

Liveweight and feed intake in dairy cattle breeding.

R.F. Veerkamp

Genetics and Behavioural Sciences Department, Scottish Agricultural College
West Mains Road, Edinburgh, EH9 3JG, Scotland

1 Introduction

Feed costs account for about 0.80 of the total variable costs associated with milk production (MMB, 1990), and therefore possible genetic differences between cows in feed intake, or in the efficiency of converting feed to valuable products, are of considerable importance to dairy cattle breeding.

Most studies investigating food intake in dairy cows have been concerned with the estimation of genetic parameters or with the derivation of economic values. Moderate amounts of variation have been found for feed intake and for the components to which feed is partitioned after digestion: yield, metabolic liveweight and liveweight change. Although some typical values are presented in Table 1, the aim of this paper is not to review these again, because Van Arendonk,

Groen, Van der Werf and Veerkamp (1995) summarise and discuss the results of the most recent experiments.

The overall objective is to discuss in detail how any genetic variation in food costs could be made use of in dairy cattle breeding. Firstly, selection for feed efficiency will be used as an example to develop the more general framework: (i) two approaches to derive economic values for the milk yield traits are compared: norms versus genetic correlations, (ii) then it is illustrated how these two methods can be combined, for example when feed intake measures come available. Secondly, an apparently contrasting approach, in which food costs are decreased by an increase in food intake capacity (Groen and Korver, 1989), is discussed. Finally, the use of linear type traits as predictors of intake and liveweight is discussed.

Table 1. Heritabilities (h^2), permanent environmental effect (c^2) and correlations for ME intake (MEIN), lactational energy (LE), metabolic live weight (MLW) and live weight change (LWC) (from Veerkamp, Emmans, Cromie and Simm, 1995).

	h^2	c^2	correlations ¹			
			MEIN	LE	MLW	LWC
MEIN	0.36	0.26	-	0.48	0.14	-0.05
LE	0.45	0.07	0.44	-	-0.18	-0.47
MLW	0.71	0.14	0.30	-0.10	-	0.30
LWC	0.10	0.16	0.23	-0.65	0.42	-

1 below diagonal genetic correlation, and above diagonal phenotypic correlation

2. Efficiency of food utilisation

2.1 Food costs related to yield

As a starting point, the most obvious method to account for the cost of feeding animals is to include it with all the returns in the breeding goal, and let H be the additive genetic value for economic merit, then:

$$H = r_m MY + r_f FY + r_p PY - c \text{ DMI}$$

where r are returns for the yield traits (MY, FY and PY are milk, fat and protein yield respectively) and c is the cost for a kg food (DMI).

Assuming that all index traits are predicted transmitting abilities from a complete multivariate BLUP analysis (or transmitting abilities are predicted accurately), optimal index weights are the sum of the partial genetic regression coefficients of each goal trait on each index trait, weighted by the economic values of the goal traits. Practically, this means that when, for example, milk, fat and protein as index measures are available only, then the index becomes:

$$I = b_m MY + b_f FY + b_p PY$$

where the index weights (b 's) are the difference between the return (r 's) for each of the yield traits and the partial genetic regression of DMI on MY, FY and PY and the cost of a kg DMI. The partial genetic regression coefficients can be derived directly from a regression of phenotype on the estimated breeding values for the index trait (Brotherstone and Hill, 1991; Veerkamp, Simm and Persaud, 1994), or, when these are not available, the partial regressions can be calculated from estimated genetic variances and covariances (for example Veerkamp, Hill, Stott, Brotherstone, Simm, 1995): $b = G^{-1} G_{*} v$, where b is the vector containing the index weights, the matrix G_{*} ($m \times n$) contains the genetic covariances between the m goal and n index traits, the symmetric matrix G ($n \times n$) is equivalent to the genetic (co-) variance matrix between the index measurements and v is the vector with the economic weights for the goal traits.

In contrast to the empirical method to derive food costs described above, most

selection indices in use are based on feeding norms to calculate food cost. For example, the ITEM in the UK uses the effective energy system described by Emmans (1994). These norms are used to calculate the extra energy needed for a kg protein for example, and subsequently a ration is formulated to derive the food costs. The difference between this method and the empirical method can be demonstrated easily, using realistic prices for the yield traits (including some costs for leasing quota, transport, cooling and processing) and for a kg dry matter of a mixed diet, then:

$$H_1 = -0.02 MY + 1.39 FY + 4.27 PY - 0.11 \text{ DMI}$$

When genetic parameters from Veerkamp and Brotherstone (1996) were used optimal index weights derived using the genetic covariances gave:

$$I_1 = +0.02 MY + 0.32 FY + 3.12 PY$$

Using the effective energy system, and a ration containing 50% each of forage and concentrate, which would cost approximately £0.11 / kg, than simple calculations resulted in:

$$H_2 = -0.03 MY + 0.66 FY + 3.84 PY$$

Because the same traits are in the goal and the index, it follows that $b = v$:

$$I_2 = -0.03 MY + 0.66 FY + 3.84 PY$$

The two indices I_1 and I_2 are different and especially the sign of the weight for MY changes. This illustrates that the two approaches discussed above produce different weights, even with a very simple index. Several obvious reasons why these weights are different for these two methods are as follows:

- estimates of genetic parameters may be inaccurate in comparison to well established norms,
- energy norms to produce one kg milk have been calculated as the heat of combustion value of that milk divided by the net efficiency. This is in contrast to genetic parameters which are not partial, consequently weights based on the genetic regression are not partial on traits absent from the breeding goal (as

should be), whereas weights based on norms assume that no other traits change.

- norms are generally developed within an animal, and therefore are often based on environmental differences (e.g. the same animal fed different amounts of food), and there is no reason why environmental effects should be in the same direction as genetic effects, ...

- genetic parameters are limited by for example the part of the lactation for which feed intake is measured, whereas norms can be used to calculate costs of a full lifetime.

Overall, it is difficult to generalise which of these two methods should be preferred. I_1 will give the maximum response given the genetic parameters are correct, but I_2 will give the maximum response when the energy norms are assumed to give the best estimate of the real marginal food costs. A subjective judgement seems the only possible solution.

However, it seems crucial to quantify how compatible the two indices are and to compare the correlations (r_{bi}) between both indices and one of the breeding goals (H_1 or H_2). Using standard selection index equations, I_2 gave 0.98 of the accuracy which was expected with I_1 . Hence, this verifies that the norms were reasonably consistent with the 'genetic model', and therefore it is not much of an issue which of these two indices should be used. However, when more complicated bio-economic models are developed (for example liveweight could be treated in a way similar to any of the milk yield traits, either using norms to calculate the food costs, or using the genetic correlation with dry matter intake) it seems sensible that consistency between these models and the genetic parameters are checked.

2.2 Yield plus dry matter intake

Neither of the two indices discussed above makes use of any knowledge of genetic variation in food utilisation, other than that some animals might have a more favourable ratio between the yield traits. If the goal is to improve this net efficiency, then dry matter intake (or a predictor of DMI) needs to be included in the index. Now it becomes more crucial which of the two methods (norms or genetic parameters) is used to derive the index weights for the yield traits.

As norms for the energy content of yield are well established in comparison to the genetic correlations between yield and intake, it seems sensible to use the economic values for the milk yield traits from these norms (I_2). However, the question now is: what to do with measures of dry matter intake. It is obvious that double counting needs to be avoided.

For example, when I_2 is used and food intake measurements come available it is tempting to include dry matter intake in the goal and use the following index for selection:

$$H = I = -0.03 MY + 0.66 FY + 3.84 PY - 0.11 DMI.$$

However, when selecting on this index, food costs related to yield are accounted for twice. It seems logical that when food costs have been included for the yield traits already (by using the norms), then only the food intake component which is independent of milk production should be included in the goal. Hence the trait DMI should be converted in the trait adjusted dry matter intake (ADMI) which is independent of the yield traits. Using the same method as described by, Kennedy, van der Werf and Meuwissen (1993) adjusting DMI genetically for MY, FY and PY is done as follows.

Taking G as the (co-) variance matrix for MY, FY and PY (most recent UK estimates):

$$G = \begin{matrix} & \begin{matrix} 376482 & 11924 & 10335 \end{matrix} \\ \begin{matrix} 11924 \\ 10335 \end{matrix} & \begin{matrix} 637 & 389 \\ 389 & 328 \end{matrix} \end{matrix}$$

G_* contains the covariances between DMI and MY, FY and PY:

$$G_* = \begin{matrix} 105495 \\ 6509 \\ 3957 \end{matrix}$$

The partial genetic regressions of DMI on MY, FY and PY can then be calculated as:

$$b = G_*' \cdot G^{-1}$$

These partial genetic regressions ($-1 * b$ is used in Q below) can be used to adjust DMI for the yield traits as $Q GL Q'$, where GL is the genetic (co-) variance matrix for dry matter intake and the yield traits. Following

the example above, the covariance matrix between ADMI, MY, FY and PY is calculated as:

$$Q = \begin{matrix} & 1 & 0.316 & -9.737 & -10.5 \\ \begin{matrix} 0 \\ 0 \\ 0 \\ 0 \end{matrix} & \begin{matrix} 1 \\ 0 \\ 0 \\ 0 \end{matrix} & \begin{matrix} 0 \\ 1 \\ 0 \\ 0 \end{matrix} & \begin{matrix} 0 \\ 0 \\ 1 \\ 0 \end{matrix} & \begin{matrix} 0 \\ 0 \\ 0 \\ 1 \end{matrix} \end{matrix}$$

$$GL = \begin{matrix} & 128304 & 105495 & 6509 & 3957 \\ \begin{matrix} 105495 \\ 6509 \\ 3957 \end{matrix} & \begin{matrix} 376482 \\ 11924 \\ 10335 \end{matrix} & \begin{matrix} 11924 \\ 637 \\ 389 \end{matrix} & \begin{matrix} 10335 \\ 389 \\ 328 \end{matrix} & \end{matrix}$$

$$Q.GL.Q' = \begin{matrix} & 56754 & 0 & 0 & 0 \\ \begin{matrix} 0 \\ 0 \\ 0 \end{matrix} & \begin{matrix} 376482 \\ 11924 \\ 10335 \end{matrix} & \begin{matrix} 11924 \\ 637 \\ 389 \end{matrix} & \begin{matrix} 10335 \\ 389 \\ 328 \end{matrix} & \end{matrix}$$

The covariances between yield and ADMI are obviously zero, and the correlation between DMI and ADMI is 0.67 only. Now DMI can be replaced by ADMI in the goal, and the norms can be used to calculate the food costs for the yield traits. The breeding goal becomes:

$$H_3 = -0.03 MY + 0.66 FY + 3.84 PY - 0.11 ADMI,$$

In practise we can measure only DMI, and therefore calculating the optimal index weights by genetic regression gives:

$$I_3 = -0.07 MY + 1.7 FY + 5.0 PY - 0.11 DMI$$

Table 2. Economic values for liveweight (maintenance costs only) and feed intake capacity (Veerkamp, unpublished).

	Liveweight (£/kg) (maintenance costs only)	Feed intake capacity (£/kg) (DMI)
Base	-0.34	0.03
6600 kg milk	-0.37	0.04
7700 kg milk	-0.43	0.06
Concentrate price +20%	-0.42	0.06
Concentrate price -20%	-0.28	0.01

Obviously, the only way to derive economic values for intake capacity is using bio-economic models, which can optimise forage to concentrate ratio in the model. It is

Had the norms and genetic correlations been consistent, than weights for I_3 should have been the same as the economic values in the goal we started of with (H_1). However, norms and genetic correlations differed slightly and for good reasons norms were chosen as base for some of the economic values. This example shows that combining these norms and selection index calculations separately, without considering both simultaneously, can be complicated. Especially when other traits, like liveweight, are added to the goal and index, there is a danger for double counting.

3. Feed intake capacity

The former section considered improving feed efficiency, and consequently feed intake, other things being equal, had a negative economic value. However, Groen and Korver (1989) suggested that selection should be to increase forage intake capacity, because the same amount of energy can then be provided from cheaper forages rather than from more expensive concentrates. Hence, the additive genetic variation for dry matter intake in a population fed a single food *ad libitum*, is assumed to reflect additive genetic differences in intake capacity, rather than differences in net efficiency.

obvious that economic values for feed intake capacity depend strongly on the assumed price ratio between forage and concentrate and on the average yield level, this is shown

in Table 2. The explanation is that the more concentrate is fed in the base situation, the more scope there is to replace concentrate by forage. One of the difficulties is to match the model with the genetic parameters. For example, where genetic parameters for dry matter intake come from a population fed a single food *ad libitum*, it can be assumed that additive genetic differences in an overall capacity to eat a 'reference food' is observed. In a bio-economic model intake capacity is often a simple function of animal weight and some food characteristics. To obtain the economic value for an increase of dry matter intake of the 'reference food', mean intake capacity for the reference diet needs to be calculated, and then the potential economic benefit can be calculated by increasing the capacities for silage, grass and concentrate with the same proportion as was needed to increase intake capacity for the reference diet by 1 kg. This all ensure that the one kg increase in the genetic parameters is equivalent to a one kg increase in the bio-economic model.

4. Linear type traits

Measurement of an individual cow's performance for liveweight and feed intake is not common practise for most breeding programmes, and therefore there is great interest in other traits which may help to predict these potential goal traits.

To overcome the high costs of measuring feed intake, measurements can be restricted to part of the lactation (Persaud and Simm, 1991), as for example is done in the Genus MOET nucleus herd in the UK. However, measurement of individual cows' intake is not feasible for most breeding programmes, which depend on progeny testing bulls via daughters recorded in many dispersed commercial herds, rather than a nucleus herd. Van Arendonk, Nieuwhof, Vos and Korver (1991) suggested measurements of food intake on growing bulls and heifers; Persaud, Simm and Hill (1991) suggested that selection on an index of fat + protein yield and live weight would be about 85 to 95% as accurate as selection on breeding

value for efficiency, though measurement of live weight is not common practice for farmers in the UK. Sieber, Freeman and Kelley (1988) found negative correlations between estimated efficiency and 7 body measurements and Gravert (1985) reported that chest circumference is an accurate predictor of feed intake. So there might be benefits from including linear type traits in a selection index for the prediction of dry matter intake, condition score and liveweight.

Investigating this option, Veerkamp and Brotherstone (1996) combined >15000 type classification records, with >1140 records on average food intake, liveweight and condition score during the first 26 weeks of lactation. Genetic correlations between liveweight and stature, chest width, body depth and rump width were consistently high (Table 3). Chest width and body depth were small to moderately correlated with dry matter intake (0.21 - 0.32 and 0.23 - 0.39 respectively). Hence, selection for liveweight and, may be for feed intake, can be done relatively cheaply: linear type traits are measured in most (inter-) national breeding programs, and appear to have high genetic correlations with the traits of interest. Also, if selection was for decreasing liveweight only, than negative aspects on feed intake can be encountered.

Table 3. Genetic correlations between the traits measured at Langhill during first 26 week of lactation and linear type measurements from both Langhill and the national data set (Veerkamp and Brotherstone 1996).

	DMI	LW	CS
STA	0.20	0.72	0.15
CW	0.32	0.99	0.74
BD	0.39	0.87	0.22
ANG	0.12	-0.71	-0.99
RW	0.18	0.79	0.33

6. Discussion

Finally, using the complete bio-economic model (rather than the simple sums used above), economic values were derived for milk, fat and protein yield, liveweight, feed intake capacity and a kg food (Table 4).

The direction of selection for DMI can be established by adding the economic values for food costs and intake capacity, and these suggest that improving feed efficiency should be the desired goal, rather than increasing intake capacity. However this is misleading for the following reasons:

- When the genetic variation for 'food costs' is corrected for the fact that norms have been used already to determine the feed costs for liveweight and the yield traits, than the standard deviation of DMI drops, and consequently the economic importance of 'food costs' drops from -39 to -26, hence, increasing food intake capacity is nearly as important.
- Although weighting food costs negatively is intended to have the effect that selection is for more efficient food utilisation, one of the problems is that no distinction is made between the energy used for the separate functions of maintenance, lactation and body tissue gain, or loss. So that, rather than improving net efficiency of food utilisation, partitioning between these components can be changed.
- There is no evidence that a large component of the variation in food efficiency is due to genetic differences in net efficiency (Veerkamp and Emmans 1995).

Hence, one of the consequences might be that selection for feed efficiency during early lactation, selects cows which merely mobilise more body tissue, rather than truly produce their milk more efficiently. This is supported by results from Veerkamp and Brotherstone (1996) who found genetic correlations of -0.66, -0.46 and -0.58 between condition score and milk, fat and protein yield and a heritability of 0.38 for condition score, respectively. The point at

which the increase in yield as a consequence of continued selection (in high input systems) diminishes in low input systems might therefore depend on the limit, which must exist, to the rate of tissue mobilisation or the amount of mobilisable tissue. Also, negative genetic relationships between yield and health or between yield and fertility might be early indications that the negative energy balance is too low, or for too long too low.

It can also be expected that intake capacity is likely to become more important in the future (assuming the same food prices). Firstly because the economic value increases at higher yield levels. Secondly because the rate of increase in energy output from selection on yield is unlikely to be matched by the rate of increase in intake during the first part of the lactation (Van Arendonk *et al.* 1991; Veerkamp, Simm and Oldham 1995). Thirdly, results from Veerkamp *et al.* (1995) (plus more recent unpublished work) suggested that with a higher percentage forage in the diet, high genetic merit animals were not capable of eating much more than control line animals, whereas on high concentrate diets high genetic merit animals have the advantages of higher intake and more body tissue mobilisation.

It is also interesting to note that under the circumstances assumed in the base model (and liveweight is not corrected for differences in condition score), feed intake capacity and liveweight are equally important, but in opposite direction. Given that these two traits are genetically correlated as well, it means that including either one of the two traits in the selection decisions might be misleading. For example a large part of what is perceived to be gained by selecting for a lower liveweight, might in fact be lost at the same time by reducing feed intake capacity.

Table 4. Economic values for milk, fat and protein yield, and liveweight (maintenance costs only) and feed intake, in £ per kg and £ per standard deviation unit.

	Milk	Fat	Protein	Intake capacity	Live weight ¹	Food costs
<i>£/kg/cow/year</i>						
5500 kg milk	-0.03	0.60	4.04	0.03	-0.34	-0.11
7700 kg milk	-0.03	0.60	4.04	0.06	-0.43	-0.11
<i>£/σ_A/cow/year</i>						
7700 kg milk	-18	15	73	21	-12	-39

¹ corrected for condition score

The results in this paper illustrate the difficulty of finding appropriate weighting factors for feed intake, liveweight and yield in dairy cattle breeding goals. The difficulties are primarily in: (i) how to account for the buffering capacity of body tissue mobilisation and related effects on health and fertility; (ii) whether to use norms or genetic correlations to derive economic values and index weights; and (iii) what measures to use in the national population.

Practically, in the UK we are considering several options, and one of the possible outcomes is to include feed intake capacity and liveweight in the total merit index, both predicted initially by linear type traits. Because selecting to improve feed efficiency could increase the gap between the rate of progress in yield and the rate of progress in intake capacity, this might be postponed till effects on condition score, health and fertility are understood more carefully. For this purpose, a project will be started (in collaboration with HFS, MDC and MAFF) to measure condition score during type classification, which would then enable us to evaluate the genetic value of this trait as predictor of reproductive performance and efficiency of food utilisation.

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