

## FEED INTAKE AND ENERGY BALANCE IN LACTATING ANIMALS

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### INTRODUCTION

There has been a long running interest in how feed intake and feed efficiency should be taken into account in breeding decisions. Initially the interest in feed intake was in trying to reduce the amount of feed required per unit of production, *i.e.* improving feed efficiency. More recently interest has shifted towards the role of feed intake and its relationship with energy balance, health, and fertility, *i.e.* robustness of animals. The similarity between selection for feed efficiency (FE) and selection for energy balance (EB) is discussed first. Secondly, nuisance factors that may suggest genetic variation in feed utilisation (FU) and other biological sources of variation are reviewed. Finally, evidence is reviewed for an association between selection for (parts of) the FU complex and reproductive performance.

### FEED EFFICIENCY AND ENERGY BALANCE

**Terminology.** Energy balance is often calculated as i) the difference between energy content of the body at two points in time, or ii) as the differences between the energy inputs and outputs over a fixed period of time. These two definitions for EB are equivalent if energy content of the body is measured perfectly, and if all energy inputs and outputs (including losses) are measured perfectly. Efficiency is generally defined as a function of inputs and outputs. If only the production (*e.g.*, yield or growth) is included in the output the terms feed conversion or gross efficiency are used. To overcome some of the disadvantages of using gross efficiency as a measure of feed efficiency (*e.g.* Veerkamp and Emmans 1995) it is suggested that feed intake should be adjusted for additional component traits, *i.e.* residual feed intake (RFI) was introduced (Koch *et al.* 1963; Luiting and Urff 1991). RFI is defined as the observed energy intake adjusted for the energy requirements (ERQ), where ERQ is calculated from component traits.

**Calculation.** The principal of calculation of FE and EB is the same; *i.e.* feed intake adjusted ERQ, although various variations on this general formula exist. For example, ERQ may be calculated from one or several component traits; ERQ and feed intake might be expressed in kg or in joules; ERQ might be expressed as a proportion of or as the deviation from feed intake. Further differences are that ERQ may be based on feeding norms, or ERQ may be calculated from within the data (*e.g.* phenotypic regressions), or from genetic covariances. However, the concept of selecting on a function of feed intake and a set of component traits remains the same for EB and FE. Genetic parameters and the effects of genetic selection follow from the genetic co-variances between feed intake and the component traits, and numerically there is no difference between calculating feed efficiency and energy balance.

**Net efficiency.** The (perceived) difference between selection for EB and FE depends on the (perceived) contribution genetic variation in net efficiency makes to the total genetic variation in feed utilisation (FU). Net efficiency means that, everything else being equal, more is produced from the same amount of food. If animals did differ in net efficiency, then some animals would appear to be in a more negative energy balance than others, but in fact they may not be because they utilise their feed more efficiently. Similarly, if there are hardly any genetic differences in net efficiency, then some animals that appear to be more efficient simply have a more negative EB. Distinguishing between EB and FE is only possible if we measure energy content of the body at the two points in time perfectly, and if we measure all energy inputs and outputs between these time points simultaneously, *i.e.* we measure net efficiency directly. Measuring net efficiency is difficult, and even results from energy chambers rely on assumptions that may not hold across genetic groups. Therefore separating out the effects of selection for EB and FE is unrealistic for animal breeders.

#### **NUISANCE VARIATION IN FEED UTILISATION**

**Recording and feeding.** The meaning of FU depends on the time period that intake and the requirements are measured, especially in lactating animals. It is possible that the use of body reserves in a part of a lactation, or over one whole lactation, buffer some animals against the effects of temporary nutritional adversity. Consequently, variation in FU, which becomes apparent during a part of the lifespan, might diminish in the longer-term *e.g.* when considered over a series of lactations and their associated dry periods. Incorrect estimates of the energy content of feed components might have an impact when measuring FU. For example, underestimating the energy content of the forage will suggest (in absolute terms) a better FU for cows with higher dry matter intake, when all cows receive the same proportion of concentrates in the diet. When concentrates are fed according to production, the amount of extra concentrates fed per kg milk will determine whether high producing cows have better or poorer FU than lower producing cows.

**Energy requirements.** Ignoring one or more important components of feed utilisation in ERQ may also suggest genetic variation. For example not adjusting for maintenance costs (*i.e.* using gross efficiency or feed conversion), means that increasing output for any other component in ERQ will increase FU, because maintenance cost are then diluted across more units of output. This also explains the difference between selection for net efficiency and gross efficiency. Selection for gross efficiency might improve apparent efficiency, whilst net efficiency might not change or might decrease simultaneously (Veerkamp and Emmans 1995). Another major source of genetic variation in FU might be differences in the equations used to calculate ERQ, *e.g.* deviation from normality or additivity. For example, high genetic merit cows are taller but have lower body condition scores than low genetic merit cows and therefore, estimates for maintenance cost at a given weight might not be comparable. Similarly different composition of growth, or milk yield might suggest genetic variation in FU. Sometimes these effects might be considered nuisance effects, and sometimes these might be of interest for selection, but when comparing genetic groups or breeds to investigate source of variation, these factors may become important.

**Feed intake and components.** FU is a function of feed intake and ERQ, and therefore genetic parameters for FU are also a function of how much variation in feed intake is explained by ERQ, and how much additional variation is added by ERQ. Generally the more components, which are included in ERQ, the lower the correlation between FU and feed intake will be. This is also seen when FU is expressed as a proportion of feed intake to ERQ, e.g. gross efficiency or feed conversion ratio (e.g. Simm *et al.* 1987). For ratio traits the coefficients of variation for ERQ (and the traits present in ERQ) and feed intake determine if feed intake or ERQ is the predominant source for variation in FU, i.e. the most dominant sources of variation depend on the current mean in the population.

**Experimental design.** The association between FU and its components is often ignored when experimental results are presented. To illustrate the effect, we used records from 600 first lactation heifers, and found phenotypic correlations of energy balance (defined as energy intake minus energy required for yield and maintenance) with milk yield and feed intake of  $-0.60$  and  $0.49$ , respectively. However, if a much smaller experiment was done and only high and low producing cows were selected *a priori*, then these correlations were  $-0.89$  and  $-0.36$ , respectively. If only cows were compared with high and low intake then the correlations were  $0.07$  and  $0.87$  respectively. Thus experiments designed to investigate a wide range of milk yields would find a strong association between yield and energy balance, because the phenotypic variation in yield is enlarged compared with the variation in intake.

**Adjustment procedure.** Kennedy *et al.* (1993) showed how the variance and covariance matrix between intake and the components (ERQ) can be used to calculate the properties of FU. These authors also showed that a distinction should be made between genetic adjustment and phenotypic adjustment when assuming that selection for RFI is independent of its components. The problem with phenotypic adjustment is that sources of genetic variation can still be the consequence of a genetic correlation between feed intake and the components, because the associations with components are only phenotypically accounted for.

#### **BIOLOGICAL SOURCES OF VARIATION IN FEED UTILISATION**

**Net efficiency in dairy cattle.** In a review of sources of variation in gross efficiency in dairy cattle, it was concluded that there are probably no large genetic differences among animals in net efficiency (Veerkamp and Emmans 1995). Detailed experiments on a limited number of animals in energy chambers could not identify genetic variation for the digestion and metabolism of gross energy, nor for the partial efficiencies with which ME is converted to different products or maintenance. Some studies which attempted to estimate partial efficiencies from experimental or field data were able to identify some genetic components of the apparent net efficiencies of energy use, but the results did not always agree. More recent studies gave the same picture (Gordon *et al.* 1995; Beever *et al.* 1998; Ferris *et al.* 1999; Schwager-Suter *et al.* 2001), which probably means that there is still little evidence to assume large genetic differences among animals in net efficiency.

**Net efficiency in other species.** In beef cattle and deer there appears to be evidence, which suggests that genetic variation in net efficiency, may exist, probably in maintenance

requirements (Semiadi *et al.* 1998; Herd and Bishop 2000; Richardson *et al.* 2001). Energy costs of protein turnover was discussed and is likely to have an effect on RFI in beef cattle (Richardson *et al.* 2001). Another source of variation in net efficiency might be the small difference in digestibility that were reported between Black-White cows versus Galloways and Highlanders (Voigt *et al.* 2000). In mice several studies reported genetic effects on net efficiency or heat production (Nielsen *et al.* 1997b; Nielsen *et al.* 1997a; Selman *et al.* 2001a; Selman *et al.* 2001b), but sometimes these effects were subjected to differences in physical activity (Klein *et al.* 1999; Mousel *et al.* 2001). No differences were observed in energy utilisation above maintenance in deer (Semiadi *et al.* 1998).

**Body composition.** Different composition of growth tissue and body tissue might play a role when comparing animals for FU. Mobilising and replenishing fat reserves has large energy costs compared with protein, whereas maintaining fat has relatively low energy costs compared with maintaining protein. However, assuming homogeneous energy cost for each kg weight or weight gain might not be appropriate. In dairy cattle, liveweight change and body condition score were an important source of variation in RFI, probably because the environmental and genetic correlations among RFI and feed intake were of opposite signs (Veerkamp *et al.* 1995). In beef cattle low correlations were reported between residual feed intake (or feed conversion ration) and carcass fat percentage (Jensen *et al.* 1992; Arthur *et al.* 2001) and carcass lean percentages (Jensen *et al.* 1992; Herd and Bishop 2000), and less than 5% of the variation in sire RFI was explained by variation in body composition (Richardson *et al.* 2001). In the latter experiment, chemical composition of gain was not affected by selection for RFI. In mice, a higher lean content in males from a selection line selected for litter size might explain the observed difference in RFI, but body composition did not explain the higher RFI of selected females compared with controls (Rauw *et al.* 2001). Also other authors contributed some of the variation in FU to variation in body composition (Archer and Pitchford 1996).

**Activity.** Activity plays a role in the energy expenditure of animals (Luiting *et al.* 1991; Bunger *et al.* 1998). Various investigations suggested that differences between RFI in chickens (Luiting *et al.* 1994), beef (Archer *et al.* 1999), and pigs (De Haer *et al.* 1993) may be caused by differences in activity. Also, in mice, line differences in maintenance energy requirements were attributed to physical activity (Klein *et al.* 1999; Mousel *et al.* 2001). Differences in thermoregulatory heat production between selection lines were excluded because differences disappeared at lower temperatures (Klein *et al.* 1999).

#### **SELECTION, FEED UTILISATION, AND FERTILITY**

**Selection for lactation.** In dairy cattle body tissue mobilisation already supports about 7 kg milk per day over an 8-week period (Reynolds and Beever 1995; Tamminga *et al.* 1997). There is good evidence that selection for a higher yield increases feed intake and simultaneously increases the energy gap between yield and intake (for reviews Veerkamp 1998; Veerkamp and Koenen 1999). A similar association between higher milk production and a poorer energy balance is also observed in sheep (Marie *et al.* 1996; Bizelis *et al.* 2000), while sows selected for higher piglet production lost more weight and more backfat than controls (Shurson and Irvin 1992; Irvin and Cootauco 1993). The current increase in litter size appears

larger than can be supported by milk production from the increase in feed intake in lactating sows (Eissen 2000). In dairy cattle the effect of this genetically poorer EB is poorer fertility. Genetic correlations between the post-partum interval till first luteal activity and EB or liveweight gain were  $-0.60$  and  $-0.80$ , respectively (Veerkamp *et al.* 2000). These results are supported by larger population studies where body condition score was used (Pryce *et al.* 2000; Dechow *et al.* 2001; Gallo *et al.* 2001; Veerkamp 2001). Reviewing the possible physiological pathways, we concluded also that reduced metabolic fuel availability, rather than direct effects of hormone concentrations, might be an important cause for the poorer fertility associated with increasing genetic merit for milk yield (Veerkamp *et al.* 2002).

**Selection for growth.** Studies in pigs indicated that selection for lean growth rate on either an *ad lib.* or restricted feeding regime did not significantly affect reproductive performance (Kerr and Cameron 1995), and that selection for growth and daily food intake may result in relatively greater genetic changes in piglet growth than in litter size from gilts (Kerr and Cameron 1996). Also, no differences were found for time till first physiological oestrus between groups selected for high or low lean growth rate (Stern *et al.* 1994; Cameron *et al.* 1999), although oestrus behaviour was lower in the high lean growth rate (Cameron *et al.* 1999). Although these studies demonstrate no important effects on fertility in gilts, effects on reproductive performance in the next litter can not be excluded. There are concerns that limited feed intake capacity and insufficient mobilisable tissue in sows selected for lean growth rate causes reduced reproductive performance in second or higher parities (Whittemore 1996; Sauber *et al.* 1998; Eissen 2000; Cameron *et al.* 2002).

**Selection for feed utilisation.** Divergent selection lines showed that selection for improved lean food conversion gave smaller litters in gilts, and selection for high feed intake gave larger litters (Kerr and Cameron 1995). Delayed physiological oestrus was observed for lines of pigs selected for high lean food conversion (low feed conversion ratio) (Cameron *et al.* 1999). Lines selected for low lean food conversion mobilised more lipid during lactation, and selection for high feed intake (directly or by selection for growth under *ad lib.* feeding) reduced lipid mobilisation as sufficient energy for lactation could be provided from intake (Cameron *et al.* 2002). This general pattern of animals that appear less efficient with food conversion or have a higher feed intake have better reproductive performance, is also observed in mice. Selection for high or low heat loss in mice increased and decreased litter size, respectively (Nielsen *et al.* 1997b). In beef cattle and sheep little attention has been given to the genetic association between FU and reproduction.

**Selection for litter size.** Selection for increased litter size also increases lactation performance (Rauw *et al.* 1999). However, the correlated response in mice was not sufficient to supply the larger litter with sufficient resources (Rauw *et al.* 1999).

## DISCUSSION

There is no doubt about the effectiveness of genetic selection to change FU and its components, despite the fact that there are several nuisance factors identified that might suggest differences in FU, where in fact these are merely a consequence of recording practises

or other unforeseen factors. However, these nuisance factors are unlikely to explain all the genetic variation in FU in the different studies. These factors will always exist, and it is already widely accepted that selection for FU is not equivalent to selection for net efficiency. Investigating the genetic covariances of FU with the other traits of interest within a population is probably the best option to test whether some unexpected sources of variation in FU play a role.

Across species there are several examples of studies that aimed to identify the most important sources of genetic variation in feed utilisation. However, together they have been unable to come up with one major source of variation in net efficiency. Activity, body composition, and protein turnover have been suggested, but results are still somewhat confusing and conflicting between studies. Hence, it is tempting to assume that many small effects improve net efficiency, and that selection for feed efficiency is working towards perpetual motion, *i.e.* efficiency of 100%. However it is more likely that selection on FU alters feed intake, the component traits in ERQ, the component traits forgotten in ERQ, and any of the nuisance factors described above.

There is clear evidence that selection for milk yield and/or direct selection for feed efficiency resulted in poorer reproductive performance in dairy cattle, mice and pigs. The subsequent negative effect on fertility is likely to come from a more negative energy balance. There are different hypotheses about the causal explanation. Some hypotheses follow the 'yield driven' argument that resources cannot keep up with requirements: the more negative EB comes from lean animals not capable of mobilising enough body reserves for lactation, or from animals not capable of eating enough to support lactation. Another line of argument is the hypothesis that the negative energy balance itself is genetically driven, simply because everything else being equal, animals in a more negative energy balance are more likely to be selected because of their higher yield. The latter seems to be most likely in dairy cows where feeding extra concentrate increases yield, but does not reduce the negative energy balance.

The implication is that selection on important components of FU should be accompanied by selection on improved fertility, and possibly health. This may be particularly important when the aim of selection is to reduce feed intake, while simultaneously increasing feed requirements. Another safe option is to derive selection indices that increase feed intake sufficiently to accommodate the increased requirements (Veerkamp and Koenen 1999).

## CONCLUSIONS

Energy balance and feed efficiency are equivalent terms, albeit with opposite sign. There is clear evidence of genetic variation in feed utilisation, but the biological sources for this variation are not crystal-clear. A conflict exists between selection for a lower feed intake per unit production to improve feed efficiency, and selection for a higher feed intake per unit production to sustain reproductive performance. Careful consideration should be given to all components of the feed utilisation complex, including fertility, health and may be energy balance, before one or more components are selected for.

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