Selection on Feed Intake or Feed Efficiency: A Position Paper from gDMI Breeding Goal Discussions

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Abstract

The widespread use of genomic information in dairy cattle breeding programs has opened up the possibility to select for novel traits, especially for traits that are traditionally difficult to record in a progeny testing scheme. Feed intake and efficiency is such a difficult to measure trait. In February 2013, the co-authors discussed how information on DMI should be incorporated in the breeding decisions. The aim of this paper is to present the overall discussion and main positions taken by the group on four topics related to feed efficiency: i) breeding goal definition; ii) biological variation in feed utilisation; iii) optimal recording of feed intake and predictor traits; and iv) unwanted correlated responses and validation.

Keywords: Feed intake, feed efficiency, animal breeding, genomic selection

1. Introduction

The widespread use of genomic information in dairy cattle breeding programs has opened up the possibility to select for novel traits, especially for traits that are traditionally difficult to record in a progeny testing scheme (Boichard and Brochard, 2012; Calus *et al.*, 2013). This is because animals from the same breed, but not necessarily offspring of progeny test bulls, can be used as a reference, or "training" population, to calibrate the genomic prediction equations (SNP Key). An example of such a training population are cows from research herds with detailed recording of unique phenotypes (Banos *et al.*, 2012).

The option of selection for novel traits prompted 15 partners from 10 countries to combine their data in the "Global Dry Matter Initiative" (gDMI) project to build one reference population with Holstein animals that are genotyped and have dry matter intake (DMI) records. DMI is an important trait that is missing in dairy cattle breeding programs. Similar projects combining data are underway in the US (http://www.dairy-efficiency.org/) and in the Scandinavian countries.

In February 2013, the co-authors met in Wageningen, The Netherlands (and US partners joined part of the discussions by teleconference). The participants discussed how information on DMI should be incorporated in dairy cattle breeding programs. Several reviews on selection for feed intake and feed efficiency in dairy cattle have been written, in the past, but also more recently

(Berry and Crowley, 2013, Pryce *et al.,* 2013, Veerkamp, 1998, Veerkamp, 2002, Veerkamp and Emmans, 1995a). The aim of this paper is to present the overall discussion and main positions taken by the group on four topics related to feed efficiency: i) breeding goal definition; ii) biological variation in feed utilisation; iii) optimal recording of feed intake and predictor traits; and iv) unwanted correlated responses and validation.

2. Breeding goal

At first sight, the inclusion of feed intake or efficiency in the breeding goal may seem a relatively simple matter. The goal is more milk with less feed. Several factors, however, complicate the inclusion of feed intake or efficiency in a balanced breeding goal.

Life-time feed efficiency, as well as including milk performance and feed intake, must also consider longevity, reproductive performance, days dry, and body weight when slaughtered (income from beef). This suggests that efficiency must be quantified at the production system level and so it might be more complex than feed efficiency at a single cow level. However, in the short term it was assumed for the discussion that a small change at the cow level will contribute to efficiency of the whole system.

More milk (i.e., output) per kg feed intake (i.e., input) suggests that feed efficiency should be presented as a ratio of input and output, i.e., gross feed efficiency or feed conversion ratio. Such traits appeal to producers since they appear easily interpretable, but ratio traits have several disadvantages in animal breeding (Veerkamp, 2002). Gross feed efficiency favours animals with high output, because maintenance costs are diluted (Veerkamp *et al.,* 1995). Even worse, increasing gross efficiency does not necessarily favour more efficient feed conversion towards milk (Vandehaar, 2012). For these reasons the outcome of the discussion of gDMI was that the ratio traits, feed conversion or gross feed efficiency, could be presented as a stand-alone trait because of its appeal. However, its direct inclusion in the overall breeding goal could be complicated and may be best represented as a linearised expression of the ratio. Then there are two options, which in an ideal world should result in a similar outcome.

The first option is to calculate residual feed intake (RFI) for all animals that have feed intake records. RFI is the measured feed intake minus the expected feed intake for milk production, growth (including body tissue mobilisation) and maintenance (as well as other energy sinks if data are available) based on feed requirement equations. RFI is popular in growing cattle (Berry and Crowley, 2013) and is probably the closest approximation of net feed efficiency at a population level for genetic/genomic evaluations. However, RFI is made to be independent of milk production and maintenance costs. Hence, these feed costs for yield, growth and maintenance should ideally also be considered in the breeding goal as traits in themselves with their respective economic values. This complexity may result in a negative economic value on body size which may affect producer acceptance. Nonetheless a negative economic value for body size is already adopted and accepted by producers in New Zealand, Ireland, and in the US ($NM - by means of reduced Stature).

The second option for linearised inclusion of feed efficiency in the breeding goal is not to predict the breeding value for RFI, but to predict the breeding value for DMI itself; this would need to be undertaken in any case if RFI is to be defined at the genetic level. The breeding goal can then be defined as the milk returns, minus the cost of DMI. Since DMI automatically includes the feed consumed for growth, maintenance and production, there is no need to separately account for the cost of differently sized animals or differences in for example the fat:protein ratio in the milk. Subsequent inclusion of body size in the breeding goal can be left to the desired outcome of the index.

It can be a lengthy discussion choosing between these two approaches and both have their own advantages and disadvantages. Both approaches however are a linear combination of the same traits, and therefore are expected to yield the same result (Kennedy *et al.,* 1993). When selecting animals based on RFI it is certain that animals with a negative RFI eat less than expected based on their outputs (assuming the definition of RFI is correct). Feed efficient animals are more difficult to identify if DMI itself is used. Also, the computation of RFI is more flexible (e.g., relationship between DMI and production or maintenance may be non-linear), but must be properly modelled (i.e., cognisance must be taken of the contribution of body tissue mobilisation to the energy kinetics). However, RFI may be more difficult to understand as it is currently not very clear what exactly RFI is and whether it is simply an accumulation of variance associated with an inaccurate statistical model. RFI might depend on lactation stage, and so within parity the correlations among, and the contributions of, the components to RFI may change. Therefore, if you use one set of parameters, RFI may not be calculated correctly. Also, RFI breeding values will be based on a small reference population, whereas alongside DMI, body size and yield can be used as predictor traits, as well as other potential predictors like milk Mid Infra-Red (MIR) (McParland *et al.,* 2011). RFI, however, is essentially a sub-index and there is already a precedence of decomposing total merit indexes into sub-indexes. Using DMI makes the index more amenable to individual herd customisation of the index by altering the economic value on feed costs for that farm. 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.

One compromise may be to include DMI in the breeding goal itself, but include RFI (maybe better to refer to it as “corrected feed intake”) as an ancillary trait where advice is given that animals with negative corrected feed intake values eat less than expected.

3. Biological variation

Many biological processes contribute to variation in feed efficiency, including variation in digestion and absorption of nutrients, mobilisation of stored body energy reserves, partitioning nutrients toward lactation versus other functions, and the efficiency of energy utilisation for lactation (Figure 1). To date, gross feed efficiency has improved through selection for increased production because a greater proportion of feed consumed is now utilised for lactation, rather than maintenance. However, more direct emphasis on selection for net or component feed efficiency may impact biological factors that more directly impact the efficiency of nutrient utilisation. Although knowledge of these underlying mechanisms is not necessary in order to implement selection for improved efficiency, understanding the biology that contributes to genetic variation in feed efficiency is useful for several reasons: 1) Understanding relationships among feed efficiency traits measured at different stages of the animal’s lifetime; 2) Identifying potential indicator traits for feed efficiency; and 3) Understanding potential correlated responses to selection for feed efficiency. Thus, an important question is “which biological functions are expected to change when selecting to improve net feed efficiency?”.

Many factors have been identified as potential contributors to variation in feed efficiency, including digestion efficiency, absorptive capacity, microbial populations, heat loss, methane production, protein and fat turnover, mitochondrial activity, immune function, thermoregulation, activity, health, etc. Recent findings in dairy and beef cattle have demonstrated between-animal variation in the ability to digest standard diets to metabolisable energy, which contributes to variation in overall RFI (Berry *et al.,* 2007a, Cruz *et al.,* 2010). However, experiments to dissect the relative importance of these component traits to overall variation in feed efficiency are extremely challenging. First, collection of adequate data sets for estimation of genetic correlations among traits is often expensive and labour intensive (Veerkamp and Emmans, 1995b). Second, the relationship of underlying traits to net feed efficiency may be highly dependent on experimental design and the environment in which they are measured. For example, composition of the diet, wastage of feed by cows, climate, body composition, timing of measurements, and measurement methods may have important impacts on the observed relationships between net feed efficiency and its underlying traits.

In summary, the gDMI group acknowledged that feed efficiency is an extremely complex trait, and understanding the underlying mechanisms contributing to its variation would be beneficial. However, because of extensive challenges associated with such research, the group focused on two areas believed to have the most direct impact on the implementation of selection for improved net feed efficiency: 1) Investigation of the genetic variation for digestibility. Selection to improve digestibility would be particularly beneficial because it is at the start of the feed utilisation chain and likely impact the production of greenhouse gases. 2) Validation of an easy-to-record proxy for RFI. The ability to continuously collect phenotypes over time will be critical to the success of selection for improved feed efficiency. Finally, the group recognised that GWAS analyses of net feed efficiency data may reveal important candidate genes or pathways for future investigations of the biological mechanisms underlying net feed efficiency.

4. Recording feed intake

When wanting to calculate RFI or DMI, an important question is when to record feed intake. To answer this question, it is important to know the correlations between different lactation stages. In Figure 2, the individual level correlations are given based on 60,688 DMI records in 3,229 lactation records from 2,365 Dutch cows. It is clear that when records are taken close together in time the repeatability is high. However, between early and late lactation and across lactations the repeatability is not so high.

Published estimates for genetic correlations between feed intake measurements across lactation originate from small datasets, are not consistent albeit associated with large standard errors (Berry *et al.,* 2007b; Buttchereit *et al.,* 2011; Coffey *et al.,* 2001; Koenen and Veerkamp, 1998; Spurlock *et al.,* 2012; Veerkamp and Thompson, 1999).

Genetic correlations were strong within a reasonable time interval; however, most estimates provided by the participants showed a genetic correlation between early and late lactation that was weaker than has been observed for the milk yield traits. This suggests that ideally feed intake should be measured in all periods of the lactation.

5. Predictors

Regardless of international collaboration, recording of feed intake will always be a limiting factor for accurate breeding values. Therefore, there is an interest in using predictors to improve the accuracy of the breeding values. DMI might be predicted by the yield traits with reasonable accuracy. However, this predicted DMI can never be used to identify genetic variation in feed efficiency as all variation between animals is due to difference in the milk yield traits. So DMI data are always required to select for improved feed utilisation.

Next to yield, an obvious group of predictor traits are the conformation traits; chest width, stature, body depth, and angularity which help to predict live weight (Coffey *et al.,* 2003), and therefore provide a good predictor for estimating feed required for maintenance. Other potential predictors are:

- Body condition score (BCS) to indicate levels of body fat and protein
- Activity data can be used to account for variation in maintenance,
- Thermal infra-red cameras can be used to collect heat measures (related to DMI)
- MIR analysis of milk samples performed regularly by milk recording agencies have been shown to be correlated to energy balance, which is mathematically related to RFI (McParland *et al.,* 2011)
- Changes in eating pattern is informative to predict disease. Eating pattern might also be affected by social hierarchy

6. Correlated responses

Milk yield and feed intake are the major determinants of energy balance. Breeding programs aiming to improve milk yield and reduce feed intake must take this into account, because a pronounced energy deficit in early lactation has a detrimental effect on fertility and health (e.g., Collard *et al.,* 2000; Lucy *et al.,* 1991).

Several authors have highlighted the critical importance of BCS (e.g., Oikonomou *et al.,* 2008), because a decline in BCS is evidence of tissue mobilisation to compensate for a negative energy balance (Bauman and Currie, 1980). A loss and gain of body fat across a lactation costs money because whilst lipid storage and mobilisation is very efficient, it does have an energetic cost since effective energy yielded by lipid loss is 39.6 MJ/kg, whereas gaining a kg requires 56 MJ (Emmans, 1994). Sometimes lipid storage and mobilisation might make economic sense (Wall *et al.,* 2008), but it is difficult to account for this in long term breeding programs. Accounting for BCS or BCS change in a breeding program, by using a restricted index, might enable selection for lower feed intake without compromising animal health and welfare. On the other hand, accounting for body energy contribution to overall lactation milk yield may also improve the ranking of bulls that produce milk with lower body energy loss and essentially higher feed intake (Coffey *et al.,* 2003). Thus, BCS is a trait with an intermediate optimum which makes the inclusion into breeding programs a complicated task (Veerkamp and Koenen, 1999).

Further studies should be conducted to get reliable estimates for genetic correlations of energy balance traits with both feed intake and functional traits. On the other hand, strong negative side effects are unlikely since breeding programs already account for fertility and longevity. Nonetheless there is some evidence of increased days open associated with improved feed efficiency (Vallimont *et al.,* 2013). The low heritability of fertility traits may result in low accuracy of selection for these traits. Therefore, unfavourable responses to selection in fertility may still occur.

Less information is available for the disease traits for which no routinely measurable indicator trait is available (e.g., metabolic disorders). Antagonistic relationships between these traits and feed intake cannot be easily negated through balanced breeding objectives. The use of combined data sets from different countries might be extremely valuable in the process of establishing these genetic associations.

7. Validation

Validation of genomic predictions is an important component of the work involved in implementing a new genomic breeding value for any trait.

One of the main limitations with developing genomic breeding values for feed intake traits is the quantity of phenotypic data available. In the review of Pryce *et al.* (2013) accuracies of genomic prediction for energy balance, DMI and RFI, estimated by cross-validation in beef and dairy cattle, ranged between 0.20 and 0.43. All of the studies had less than 5,000 animals and less than 700,000 SNP/cow. Increasing the size of the reference population should increase the accuracy of genomic prediction. Using the formula of Daetwyler *et al.* (2008) 25,000 individuals with phenotypes would be required to achieve an accuracy of 0.8 on the assumptions that 600,000 informative SNP are available and the heritability is 0.4. This is obviously challenging for expensive-to-measure traits such as RFI and DMI, but is an area that international collaboration may be beneficial.
Validation of genomic predictions estimated at different life stages are also very important. For example, Davis *et al.* (2013) have recently validated genomic predictions of growing heifer RFI estimated by Pryce *et al.* (2012) in an independent population of lactating New Zealand Holsteins.

8. Conclusions

This international consortium has created the world’s largest collection of data for feed intake on genotyped dairy cattle. This has enabled the possibility of including feed intake or some measure of feed efficiency in dairy cattle breeding programmes. The preference is a linearised measure of feed efficiency, either DMI directly, or RFI concurrent with the appropriate cognisance of the energy cost of milk production, composition and live weight. Measuring feed intake will remain a challenge, especially since recordings at several lactation stages seems to be required. The fact that it is now possible to estimate accurate genomic breeding values using combined reference populations, adds to the urgency of determining how best to use the new information in the breeding goal, without creating unwanted correlated responses in other traits.

9. Acknowledgements

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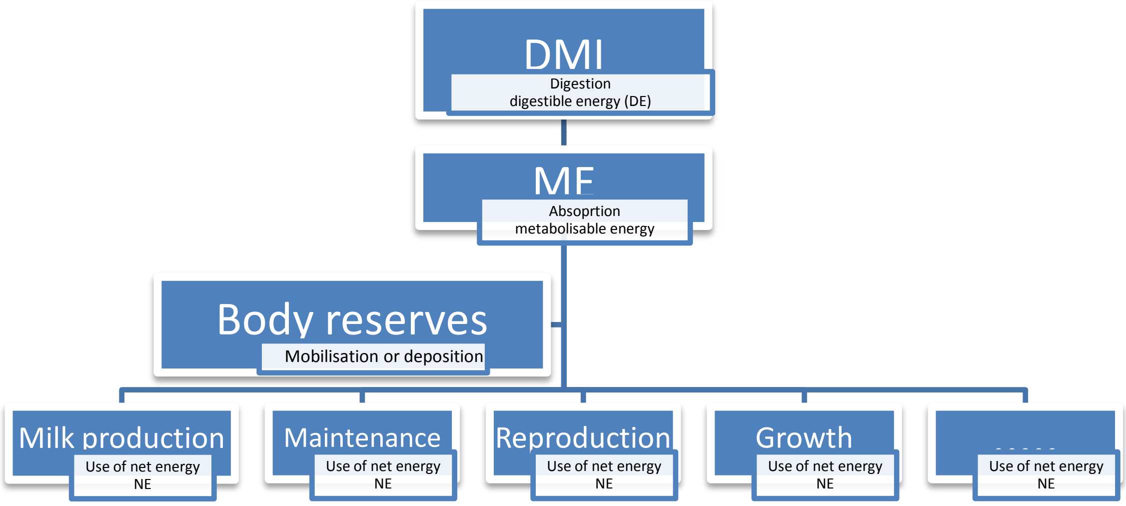

Figure 1. Schematic representation of feed utilization in dairy cow.

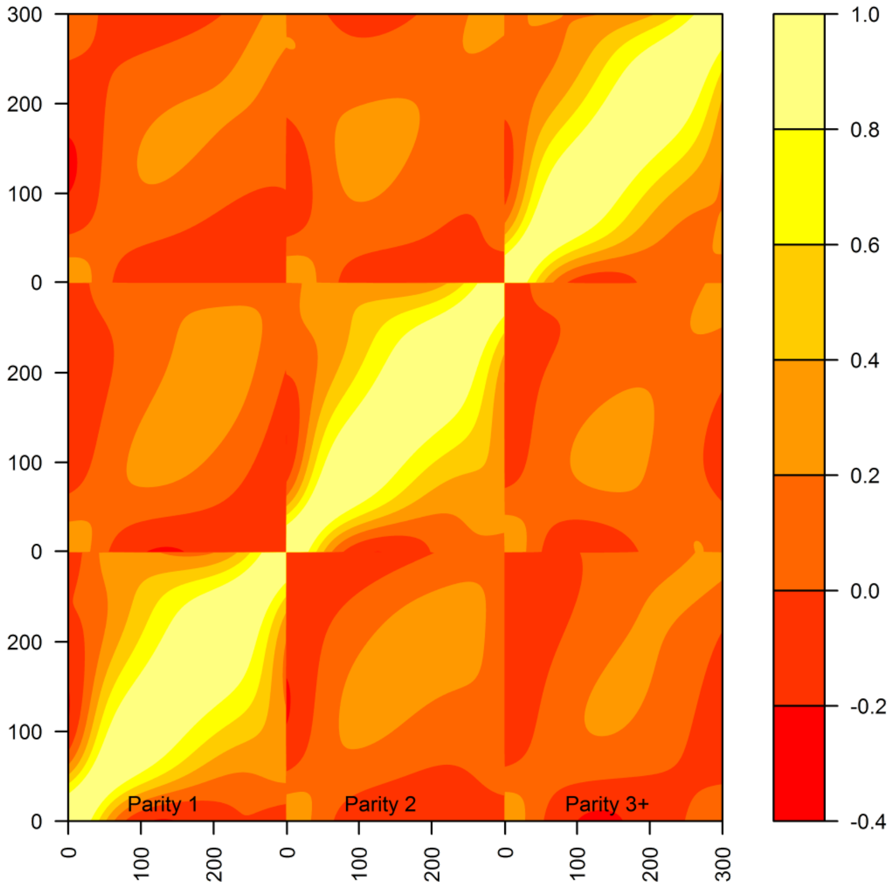

Figure 2. Individual cow correlations of measuring feed intake within and across the first three parities.