and J.B. Cole. 2007. Genetic Evaluations for mixed-breed populations. J. Dairy Sci. doi:10.3168/jds.2006-704.

Veerkamp, R.F., M.P. L. Calus, G. De Jong, R. Van Der Linde, and Y. De Haas. 2014. Breeding value for dry matter intake for Dutch bulls based on DGV for DMI and BV for predictors. In: Proceedings of 10th World Congress of Genetics Applied to Livestock Production.

Veerkamp, R.F., Y. de Haas, J.E. Pryce, J. E., M. Coffey, D. Spurlock, and M.S. Vandehaar. 2015. Guidelines to measure individual feed intake of dairy cows for genomic and genetic evaluations. ICAR Technical Series 19:191-198.

Veerkamp, R.F., J.E. Pryce, D. Spurlock, D. Berry, and M. Coffey. 2013. Selection on feed intake or feed efficiency : A position paper from gDMI breeding goal discussions.

Veerkamp, R.F., G. Simm, and J.D. Oldham. 1994. Effects of interaction between genotype and feeding system on milk production, feed intake, efficiency and body tissue mobilization in dairy cows. Livest. Prod. Sci. doi:10.1016/0301-6226(94)90202-X.

Waghorn, G.C., K.A. Macdonald, Y. Williams, S.R. Davis, and R.J. Spelman. 2012. Measuring residual feed intake in dairy heifers fed an alfalfa (Medicago sativa) cube diet. J. Dairy Sci. doi:10.3168/jds.2011-4670.

Wallén, S.E., Prestløkken, E., Meuwissen, T.H.E., McParland, S. and Berry, D.P., 2018. Milk mid-infrared spectral data as a tool to predict feed intake in lactating Norwegian Red dairy cows. J. Dairy Sci. 101(7):6232-6243.

Williams, Y.J., J.E. Pryce, C. Grainger, W.J. Wales, N. Linden, M. Porker, and B.J. Hayes. 2011. Variation in residual feed intake in Holstein Friesian dairy heifers in southern Australia. J. Dairy Sci. 94:4715–4726.

Table 1. Heritability (h^2) estimates for different indicator traits of feed efficiency in dairy cattle.

Trait	Paper	$h^2 \pm$ SE
Dry matter intake	Vallimont et al. (2010)	0.18 ± 0.06
	Williams et al. (2011)	0.17 ± 0.10
	Liinamo et al. (2012)	0.23 ± 0.12
	Tetens et al. (2014)	0.37 ± 0.04
	Shonka et al. (2015)	0.52 ± 0.13
	Bilal et al. (2016)	0.12 ± 0.01
	Byskov et al. (2017)	0.37 ± 0.06
	Lu et al. (2018)	0.23 ± 0.02
Energy intake	Köck et al. (2018)	0.07 ± 0.03 to 0.13 ± 0.02
Energy-corrected milk	Köck et al. (2018)	0.08 ± 0.03 to 0.12 ± 0.02
Residual Feed Intake	Hurley et al. (2017)	0.04 ± 0.08 to 0.11 ± 0.08
	Van Arendonk et al. (1991)	0.19 ± 0.12
	Krover et al. (1991)	0.22 ± 0.11
	Jensen et al. (1995)	0.36 ± 0.17
	Svendsen et al. (1993)	0.02 ± 0.08
	Vallimont et al. (2011)	0.01 ± 0.05
	Williams et al. (2011)	0.27 ± 0.12
	Byskov et al. (2017)	0.23 ± 0.05
	Lu et al. (2018)	0.16 ± 0.02

$h^2 \pm$ SE: heritability $\pm$ standard error.

Table 2. Genetic correlations (r_g) between different indicator traits of feed efficiency and production traits in dairy cattle.

Feed efficiency trait	Production trait	Paper	$r_g \pm SE$
Dry matter intake	Milk yield	Gonzalez-Recio et al. (2014)	0.10 ± 0.11
		Vallimont et al. (2010)	0.51 ± 0.32
	Fat yield	Gonzalez-Recio et al. (2014)	-0.03 ± 0.10
		Vallimont et al. (2010)	0.53 ± 0.34
	Protein yield	Gonzalez-Recio et al. (2014)	-0.11 ± 0.08
		Vallimont et al. (2010)	0.55 ± 0.37
	Somatic cell score	Vallimont et al. (2010)	-0.15 ± 0.28
	Body weight	Liinamo et al. (2012)	0.54 to 1.00
		Vallimont et al. (2010)	0.52 ± 0.35
	Body condition score	Gonzalez-Recio et al. (2014)	0.37 ± 0.32
		Liinamo et al. (2012)	0.11 to 0.45
		Vallimont et al. (2010)	0.37 ± 0.46
Residual Feed Intake	Milk yield	Veerkamp et al. (1994)	-0.11 to 0. 07
		Gonzalez-Recio et al. (2014)	0.07 ± 0.08
	Fat yield	Gonzalez-Recio et al. (2014)	0.02 ± 0.07
	Protein yield	Gonzalez-Recio et al. (2014)	0.03 ± 0.07
		Veerkamp et al. (1994)	-0.11 to -0.02
	Lactose	Veerkamp et al. (1994)	-0.19 to -0.05
	Body weight	Korver et al. (1991)	0.03
		Van Arendonk et al. (1991)	0.01
	Body condition score	Gonzalez-Recio et al. (2014)	0.71±0.32
		Veerkamp et al. (1994)	0.33 to 0.36

Table 3. Accuracies of genomic predictions for indicator traits of feed efficiency.

Trait	Paper	Average accuracy
Dry matter intake	de Haas et al. (2012)	0.35
	de Haas et al. (2015)	0.37
	Mujibi et al. (2011)	0.20
	Boloorma et al. (2013)	0.32
Residual feed intake	Pryce et al. (2012)	0.40
	Mujibi et al. (2011)	0.43
	Boloorma et al. (2013)	0.43