GENETIC IMPROVEMENT OF ECONOMIC PERFORMANCE IN DAIRY CATTLE

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ABSTRACT

The aims in this thesis were to investigate the use of more comprehensive breeding goals in dairy cattle, to investigate the possible importance of genotype by environment interaction and to identify possible sources of genetic variation in feed utilisation.

On the basis of a literature review, longevity was examined as a component of the breeding goal, and four linear type traits (foot angle, udder depth, teat length and angularity) with the closest genetic association with longevity were used as index measurements. Economic values were derived for protein, fat and milk yield and for longevity using dynamic programming. The relative economic values derived were, in genetic standard deviations relative to protein yield, 1.0, 0.2, -0.2 and 0.8, respectively. Three additive indices were derived, assuming that the breeding goal was for: (i) yield only (YIN), (ii) longevity only (LIN) or (iii) yield and longevity, hence profit (PIN). Selection on PIN was expected to give a 5% higher annual rate of genetic progress in economic merit compared with selection on YIN, and PIN was robust to most assumptions made in the calculations.

Genotype by environment interaction was investigated for a range of traits. Selection (S) and Control line (C) cows, housed and managed at the Langhill Dairy Cattle Research Centre, have been offered *ad libitum* complete mixed diets, with proportions (in total DM) of concentrates, silage, brewers' grains of either 20:5:75 (LC; 1.0 tonne concentrate per annum) or 45:5:50 (HC; 2.5 tonne concentrate), over a full lactation. No diet by genetic line interactions were observed for a number of traits describing milk production, feed intake, efficiency and body tissue mobilisation. However, regression coefficients of milk yield and condition score on pedigree index for fat plus protein yield were significantly different between LC and HC. Phenotypic and genetic variances were generally larger on HC than on LC, but difficulties in separating the permanent environmental variance from the additive genetic variance might have obscured some of the comparisons. Genetic correlations between HC and LC were high for most traits, and only for fat yield the value was below 0.80.

Residual feed intake (defined as energy intake minus predicted energy requirements based on lactational performance, metabolic live weight and live weight change) was investigated to identify sources of genetic variation in feed utilisation. When the energy requirement for each cow was estimated from phenotypic regressions then the heritability for residual feed intake was estimated to be between 0.30 and 0.38. When partial genetic regressions were used, than the heritability of residual feed intake was only 0.05. This difference between the heritability for 'genetic' residual feed intake and phenotypic residual feed intake was a consequence of (i) the antagonistic genetic and environmental correlations between live weight change and energy intake and (ii) a strong bias downwards in the estimation of the heritability for genetic residual feed intake. These results suggest that predicted energy requirements did not take account of all the genetic variation in feed intake and possibly some variation in partial efficiencies exists.

Future investigations into more comprehensive breeding goals should consider the whole genetic complex of yield, intake, live weight and body tissue mobilisation and not any one of the components only. Possible interactions - within and across lactations - between this complex and different management and feeding levels need to be investigated further, even though only limited evidence was found in this study of the existence of genotype by environment interaction.

ACKNOWLEDGEMENTS

Data from the Langhill project was used in this study and experiments were designed and set up prior to my arrival. Hence, I am indebted to all the persons involved in the initiation of this program.

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PREFACE

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Charles and Mieke, brothers and friends and many others who showed their interest have been a great stimulation throughout the whole period of this study. However, most of all, I am thankful for Gerlien her support, help and encouragement, she has made the time in Scotland very special.

Some of the published papers from the time period of this thesis are included in the Appendix and a complete list of publications is given on the next pages.

PUBLICATIONS

Refereed publications:

Hastings, I.M. and Veerkamp, R.F. 1993. The genetic basis of response in mouse lines divergently selected for body weight or fat content. I. The relative contributions of autosomal and sex-linked genes. Genetical Research, Cambridge, 62: 169-175.

McGowan, M.R., Veerkamp, R.F. and Anderson, L. 1994. Effects of genotype and feeding system on reproductive performance in dairy cattle. (Submitted)

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Veerkamp, R.F., Emmans, G.C., Cromie, A.R. and Simm, G. 1994. Variance components for residual feed intake in dairy cows. Livestock Production Science (In press; Chapter 5).

[1] Veerkamp, R.F., Emmans, G.C., Simm, G. and Oldham, J.D. 1994 Energy and protein utilisation of cows of high and low genetic merit for milk solids production on a high and low input diet. Huisman *et al.* (editors) Biological basis of sustainable animal production, Proceedings of the Zodiac symposium, Wageningen the Netherlands, April 13-15, 1993, EAAP publication No. 67, page 154 - 160, Wageningen Pers, Wageningen, The Netherlands.

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Veerkamp, R.F., Hill, W.G., Stott, A.W., Brotherstone, S. and Simm, G. 1994. Selection for longevity and yield in dairy cattle using transmitting abilities for yield and type. (Submitted; Chapter 2).

[1] Veerkamp, R.F., Simm, G. and Oldham, J.D. 1994. Effects of interaction between genotype and feeding system on milk production, feed intake, efficiency and body tissue mobilisation in dairy cows. Livestock Production Science 39: 229-241. (Chapter 3)

[1] Veerkamp, R.F., Simm, G. and Persaud, P. 1994. Potential value of linear type traits for the prediction of intake, efficiency and profitability in dairy cattle. Livestock Production Science 38: 179-189.

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[1] Reprint or copy in Appendix.

Conferences:

Simm, G., Veerkamp, R.F. and Oldham, J.D. 1992. Breeding more profitable dairy cows - the Langhill experience. Proc. 8th World Holstein Friesian Conference, Hungary.

Simm, G. and Veerkamp, R.F. 1994. Scientific advances in cattle breeding. RADBF dairy farming conference. Stoneleigh, 1-2 March.

[1] Stott, A.W., Veerkamp, R.F. and Emmans, G.C. 1994. Modelling to establish the economic value of longevity in the dairy cow. Proc. 44nd Meeting European Association of Animal Production, Edinburgh, Paper No. C2.16.

Veerkamp, R.F. and Simm, G. 1994. Breeding more profitable dairy cows: profit indices for the UK. National training conference for ADAS dairy consultants, Cheltenham: 7 - 8 June.

[1] Veerkamp, R.F., Brotherstone, S., Stott, A.W., Hill, W.G. and Simm, G. 1994. Profit indices for UK dairy cattle. British Cattle Breeders conference, Cambridge 10 - 13 January, 49: 64-71.

[1] Veerkamp, R.F., Brotherstone, S., Stott, A.W., Hill, W.G. and Simm, G. 1994. An index combining transmitting abilities for type and yield to select for yield and longevity. 5th World Congress on Genetics Applied to Livestock Production Science, Guelph, 17: 69-72

[1] Veerkamp, R.F., Emmans, G.C. and Simm, G. 1994 Sources of genetic variation in efficiency of dairy cows. Proc. 45nd Meeting European Association of Animal Production, Edinburgh. Paper No. NGC4.3 (Main paper).

Veerkamp, R.F., Simm, G., Oldham, J.D. and Persaud, P. 1991. Breeding for milk fat and protein production: consequences for efficiency of production. Proc. 42nd Meeting European Association of Animal Production, Berlin. Paper No. C4.12.

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Veerkamp, R.F., Simm G. and Oldham, J.D. 1994. Genotype by environment interaction - experience from Langhill. BSAP Occasional Meeting, Greenmount College, Northern Ireland, 1-2 November.

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INTRODUCTION

Many components contribute to profitability of dairy cattle enterprises (e.g. Gill and Allaire, 1976b; Ostergaard *et al.*, 1990). However, in most countries breeding is still based mainly on improving milk component yields. Selection for milk solids production does improve profitability of dairy cows within a single lactation (Simm *et al.*, 1994, Appendix), though selection on yield components alone does not automatically maximise the rate of genetic gain in overall profitability. For example, Gibson (1986) concluded that when selecting for milk yield, gross energetic efficiency (energy in milk per unit energy in feed) was increased but at a diminishing rate. Recent estimates of genetic correlations under *ad libitum* feeding (Persaud *et al.*, 1991) showed that the correlated response from indirect selection for gross energetic efficiency by selection on fat plus protein yield is expected to be only 47-75% of that from direct selection for efficiency. There are also indications that selection for milk production alone might be inconsistent with the health and reproduction of the animals (Christensen, 1989a and b; Solbu and Lie, 1990; Simianer *et al.*, 1991; Eriksson, 1991).

Investigation of a 'broader' definition of the breeding goal (often called 'total merit') and, hence, new selection criteria, is particularly relevant now considering:

- (i) the surplus of dairy products in many western countries. Quotas or price constraints have made higher production *per se* less attractive, and reducing costs of production more attractive;
- (ii) growing public concern for the health and welfare of farm animals, as well as the direct economic consequences of disease;
- (iii) new breeding schemes, initiated in the UK and elsewhere, which involve centralised nucleus herds of dairy cattle, rather than progeny groups dispersed over many commercial herds. These centralised schemes permit direct recording of 'new' traits for selection, e.g. feed intake, health events.

For these reasons, this thesis can be seen as having the general aim of investigating methods to improve the rate of genetic gain in total merit of dairy cows. Chapter 1 is a general review and discusses possible methods for the derivation of economic values for possible goal traits. Furthermore, the possible importance in a breeding program of (i) health and reproduction and (ii) longevity of dairy cows was reviewed. In Chapter 2, results from this review were used and a selection index was derived in which linear type traits - used to predict longevity of dairy cows - were combined with milk, fat and protein yield.

Data from the Langhill Dairy Cattle Research Centre were used in Chapter 3 to investigate the consequences of selection on fat plus protein yield only and the effects of interaction between genetic merit for fat plus protein yield and feeding system. Several traits describing milk production, feed intake and body tissue mobilisation were studied. Variance components and the genetic correlation between the same trait expressed on two different feeding systems were estimated in Chapter 4 and sources of genetic variation in feed intake and residual feed intake were investigated in Chapter 5.

The final chapter (Chapter 6) is a general discussion in which additional literature results were combined with the results from Chapter 3 and Chapter 5 to identify sources of genetic variation in feed efficiency. Conclusions were drawn on appropriate components for future breeding goals and suggestions are made for further research.

CHAPTER 1

BREEDING FOR ECONOMIC PERFORMANCE IN DAIRY COWS - A REVIEW

Selection index theory (Hazel, 1943) is widely accepted as method to combine several traits of economic importance in an index. In principle, the construction of a selection index is straightforward, requiring:

(i) a list of traits of economic importance ('goal' traits);

(ii) relative economic values of these goal traits;

(iii) a set of measurements (index traits) which can be obtained on candidates for selection and/or their relatives to predict their merit for goal traits. These may be the same as, or different from, goal traits.

(iv) Genetic and phenotypic parameters for (some of the) goal traits and for index measurements. These are heritabilities and correlations which indicate the extent to which different traits are under genetic control and the strength of the associations between the traits.

This chapter is a general review and possible methods for the derivation of economic values are discussed. Furthermore, the potential value of (i) health and reproduction traits and (ii) longevity of dairy cows in a breeding program was reviewed, by collating economic values and genetic parameters for these traits. Genetic correlations with measurements available nationally - yield and linear type traits - have been collated, to review the usefulness of these traits as predictors in a selection index.

1.2 Derivation of economic values.

1.2.1 Profitability perspectives.

Profitability is often defined as a function of several costs (C) and returns (R) - a profit function. Harris (1970) gave three possible profit functions: (i) maximise profit (R - C), (ii) minimise costs per unit of product (C/R), (iii) maximise revenues per unit cost (R/C). Dickerson (1970 and 1976) argued that the only reasonable breeding objective was economic efficiency, defined as the ratio of production income divided by production costs. Moav (1973) pointed out that different perspectives yield different economic values. Pearson (1986) justified the use of profit (income minus expenses) as the choice for dairy cattle selection objectives, since (i) profit is more understandable for producers, (ii) dairy cattle breeding programs in temperate zones focus on the producers perspective and (iii) results from Balaine *et al.* (1981a) showed a high correlation between animals ranked on returns - costs and the ratio of costs to returns. Brascamp *et al.* (1985) produced a possible solution to this problem and showed that when assuming a 'normal profit' market situation, economic values are equivalent for the three definitions of profitability. Smith *et al.* (1986) went a step further and showed that increased production due to genetic improvement should be evaluated against increasing the size of an enterprise or, in a fixed output situation, against reduction of the number of animals. Smith *et al.* (1986) were able to show that for a given profit equation, rescaled relative economic merit was identical, whether evaluated at fixed or scaled output, fixed or scaled input, and fixed, scaled or zero profit (Gibson, 1989a). The rescaled economic values were equivalent to increased economic efficiency as proposed by Dickerson (1970). Van Arendonk and Brascamp (1990) were able to show that the equivalence between optimising cow profitability and product profitability also holds in situations with more than one product, when the same output or input restriction is applied. Groen (1989) suggested that the individual producers interest (profit maximisation) should be chosen, because producers are the main decision makers in the agricultural industry. Groen and Ruyter (1990) reviewed derivation of economic values for milk production traits and concluded that profit maximisation seems to be the uniform choice in dairy cattle breeding.

1.2.2 Neo-classical production theory.

Amer and Fox (1992) and McArthur (1987) criticised the general use of profit functions and rescaling as discussed by Brascamp *et al.* (1985) and Smith *et al.* (1986). The major criticisms were, among others:

- re-optimisation of management and the enterprise is needed after genetic change, because farmers will always try to optimise their profit. Hence, genetic gain results in new (non linear) total, marginal and average cost functions and not simply in a constant change in marginal costs and marginal returns.
- economic values at different bases (national interest, farm or animal) are proportionally related to each other. Once the effect of a genetic change on profit per farm is known, economic values for other bases are proportionally equivalent.
- assuming that farmers are profit maximisers then, by definition, profit cannot be increased by rescaling the size of the enterprise, (if it was so this would have been done already). Therefore the rescaling argument of Smith *et al.*

(1986) - that any profit from genetic change which could have been made by rescaling the size should not be attributed to that genetic change - seems to be in conflict with the assumption that farmers are profit maximisers.

- who receives the benefits from genetic improvements (e.g. consumers or producers or the sum of these two: society) depends on the supply and demand curves. Therefore the concept of perspectives linked to different bases seems an over simplification.

The theoretical framework for derivation of economic values outlined by Amer and Fox (1992) has practical implications in that (i) when the effects of genetic improvement are evaluated at the level of farm, different bases and the need for their equivalence are irrelevant and (ii) optimisation of management should be considered after introduction of improved genetic merit. But as Amer (1994) commented, there is no simple prescription as to the most appropriate method for deriving economic values, and there has to be a (subjective) trade off between complexity of the models and the use of simplifying assumptions.

1.2.3 Input or output restriction.

Under quota systems where output per farm is restricted for one or more components of the breeding goal, rescaling as proposed by Smith *et al.* (1986) is not applicable, because returns are a discontinuous function of the outputs (Gibson, 1989a). Both Groen (1989) and Gibson (1989a) accounted for output restrictions and showed that economic values were affected by quotas. Gibson (1989a) introduced an approximate rescaling method when output restrictions applied for milk production traits. He showed that the economic value of the restricted output component is reduced with the average profit per unit output. More generally rescaling rules for restricted output for one or more output components were introduced by Van Arendonk and Brascamp (1990). Alternatively, it can be assumed that the small changes expected in individual traits would leave the number of animals in a typical herd unchanged and that quota can be freely leased when herds are 'above quota'. Making these assumptions allows quota to be accounted for as a marginal cost (Chapter 2).

1.2.4 Methods to derive economic values.

The normative approach

Groen (1989) classified two approaches for deriving economic values: (i) the positive approach or data evaluation and (ii) the normative approach or data simulation. The normative approach sets up a profit equation and economic values are derived by (i) partial differentiation of the equation with respect to the trait of interest (Moav and Hill, 1966) or by (ii) evaluating the effect of one unit change of the trait. The second option can be (a) accompanied by dynamic programming (Van Arendonk, 1985b; Rogers *et al.*, 1988a; Boichard, 1990), (b) accompanied by linear programming or (c) without optimisation of the profit function, but simply evaluating the effect on the total output of one unit change of a trait. When the normative approach becomes a complicated structure of equations, it is called 'bio-economic' modelling (Tess *et al.*, 1983). Bio-economic models are often so complex that only method (c) can be used to derive economic values (Groen, 1989). Dekkers (1991) pointed out that method (c) should re-optimise the management system after the change in genetic merit, as economic values need to be derived from an optimised production system (McArthur, 1987). However Dekkers' results indicated that economic values for involuntary culling, conception rate and milk production were robust to sub-optimality of culling and insemination decisions, provided optimum culling levels before genetic change are specified.

The positive approach

Several authors (Andrus and McGilliard, 1975; Balaine *et al.*, 1981a and b; Gill and Allaire, 1976a; Tigges *et al.*, 1986; De Haan *et al.*, 1992; Simm *et al.*, 1994 Appendix; Veerkamp *et al.*, 1994, Appendix) used comprehensive profit functions to calculate profitability of individual animals. Extensive comparisons of these functions are reviewed by Pearson and Miller (1981) and Allaire and Thraen (1985). Profit functions differed primarily in the complexity and the number of actual measurements included. For example, the profit functions used by Veerkamp *et al.* (1994) were primarily based on real records on the cow and therefore accounted for variation in feed intake and utilisation of feed, whereas most others used fixed relationships between production (and sometimes live weight) to predict feed intake. The profit function used by De Haan *et al.* (1992) was different since it included lost opportunity costs for a replacement cow, as suggested by Van Arendonk (1991). Most profit equations were based on data from experimental herds and were used only to identify the correlations or coefficients of determination between several 'nationally available' traits and total merit of dairy cows.

Profit functions can also be used to estimate economic values. Hazel (1943) defined economic values as the partial genetic regressions of overall merit on the goal traits, but there seems to be general confusion on how to obtain economic values from profit functions based on real data. For example, Niebel (1986) suggested that regression could be based on overall farm records or on phenotypic measurements, and De Haan *et al.* (1992) regressed phenotypic measurements of profit on phenotypic linear type traits. Rogers *et al.* (1988b) regressed BLUP sire evaluations on predicted transmitting abilities (PTAs) for milk yield and type. But these are biased estimates of the genetic relationship, as shown by Blanchard *et al.* (1983). These authors also showed that the correlation between Y_{pta} and X_{pta} (X_{pta} and Y_{pta} are predictors of genetic merit for trait X and Y) are biased by the repeatabilities for Y_{pta} and X_{pta}, respectively. To obtain partial genetic regression coefficients of longevity on type Brotherstone and Hill (1991b) regressed phenotypic survival measurements on transmitting abilities for type. This seems the most appropriate way to obtain economic values of a phenotypic profit function, because whenever primarily sib information is included in X_{pta}, no environmental covariances are expected between X and Y. Hence, estimated coefficients from a partial regression of phenotypic merit (a profit function based on phenotypic measurements) on transmitting abilities (excluding information included in the profit function) gives economic values for goal traits.

Positive or normative approach ?

Groen (1989) stated that the positive approach is less suitable than the normative approach, because it uses current prices. Although this argument is less likely to hold when biological traits are recorded and different pricing schemes are attached to those records (Simm *et al.*, 1994, Appendix), a disadvantage of the positive approach is that it calculates economic values in a given situation, where economic values should be calculated under optimal management situations. Further problems with the positive approach are: (i) small data sets give economic values with large sampling errors, and (ii) biases can be introduced due to sampling. Furthermore interpretation of the economic values is often difficult because of correlations between the 'independent' variables.

Nevertheless there are some disadvantages with the normative approach as well. The normative approach becomes vulnerable when relationships between traits are only partly known. Most bio-economic models are based on 'AFRC type' equations and Gibson (1992) mentioned some of these disadvantages. Firstly, the vast majority of the available equations are based on experiments where the same cows are fed different diets or amounts of feed. So the estimated equations only reflect nutritional effects and no genetic relationships. Secondly, other data come from experiments where cows have different phenotypic levels of production and are fed different nutritional diets. In these data it is difficult to decide the extent to which imposed differences in diets across performance levels pre-determine the observed relationships. Also most of the observed relationships are purely phenotypically based. Some evidence to support these statements comes from a comparison between two selection lines (Veerkamp *et al.*, 1993, Appendix). A three percentage point lower residual feed intake was observed for animals selected for fat + protein yield, compared with a control line. This significant difference suggests that selection has an impact on 'AFRC type' equations and therefore the general ability of bio-economic models to predict economic consequences of selection might be questioned. For example, when the same set of 'AFRC' equations used for the calculation of residual feed intake, was used to predict the consequences of selection for fat + protein yield an obvious bias would have been introduced.

1.2.5 Generality of economic values.

The previous sections made it clear that obtaining economic values is not easy. Fortunately, VandePitte and Hazel (1977) showed that only large changes in economic values may lead to losses in efficiency of selection. Most loss in efficiency is likely to come from omitting important traits (measured as the product of the economic value and heritability) or giving the unimportant traits too much emphasis or selecting important traits in the wrong direction (Smith, 1978). Gibson (1989a and 1989b) investigated the effect of different pricing systems, quota systems and methods of evaluation on the relative economic values for weights of carrier, fat, protein and lactose. His conclusion was that relative economic values, based on different payment systems, different costings and different scaling methods, differed remarkably, and that selection response differed when using incorrect economic values. In more practical situations, however, the reduction in genetic progress (Gibson *et al.*, 1992) was limited, and a single set of economic values was suitable for all markets in Canada at one time.

As an alternative to deriving economic values, Brascamp (1984) reviewed methods to weight goal traits according to the desired gain for these traits. Gibson and Kennedy (1990) have argued that selection should always be for economic gain and not for desired gains.

1.3 Health and reproduction

1.3.1 Economic values for health and reproduction.

Costs as a consequence of health events normally include costs for discarded milk, drugs used to treat the mastitis and increased labour. Decreased sale value and costs of increased replacement should also be accounted for (e.g. Strandberg and Shook, 1989). Economic losses due to mastitis are estimated to be substantial and are reported to be from 240 kg milk per case of mastitis in Denmark, 400 - 470 kg milk per case in the USA and up to 2167 kg milk per veterinary treated cow with sub clinical mastitis in Sweden (see review by Eriksson, 1991). Similarly, costs increased by 115 to 185 kg milk equivalent for each unit change in average log somatic cell count (i.e. per doubling of the actual average somatic cell count). Esslemont and Peeler (1993) gave values of £50, £248 and £1464 for mild, severe and fatal cases of clinical mastitis (incidence 13%, 8% and 1%), respectively. The cost of higher somatic cell counts (SSC) defined as 350 000 - 450 000 and > 450 000 was found to be £42 and £84 respectively (Lucey *et al.*, 1986). Selection index calculations by Strandberg and Shook (1989) showed that including SCC or mastitis in an index was expected to reduce the rate of genetic gain in yield traits by 1 to 2% and to slow the rate of increase in clinical mastitis by 20 to 25%.

Based on the observations from the University of Reading's 'DAISY' dairy herd health and fertility monitoring scheme, the costs of an extra day (>360 days) on a cow's calving interval is typically around £3.00 for a high yielding herd (Esslemont and Peeler, 1993), a net results of lost milk yield (around £-2.10 per day), less concentrate needed (£+.51), slippage in calving pattern (£-0.50), fewer calves sold (£-0.27) and extra cost in the dry period (£-0.40).

Lameness has an effect on reproduction, culling, milk yield, milk withdrawn and in the worst situation, single cases of interdigital, digital or sole ulcers could cost as much as £80, £392 and £392 respectively (Esslemont and Peeler, 1993). This could add up to as much as £60 per cow per year (assuming incidence of all three diseases is 9%).

1.3.2 Genetic parameters for health and reproduction.

Heritability estimates for milk fever, mastitis and ketosis are given in a comprehensive review by Emanuelson (1988). Heritability estimates for diseases recorded directly through clinical registrations were generally below 0.05, though estimates for somatic cell counts and ketone bodies were slightly higher. Simianer *et al.* (1991) reported heritabilities in the range of 0.05 to 0.13 for (i) mastitis, (ii) ketosis or (iii) any disease observed. Genetic correlations between somatic cell counts and clinical mastitis range from 0.5 - 0.8 and heritabilities are found to be slightly higher than for clinical mastitis (Emanuelson *et al.*, 1988). Somatic cell score is the log of somatic cell counts and Welper and Freeman (1992) reported a heritability of 0.16 for this indirect measurement of mastitis.

Several factors affecting lameness in cattle are more fully discussed by Greenough (1991), and heritability estimates are reported by Peterse and Antonisse (1981), Petersen *et al.* (1982), Nielsen and Smedegaard (1984), Smit and Verbeek (1984), Peterse (1986a, b). The most common cause of lameness is referred to as 'footrot'. There was conflicting evidence of breed differences for this infectious disease, but heritabilities were reported to range from 0.08 to 0.27. Also, laminitis or 'sole ulcer' was found to be lowly heritable and estimates for the heritability range from 0.10 to 0.20.

Heritability estimates for fertility traits were similar to estimates for diseases (for numerous references see: Philipsson, 1981; Freeman, 1986; Van Arendonk *et al.*, 1989; Weller and Ron, 1992; Hayes *et al.*, 1992) and are most often below 0.10. For example heritability estimates for conception rate ranged from 0.02 to 0.04 for heifers and from 0.01 to 0.02 for cows (Weller and Ron, 1992). For days to first service, days open and number of services per conception heritability estimates were 0.03, 0.05 and 0.03 (Hayes *et al.*, 1992), respectively. In heifers, the heritabilities for direct and maternal calving ease (4 categories from unassisted to surgical intervention) were around 0.05 and in cows around 0.02 (Cue and Hayes, 1985; Cue *et al.*, 1990) and there appears to be a genetic antagonism between direct and maternal effects for calving ease (Freeman *et al.*, 1981; Dwyer, 1984 cited in Dadati *et al.*, 1985; Cue and Hayes, 1985).

1.3.3 Genetic correlations with yield

Compared with low pedigree index heifers, a group of heifers selected on high pedigree index had 9% more digestive disorders, 5% more foot rot, 11% more cases of udder oedema and 2% more lactations affected by mastitis (Shanks *et al.,* 1978), for this reason a negative genetic association between yield and general health is expected. Estimated genetic correlations seem to support this hypothesis, for example genetic correlations between milk yield and observations on (i) mastitis, (ii) ketosis and (iii) presence of any disease, were above 0.5 (Simianer *et al.*, 1991), indicating a strong undesirable relationship between disease and production. Emanuelson (1988) reviewed estimated genetic correlations between production and mastitis, somatic cell counts and ketosis and found values between -0.10 and 0.66, -0.07 and 0.60, and 0.19

and 0.30 respectively. More recent parameters were reviewed by Simianer (1993), but his findings matched the parameters reported by Emanuelson (1988) in that the genetic relationship between yield and health is undesirable.

Relationships between fertility and yield are found to be negative, but management decisions and biological effects are often confounded in field data - high producing cows are likely to be inseminated later and high yielders are likely to get more opportunities for insemination. This might have increased negative relationships between yield and fertility traits (Philipsson, 1981; Freeman, 1986). To remove this selection effect on the estimated parameters Van Arendonk *et al.* (1989) included the data upon which these selection decisions are made in the REML analysis, which should remove the bias (Meyer and Thompson, 1984). But even then these authors found unfavourable genetic correlations from -0.08 to 0.33 between 'interval to first insemination' and yield, and from 0.21 to 0.76 between 'number of days open' and yield.

Given the difficulty of estimating genetic correlations between yield and reproduction from field data, selection experiments with a control and selection line could provide useful information on the genetic relationship between yield and fertility. However, there is conflicting evidence from several long term selection experiments, Bonczek *et al.* (1992) found superior performance for control line cows (primiparious) for the interval of calving to first service, the interval of calving to conception and for the length of gestation, compared with a selection line selected for yield only. Nevertheless, Bertrand *et al.* (1985) found no significant genetic group differences in number of services or number of reproductive examinations. Legates and Myers (1988) found no definitive trend in differences between genetic groups for days open. A comparison of genetic groups by Rothschild *et al.* (1981) for numbers of oestruses and services, age at first oestrus, or age at first calving in heifers and gestation length showed only a significant difference for the latter trait.

1.3.4 Genetic correlations with type traits

The potential for improving udder health (mastitis or somatic cell counts) using udder measurements has been studied (Thomas *et al.*, 1984; Seykora and McDaniel, 1986; Monardes *et al.*, 1990; Rogers *et al.*, 1991a) and a summary of published genetic correlations is given in Appendix 1A. Thomas *et al.* (1984) and Seykora and McDaniel (1986) used comprehensive measurements of udder characteristics for the prediction of somatic cell counts or mastitis, but most traits did not correspond to current linear type traits available, which makes practical implementation difficult. Using the current type classification system, genetic correlations between somatic cell counts and (i) udder depth (-0.21 to -0.64), (ii) fore udder attachment (-0.09 to -0.47) and (iii) teat placement (0.00 to -0.51) were negative and between SCC and teat length (0.16 to 0.20) tended to be positive (Rogers *et al.*, 1991a) (a deeper udder, more loosely attached, with longer teats placed further apart gave higher SSC).

Minor but significant phenotypic effects were observed between reproductive performance (days open and number of inseminations) and foot angle and rump width (Shapiro and Swanson, 1991). Highly favourable genetic correlations with calving interval were observed for chest floor (-0.42), rear udder (-0.37), capacity (-0.34) and highest antagonistic correlations with calving interval were for dairyness (0.43) and dairy character (0.38) (Dadati *et al.*, 1986). However, no other publications were found with genetic relationships between reproductive measurements and linear type scores currently in use. There was a tendency for the genetic correlations between type and the direct effect of calving ease to be opposite in sign to the genetic correlations between type and maternal effect of calving ease (Cue *et al.*, 1990) (Appendix 1B).

1.4 Longevity

1.4.1 Economic value for longevity

Herd life has been found to be a trait of major economic importance by several authors (Gill and Allaire, 1976a; Bakker *et al.*, 1980; Balaine *et al.*, 1981b; Congleton and King, 1984; Van Arendonk, 1985b; Rogers *et al.*, 1988a; Allaire and Keller, 1990; Klaassen *et al.*, 1992). Various measurements of herd life based on availability of measurements in national data sets include: presence or not of an animal at a fixed age (Everett *et al.*, 1976a), presence or not in a fixed lactation (Brotherstone and Hill, 1991a), survival score within each consecutive lactation (Madgwick and Goddard, 1989) and length of productive life (Rogers *et al.*, 1991b). The benefit from a longer herd life comes from (i) lower replacement costs, (ii) increased income caused by a higher proportion of the cows producing at mature level, (iii) reduced amount of feed necessary for non producing heifers and (iv) a better possibility of culling low producing cows (Rendel and Robertson, 1950). Several authors have used different approaches to estimate the economic value of herd life (or related traits).

The positive approach has been used by Andrus and McGilliard (1975), who calculated index weightings by partial regression of profit per year of herd life on phenotypic measurements of seven other traits, including herd life. Congleton and King (1984) used an extensive dynamic herd model to estimate the economic benefits from increased herd life. This model included relationships between cow age, milk production, labour requirements, health costs, reproductive diseases, mastitis and fertility. Economic values for herd life were calculated by lowering the (fixed) culling criteria for cows. They concluded that the economic value of herd life was insensitive to higher feed prices, poor management, decreased salvage value, trend of improving management, but high salvage value and low feed price decreased the value of extended herd life. Esslemont and Peeler (1993) calculated the cost of each cow involuntarily culled to be £590 in a 100 cow herd. Hence, decreasing involuntary culling by 1% will increase the margin per cow by £5.90. Van Arendonk (1991) showed that the economic value for herd life is over-estimated when using a profit function (positive approach) without allowing for opportunity costs. Opportunity costs account for the fact that a cow will be replaced by an average cow to keep the number of cows fixed. With higher average milk yield, higher depreciation costs (ratio of the replacement costs per cow per year to total fixed costs per cow per year) and lower average herd life, the economic value of herd life increases when keeping the economic value of yield constant (Allaire and Gibson, 1992). These authors used the normative approach and economic efficiency as a perspective, because Van Arendonk and Brascamp (1990) showed equivalence between perspectives when using this ratio. In terms of economic weights standardised by genetic variation (s.d.), generally milk production is found to be twice as important as herd life, which is consistent with the conclusion of Burnside *et al.* (1984).

All studies estimating the economic value of longevity discussed thus far, did not regard the advantage of better possibility of culling low producing cows with increased herd life as suggested by Rendel and Robertson (1950). Van Arendonk (1985c) and Rogers *et al.* (1988a and b) used dynamic programming to determine the economic consequences of changes in involuntary culling rate, whilst optimising voluntary culling. They found that the economic weight for herd life was 50% higher than without voluntary culling and variation in production between cows. Dekkers (1991) came to the same conclusion and showed that when omitting changes in voluntary culling (as a consequence of improved involuntary culling) economic values were 30% underestimated for involuntary culling.

1.4.2 Selection criteria for longevity.

A decrease in involuntary culling together with an increase in voluntary culling may give economically optimal results (Van Arendonk, 1985a; Rogers *et al.*, 1988a). Voluntary culling is a function of management only so that a reduced level of involuntary culling will be the desired breeding goal. Lack of widespread recording and unreliable recording of culling reasons (Madgwick and Goddard, 1989) makes it difficult to directly incorporate involuntary culling as a trait in breeding programs. As an alternative, herd life is often adjusted for milk yield to calculate functional herd life (HLF) (Ducrocq *et al.*, 1988). Functional herd life is thought to be a function of involuntary culling only (hence, all voluntary culling is assumed to be on yield), whereas true herd life (HLT) is a function of voluntary and involuntary culling. Several different approaches have been used to convert observed true herd life measurements to functional herd life; Boldman *et al.* (1992) used the within herd rank of a cow's yield in the latest lactation as a covariate. Short and Lawlor (1992) used the same correction procedure, but used first lactation yields instead. The first lactation was chosen because the latest lactation is likely to be affected by diseases and therefore might not reflect the real production ranking of the animals. Luijkx *et al.* (1992) used the genetic and phenotypic variances and covariances among herd life, yield and linear type traits to calculate the variance/covariance matrix conditional upon milk yield. Kennedy *et al.* (1993) showed that when variances and covariances are known between herd life and production, a selection index including herd life and production can account for the adjustment of herd life for milk yield.

An unfavourable aspect of functional herd life is that herd life is not only adjusted for the fact that farmers cull on yield, but also is adjusted for possible undesirable effects (genetic and environmental) of a higher yield on herd life. Dekkers (1993) concluded that the direct effect of production on herd life will be large enough to advocate adjustment of herd life for phenotypic production. Nevertheless, it will be intrinsically difficult to separate from field data (i) the effect of voluntary culling for yield (and the farmer's perception of the value of a cow) and (ii) the effect of yield on involuntary culling and therefore it will be difficult to make a sound decision if selection should be in principal for true or functional herd life. But, perhaps selection experiments on yield and/or intensive recording of culling reasons in field data can provide answers about the magnitude of the genetic effect of yield on involuntary and voluntary culling.

1.4.3 Genetic parameters for longevity

Heritability estimates for the various measurements of herd life range from 0.00 to 0.10 with an average value of about 0.04 (Dentine *et al.*, 1987; Madgwick and Goddard, 1989; Brotherstone and Hill, 1991a; Short and Lawlor, 1992; Boldman *et al.*, 1992; Luijkx *et al.*, 1992). Hudson and Van Vleck (1981) adjusted components of variance of true herd life to estimate variance components for functional herd life and calculated that heritability of HLT is reduced by 35% to estimate the heritability for HLF. On the basis of analytically derived equations Dekkers (1993) concluded that heritability estimates of HLT are larger than the heritability for involuntary culling, when the standardised partial regression of herd life on milk yield was greater than 0.15.

Genetic correlations between different measurements of herd life are large within large data sets. Everett *et al.* (1976b) found genetic correlations between stayability to 48 months and stayability to other ages to be 0.86 or greater. Genetic correlations between survival till the second, third or fourth lactation were 0.73 to 0.91 (Brotherstone and Hill, 1991a) and genetic correlations among survival to the second lactation, 54 months of age, 85 months of age, HLT and HLF ranged from 0.71 to 0.99 (Boldman *et al.*, 1992; Short and Lawlor, 1992). Some of these high correlations might be explained because the traits are not independent, i.e. survival till the third lactation is conditional on survival to the second lactation and so on. Survival score as defined by Madgwick and Goddard (1989) overcomes this problem, because it excludes an animal from the data set after the first culling record. Approximated correlations among several survival scores ranged from 0.24 - 1.0 (average 0.85) during the first 3 years after calving. Correlations among the later survival scores were lower but this is presumably due to higher sampling errors in the smaller data sets.

1.4.4 Genetic correlation between yield and longevity.

The low heritability of herdlife, and the fact that it is expressed late in life will give low responses to direct selection for herdlife. For these two reasons, there is much interest in using correlated traits for a possible selection index. Milk production would be the first possible predictor of longevity for a selection index, because several authors reported positive correlations between production traits and measures of herd life, ranging from 0.2 to 0.4 and from 0.4 to 0.6 for phenotypic and genetic correlations respectively (in Honnette *et al.*, 1980). But as discussed before, these moderate to high positive correlations might be inflated through culling decisions in commercial data. Based on evidence that higher yields appear to coincide with higher disease susceptibility (Christensen, 1989a; Solbu and Lie, 1990; Simianer *et al.*, 1991; Eriksson, 1991), the underlying biological relationship between yield and herd life might even be unfavourable.

1.4.5 Genetic correlations between type and longevity.

Type scores have also received a great deal of interest as possible predictors of herd life. Burnside *et al.* (1984) reviewed the usefulness of descriptive type traits as predictors of longevity, and could not come to a definite answer at that stage. In 1983 linear type scores were introduced in the UK (and elsewhere) and several subsequent studies have related linear type traits to herd life. An overview of the reported genetic correlations with measurements of herd life is given in Appendix 1C. A distinction should be made between pedigree registered and non pedigree cows. Brotherstone and Hill (1991b) found differences between pedigree and non pedigree herds for rear legs side view, teat position side view and foot angle. Nevertheless, they concluded that there was no evidence that regressions and correlations are substantially lower for the non-pedigree than for pedigree progeny. In contrast, Dentine *et al.* (1987), Rogers *et al.* (1988b) and Short and Lawlor (1992), found different relationships between type and measures of herd life in pedigree and grade cows. Especially body traits like stature, chest width and body depth appear to have a positive genetic relationship with herd life in pedigree herds and a negative relationship with herd life in non-registered herds. As breeders in pedigree herds have an obvious interest in type classification, correlations within these herds might be a consequence of selection decisions of breeders (they keep daughters from bulls which have high estimated breeding values for 'fashionable' type traits). For this reason, relationships between herd life and linear type traits estimated from non pedigree herds might be given more weight than genetic correlations based on pedigree cows.

A second distinction is made in relationships between linear type traits with either functional or true herd life. Although high genetic relationships are observed between these two different measurements of herd life, genetic relationships with type seem to be affected more. Especially some of the udder traits and angularity appear to have opposing genetic correlations with milk yield and herd life. Consequently, genetic correlations between functional herd life and the udder traits are larger than the correlations with true herd life. Some studies incorporate quadratic terms for the type traits because an economic optimum is perceived. Brotherstone and Hill (1991a) found no evidence for an intermediate optimum using genetic regressions, although most type traits showed a clear optimum when herd life was regressed on phenotypic measurements of type (Brotherstone and Hill, 1991a; Foster *et al.*, 1989).

1.5 Conclusions

Enhancing dairy breeding goals with traits other than the yield components seems sensible, not only because of the economic importance of traits like feed intake and herd life, but also because some of the benefits of selection on yield might be offset by an increase in health and reproduction problems. Hazel's (1943) approach is generally accepted as the best method to combine several traits of importance into a breeding objective.

The theory of deriving economic values for possible traits in the breeding goals has been discussed by several authors. Several simplifying assumptions are usually made by animal breeders and some of these assumptions have been made more implicit by Amer and Fox (1992). The criticism of re-optimisation of management after genetic change has been implemented in Chapter 2. In this Chapter economic values for longevity have been calculated re-optimising (i) feeding and (ii) voluntary culling after changes in genetic merit.

In the short term, predicted transmitting abilities for linear type traits and milk yield components are available only for progeny tested bulls. Therefore there is not much scope for traits other than production to be included in the breeding goal of dairy cattle unless reliable genetic correlations with type traits are available. Potentially, genetic correlations could exist because the linear type traits describe biological extremes and therefore could be correlated to other traits of economic importance. In the literature there was some evidence of the usefulness of linear type traits for the prediction of longevity and for this reason linear type traits were included in a selection index in Chapter 2.

As health and fertility have a low heritability and there is limited evidence of genetic correlations between type and these traits, these traits are not further discussed in this thesis. Genotype by environment interaction and genetic sources of variation in feed utilisation will, however, be considered.

APPENDIX 1A

Genetic correlations between type measurements and somatic cell counts.

Source[1]:	1)	1)	2)	2)	3)	3)	3)	3)	3)	3)	4)
#sires:			323	232	218	437	216	458	301	261	712
#records:	7000	7000	5000	5000	5335	16281	4294	18177	>50000	>30000	-
trait[2]:	SCC	SCS	SCC	SCC	SCC 1	SCC 1	SCC 2-3	SCC 2-3	SCC 1	SCC 2-3	SCS
Method[3]:	HEND	HEND	REML+	REML	REML	REML	REML	REML	REML+	REML+	PTA
			unequal						unequal	unequal	
TM			-.04	.02		-.23		-.04	-.19	.08	
ST					-.13	-.10	-.06	.05	-.11	.06	-.11
CW/stren					.02	-.07	.00	-.01	-.06	.11	-.11
BD					-.13	-.05	-.14	.02	-.05	.08	-.10
ANG						.13		.19	.18	.07	.08
RA					.24	.11	.12	.15	.08	.07	.04
R/thurl					.01	-.14	-.07	-.09	-.21	-.06	-.18
RLS					-.02	.00	.09	-.18	-.10	-.07	.01
RLR					.22		.20				
FA					.18	.00	-.03	.02	-.06	.14	-.07
FUA			.07	-.16	-.42	-.47	-.35	-.09	-.41	-.16	-.31
RUW					-.12	-.06	.27	.08	-.15	.05	-.17
US	.12	.20	.15	-.15	.00	-.02	-.12	.08	-.12	.06	-.16
UD	-.25	-.42			-.21	-.35	-.64	-.19	-.42	-.26	-.28
TPR	.10	.16	.28	.01	-.51	-.18	-.24	.00	-.31	-.12	-.21
TPS	.41	.54	.30	.03							
TL	.13	.32							.20	.16	
RUH					-.30	-.08	.13	.5	-.19	.08	-.13

[1] Sources: 1) Seykora and McDaniel (1986); 2) Monardes *et al.* (1990); 3) Rogers *et al.* (1991a); 4) Schutz *et al.* (1993).

[2] Traits: SCC n is somatic cell counts in lactation n; SCS is somatic cell score, log of SCC.

[3] Methods: REML is maximum likelihood (+ is for unequal design estimation); PTA are Pearson correlations between estimated breeding values.

APPENDIX 1B

Correlations between type traits and reproductive measurements.

Source[1]:	1)	1)	1)	2)	2)	2)	3)	3)	3)	3)
#sires:	775	3546	250	2548	3312	53	107	107	148	148
#records:	7193			22791	128857		>24000	>24000	>26000	>26000
trait[2]:	DCE	DCE	DCE	CIV	CIV	CIV	DCE	MCE	DCE	MCE
	heifers	heifers	heifers	1 to 2	1 to 2	1 to 2	heifers	heifers	cows	cows
Method[3]:	Hend.	PTA	PTA	Hend.	PTAs	PTAs	REML+	REML+	REML+	REML+
						R > 55%	unequal	unequal	unequal	unequal
TM	-.33			-.25	-.06	-.37	-.14	.08	.18	-.40
ST	-.10	-.05	-.16	-.23	-.02	-.37				
CW/stren	-.11	-.01	-.02	-.13	-.01	-.09				
BD										
ANG	-.17	.00	.00	.38	-.02	-.15	-.13	-.10	-.02	0.08
RA	.03	-.04	-.11	.11	.00	.09	.43	-.16	.22	-.26
R/thurl	-.15	.05	.07	-.13	.00	-.05	.33	-.05	..	..
RLS	.24	.03	-.03	-.08	-.03	-.21	-.15	.02	-.19	-.09
RLR										
FA										
FUA	-.35	-.09	-.10	-.21	-.05	-.17				
RUW	-.22	.07	.01	-.37	-.04	-.25				
US										
UD										
TPR										
TPS										
TL										
RUH										

[1] Sources: 1) Dadati *et al.* (1985); 2) Dadati *et al.* (1986); 3) Cue *et al.* (1990)

[2] Traits: DCE and MCE direct and maternal calving ease; CIV calving interval

[3] Methods: REML is maximum likelihood (+ is for unequal design estimation); PTA are Pearson correlations between estimated breeding values; Hend. one of the Hendersons methods

APPENDIX 1C

Genetic correlations between linear type traits and herd life.

Source[1]:	1	1	1	2	2	2	2	2	3	3	4	4	4	4	4	4	4	4	4	4	5	5
sires:	168	167	97	722	722	722	-	-	617	617	1176	1405	1176	1405	1176	1405	1176	1405	1176	1405	389	389
#records:	-	-	-	19294	19294	19294	18 388	>90000	53830	53830	80126	45 515	80126	45 515	80 126	45 515	80 126	45 515	80 126	45 515	109456	109456
trait[2]:	S1 lact.	S54 m.	HLF	S2 lact	S3 lact.	S4 lact	S3 lact.	S4 lact	HLT	HLF	S2 lact.	S2 lact.	S54 m.	S54 m.	S84 m.	S84 m.	THL	THL	FHL	FHL	THL	FHL
adj. yield:	Yes	Yes	Yes	No	No	No	No	No	No	Yes	No	No	No	No	No	No	No	No	Yes	Yes	No	Yes
Data[3]:	grade	grade	grade	reg.	reg.	reg.	reg.	comb.	grade	grade	Reg	grad	Reg	grad	Reg	Grad	Reg	Grad	Reg	Grad	Com	Com
Method[4]:	Calo	Calo	Calo	REML	REML	REML	L.S.	L.S.	REML	Anal.	REML	REML	REML	REML	REML	REML	REML	REML	REML	REML	REML	Anal.
TM	-.41	.33	.48	.65	.62	.43	.29	.35			.53	.07	.49	.19	.38	.09	.47	.17	.54	.12		
ST	-.29	-.01	.25	.08	.02	.04	-.03	.00	-.23	-.21	.25	-.16	.14	-.06	.03	-.03	.12	-.09	.18	-.19	.12	.06
CW/stren	-.05	.11	.05	.23	.22	.04	.04	-.13			.04	-.35	-.02	-.24	-.16	-.19	-.06	-.27	-.01	-.32	|-.06	-.16
BD	.03	.02	-.03	.33	.30	.15	.16	-.03	-.21	-.20	.05	-.29	-.02	-.14	-.19	-.18	-.06	-.21	-.03	-.32	|	
ANG	-.08	.04	.11	.07	.02	.16	.04	.13	.00	-.16	.43	.30	.45	.37	.30	.08	.42	.25	.27	.06		
RA	.13	-.16	-.33	-.38	-.32	-.16	-.15	.03	.16	.09	.06	.02	.08	.04	.13	.21	.09	.12	.01	.10	.13	.09
R/thurl	-.11	.09	.22	.26	.22	.12	.09	-.11	-.12	-.18	.13	-.05	.05	-.05	-.11	.03	.01	-.06	.04	-.16	-.01	-.01
RLS	-.08	-.12	.05	.03	.10	.10	.01	-.05	.07	.08	-.06	.00	-.07	.00	-.11	.01	-.08	.00	-.08	-.02	.03	-.05
RLR				.21	.04	.01	.09	.06	-.01	-.06												
FA	-.12	.34	.20	.35	.26	.22	.13	.09	-.16	-.12	.19	-.10	.22	-.16	.22	.07	.23	-.07	.26	-.06		
FUA	-.45	.34	.34	.28	.45	.29	.24	.06	.47	.46	.30	.08	.31	.17	.33	.09	.31	.17	.47	.24	.01	.16
RUW	-.06	.11	.06	.37	.47	.52	.21	.12	.13	-.07	.35	.12	.31	.23	.25	.10	.32	.20	.32	.10		
US	-.34	.26	.38	.27	.24	.12	.07	.02	.23	.22	.36	.09	.37	.17	.35	.08	.38	.17	.43	.18	.05	.17
UD	-.60	.31	.51	.08	.24	.18	.18	.14	.38	.47	.28	.14	.25	.06	.38	.23	.30	.20	.50	.39	.14	.41
TPR	-.49	.38	.51	.40	.37	.32	.09	.03	|.15	.17	.36	.08	.37	.13	.32	-.05	.36	.06	.42	.08	.05	.15
TPS				.49	.38	.38	.08	-.02	|													
TL				-.37	-.44	-.41	-.29	-.19													-.04	-.16
RUH	-.13	.23	.05						13	.25	.34	.30	.30	.27	.31	.32	.33	.33	.37	.14	.26	.18

[1] Sources: 1) Rogers *et al.* (1990); 2) Brotherstone and Hill (1991 a and b); 3) Boldman *et al.* (1992); 4) Short and Lawlor (1992); 5) Luijkx *et al.* (1992)

[2] Traits: S. is survival till n lactation or n months; HLT true measured herd life; HLF functional herd life (HLT corrected for yield)

[3] Data: Pedigree registered or graded cattle or combined

[4] Method: Calo *et al.* (1973) corrected correlations between PTA's; REML, multivariate sire model; L.S. least square, regression of phenotype for survival on PTA for type; Anal. Correlations between type and FHL are derived from estimates for THL.

CHAPTER 2

AN INDEX COMBINING TRANSMITTING ABILITIES FOR TYPE AND YIELD TO SELECT FOR YIELD AND LONGEVITY.

2.1 Introduction

Herd life has been found to be a trait of major economic importance by several authors (Chapter 1). The benefits from a longer herd life come from (i) lower replacement costs, (ii) increased income as a result of a higher proportion of the cows producing at the mature level, (iii) reduced amount of feed necessary for non-producing heifers, and (iv) more opportunities for culling low producing cows (Rendel and Robertson, 1950).

Type scores have received a great deal of interest as possible predictors of herd life. Burnside *et al.* (1984) reviewed the usefulness of descriptive type traits as predictors of longevity, and could not come to a definite answer at that stage. In 1983 linear type scores were introduced in the UK (and elsewhere) and several subsequent studies have related linear type traits to herd life (Rogers *et al.*, 1990; Brotherstone and Hill, 1991a and b; Boldman *et al.*, 1992; Luijkx *et al.*, 1992; Short and Lawlor, 1992). In these studies correlations between type and different measures of longevity ranged from -0.60 to 0.65 (Chapter 1). The genetic correlations between functional herd life (herd life corrected for milk yield) and udder traits were larger than the correlations with true herd life (Boldman *et al.*, 1992; Short and Lawlor, 1992).

The objectives of this study were (i) to estimate economic values for involuntary culling in dairy cows using dynamic programming (Stott, 1994) and (ii) to construct a selection index incorporating predicted transmitting abilities for linear type traits and milk, fat and protein yield. Because no predicted transmitting abilities (PTAs) for direct measures of longevity are yet available in the UK, PTAs for the type traits were used to predict longevity.

2.2 Material and methods

Economic values: There are several different viewpoints which can be taken in calculating economic values (e.g. national returns, individual producers returns). In this study they were derived from the individual producer's viewpoint, because producers are the major decision makers in the dairy industry (Pearson, 1986; Groen, 1989). The perspective of individual producers will be to improve profitability (Moav, 1973). A dynamic programming model (Van Arendonk, 1985a; Stott, 1994) was used to calculate economic values for the goal traits - milk, fat and protein yield and percentage involuntary culling up to lactation four. The economic value for each goal trait was calculated as the change in the net present value of a replacement heifer (£ per unit, expressed as an annuity) as a consequence of a unit increase in the goal trait concerned, whilst keeping the output of the other goal traits constant. The dynamic programming model is more fully discussed by Stott (1994) and only modifications in the version used are discussed here. More information on the assumed key parameters and some validation of the current model is given by Stott *et al.* (1994, Appendix).

In this model the cows' daily energy requirements were calculated from energy needed for maintenance (based on live weight), energy required or gained from live weight change, energy required for pregnancy and the energy required for fat, protein and lactose production during lactation. All equations used for the daily rationing came from a program which is used by a commercial feed company. In general, the equations were based on the effective energy system (Emmans, 1994). Based on the calculated energy requirements a least cost cow ration was formulated combining grass or silage and concentrates. Dry matter intake capacity was based on (i) live weight of the cow and (ii) dry matter percentage and digestibility of the feed.

Finally, dynamic programming was used to optimise the 'keep or replace' decisions (Van Arendonk, 1985a). Decisions were taken annually over a sequence of 20 annual stages and a maximum of 12 lactations was assumed with 15 yield states (chance nodes) within each lactation (Stott, 1994). The influence of the repeatability of milk yield on the replacement decision was accounted for using the method of Bayesian updating (Lindley, 1965). In the absence of reliable UK information, the probabilities of involuntary replacement used were those of Van Arendonk (1985b). All other physical and financial assumptions were based on UK estimates for future prices (S. J. Amies, personal communications).

A price ratio for weight of fat:protein of 1:1.5 was assumed and costs of transport and processing were assigned to each extra kg milk (strictly speaking milk less fat and protein or 'carrier'). In the absence of evidence suggesting otherwise, it was assumed that the expected small changes in individual traits would leave the number of animals in a typical herd unchanged. It was also assumed that quota can be freely leased when herds are 'above quota', reflecting current industry practice. The dynamic programming model was therefore based on a fixed number of animals in the herd, with quota considered as an opportunity cost associated with fat production. A sensitivity analysis of the economic values was used to examine the effect of these assumptions. The economic values for longevity were derived by proportionally decreasing the chance that a cow was involuntarily culled in the first four lactations by one percent and a value of £5.52 per % was found. For the yield traits, the daily milk production was proportionally increased whereas the outputs of the other two components were kept constant. Values derived were £-0.03, £0.60 and £4.04 per kg for milk, fat and protein yield respectively. These economic values reflect the annual benefit in economic margin over the next twenty years from a permanent change in each of the goal traits.

Genetic parameters: The calculated economic value was for a change in involuntary culling, and hence, genetic correlations between linear type traits and longevity (survival) adjusted for yield (Brotherstone and Hill, 1991b) were used. Genetic and phenotypic parameters (Table 2.1) were the most up to date estimates for the UK population from Brotherstone and Hill (1991b) and S. Brotherstone (personal communication). Only four of the 16 linear type traits were chosen for the index, based on the genetic correlations with survival and using stepwise elimination and inclusion. Theoretically, type traits which have a low genetic correlation with longevity could appear important due to correlations with other traits in the index or goal. Including these traits in the index, however, will make the index vulnerable to imprecise estimates of genetic correlations and, in the worst situation, the real response might even decrease (Sales and Hill, 1976).

Derivation of index weightings: Although not fully practical yet, as a starting point it seems appropriate to assume that all index traits are predicted transmitting abilities from a complete multivariate (animal) model run. In that situation, optimal index weights are the sum of the partial genetic regression coefficients of each goal trait on each index trait, weighted by the economic value of the goal traits (Hazel, 1943). The partial genetic regressions can be derived directly from a regression of phenotype on the estimated breeding values for the index trait (Brotherstone and Hill, 1991b), or, when these are not available, the partial regressions can be calculated from estimated genetic variances and covariances:

$$R = G^{-1} G_{ig}$$

where R is a matrix of partial genetic regression coefficients of m goal traits on n index traits and the matrix G_{ig} (m x n) contains the genetic covariances between the m goal and n index traits. The symmetric matrix G (n x n) is equivalent to the genetic (co-) variance matrix between the index measurements. The index weights are then $b_{pin} = R\ v$, where v is the vector with the economic weights for the goal traits and

b_{pin} is the vector containing the index weights. If index traits and goal traits were the same, then $G_{ig} = G$ and $b_{pin} = v$.

This method was used to calculate index weighting factors for three different indices, assuming that the breeding goal was for: (i) yield only (YIN), (ii) longevity only (LIN) or (iii) yield and longevity, and hence profit (PIN). For practical use, some re-scaling was done to the weighting factors as these have to be applied to published PTAs for milk, fat and protein expressed in kg and for the type traits expressed in standard deviation (of PTAs) units.

The consequences of selection on different indices (or 'desired gains') were presented for a 0.22 standard deviation change in the index. This value was chosen because it approximates the annual selection response in a 'typical' four pathway dairy cattle breeding scheme (Robertson and Rendel, 1950). However, it should be realised that it remains difficult to predict the precise responses to selection on breeding values. For example a reduction of about 0.75 can be expected due to the a reduction in genetic variation due to selection (Dekkers, 1992).

<u>Sensitivity analysis:</u> Index weights for PIN were calculated using parameter values from an assumed base situation. However, if *real* values (e.g. for economic values) are different from the base values, then the calculated index weightings in the base situation (for PIN) might not give the optimum response in the *real* situation. For this reason, efficiency of the PIN was calculated for several situations different from the base. Efficiency of selection was calculated as:

Efficiency = (accuracy with PIN in real situation) /
(accuracy with optimum index for real situation)

The accuracy of any index is calculated as:

$$r_{hi} = b' \, G \, v \, / \, (b' \, P \, b \, v' \, C \, v)^{0.5}$$

where,

b = vector with weighting factor for each index trait
P = variance- and covariance matrix between sib means for the index traits
G = matrix with genetic covariances between index and goal traits
C = matrix with genetic covariances between goal traits
v = vector with economic value of each goal trait

Sensitivity was tested in three ways. Firstly, individual economic values were increased and decreased by 50% and then 100%, to test the importance of inaccurate estimates for the economic values.

Secondly, the assumption that complete multivariate PTAs were included in the index was examined. In practice, PTAs for type and yield traits are often estimated separately in multivariate BLUP evaluations, or the PTAs come from complete univariate analysis for all yield and type traits. In these situations, when PTAs are known with an accuracy smaller then unity, then (i) there might still be a bias due to an environmental covariance between records for type and for yield, and (ii) some PTAs might have higher accuracy than others (for example when heritabilities for the index traits are different or different number of records are available for each index trait). Consequently, the genetic correlations between index traits might still contribute to the accuracy of the PTAs for these traits. For these reasons, the efficiency of PIN was compared with the optimal index, when PIN weights were applied to (i) progeny records, or (ii) PTAs coming from univariate BLUP evaluations, or (iii) PTAs coming from two multivariate BLUP evaluations, one for the type and one for the yield traits. The total weight for phenotypic records in the *base* situation is:

$$b = P_i^{-1} G_i b_{pin}$$

where P_i is the (co-) variance matrix between the index measurements and the matrix G_i contains the genetic (co-)variances between the index traits. The elements of the matrices P_i and G_i depend on which of the three situations above are evaluated. For example, if phenotypic records are used as index measurements P_i and G_i are redundant, and when PTAs come from complete univariate BLUP evaluations, all the off-diagonals are zero. The optimal weights in the *real* situation were calculated as $b = P^{-1} G v$ (Hazel, 1943). A sire model was assumed, and the number of half sib progeny records was set at 10000, 1000, 50, 5 or 1.

Finally, sensitivity for errors in the estimated genetic correlations between type and longevity was evaluated. The *real* genetic correlations were assumed to be minus and plus 50% and 100% (set to zero) of the values in Table 2.1 and accuracy of PIN was compared with the accuracy of the optimum index.

2.3 Results

The weighting factors calculated for the indices are given in Table 2.2, for two different breeding objectives: increasing margins from yield only or increasing profit -

a combination of yield and longevity. A third objective, longevity, is given for explanatory reasons. Weights for the yield index (YIN) are equivalent to the economic values of the yield traits and no importance is given to the type traits, as expected, because PTAs were assumed to come from complete multivariate BLUP evaluations. When selection is for longevity, animals which have breeding values for steeper foot angle and are more angular are favoured. PTAs for a shallower udder and shorter teat length are also favourably related to longevity. The index weights for profit are the sum of the weights for yield and longevity.

If selection is for yield only, then 0.22 standard deviations change in the index gives a response of £15.3 which is a result of 119 kg milk, 5.0 kg fat and 3.9 kg protein (Table 2.3a). When selection is for profit then a slightly lower rate of genetic gain is achieved for the production traits, but longevity is genetically improved (rate of genetic gain is 0.23 less cows culled involuntarily in the first four lactations in a 100 cow herd). This is predicted to increase the annual selection response in profit by 5% compared to selection on a combination of milk, fat and protein only. The benefit from selection on PIN is shown, for example, when the selection responses for udder depth (UD) are compared (Table 2.3b). Selection for milk yield will result in deeper udders and selection for longevity will result in shallower udders, but selection on PIN will give a balanced rate of genetic gain, based on the economic values of longevity and yield. Another observation is that teat length (TL) is not expected to change following selection on PIN, even though it has a negative weighting in the index.

Table 2.4 shows that the index proposed (PIN) is robust to large changes in the economic value of milk and fat. Most of the loss in efficiency of the profit index appears when the economic value of protein is overestimated. Table 2.5 shows efficiency of PIN weights when applied to (a) phenotypic sib means, (b) univariate PTAs or (c) PTAs coming from two multivariate analyses. These weights gave selection efficiencies larger than 0.96 when all animals measured have both type and yield records available, but efficiencies decreased with decreasing number of records. Only in the situation where there are a lot of progeny with milk records and hardly any progeny with type records, or vice versa, do alternative index weights increase efficiency of selection by more than 0.05. This loss in efficiency is partly overcome by applying the index weights to PTAs (Table 5b and c), however, in all cases there is a considerable loss in efficiency when the number of milk records is low and the number of type records is high. Efficiency of PIN remains greater than 0.972 when the real genetic correlations are minus or plus 100% different from the estimated genetic correlations (Table 2.6).

2.4 Discussion

The objective of this Chapter was to demonstrate how longevity and yield could be incorporated into a dairy cattle breeding goal, using predicted transmitting abilities (PTAs). To achieve this objective, PTAs for four linear type traits and three milk production traits were combined in an economic profit index, PIN. Selection on PIN is expected to give a 5% higher annual rate of genetic progress in profit compared with selection on an index combining PTAs for milk, fat and protein only. The extra benefit comes from the longer herd life of cows. The results are discussed against this background.

Economic values: For milk, fat, and protein yield and longevity the economic values were derived with a dynamic programming model. The bio-economic part of this model fed a least cost ration, based on forage and concentrate and the dynamic programming optimised voluntary culling. This has the advantage that there is no need to assume an infinitely small change in genetic merit of a trait, as is normal practice when the partial derivative is taken from a profit equation to calculate economic values for a trait. At present, assuming an infinitely small change in genetic merit for yield seems unrealistic in the UK. Large changes in genetic merit are expected, largely as a result of the wide availability of imported semen from high merit bulls, and a greater awareness amongst farmers of the economic benefits of genetic improvement. Therefore, it seems relevant to re-optimise management after the genetic change, as suggested by Amer and Fox (1992).

Several authors have used different approaches to estimate the economic value of herd life (or related traits). Esslemont and Peeler (1993) calculated the cost of each cow culled involuntarily to be £590 in a 100 cow herd - equivalent to a £5.90 increase in the margin per 1% reduction in involuntary culling This is close to the economic value, derived in this study, of £5.52 per 1% improvement. Van Arendonk (1991) showed that the economic value for herd life is over-estimated when using a profit function (using real data - the 'positive approach') without allowing for opportunity costs. Opportunity costs account for the fact that a cow will be replaced with a heifer to keep the number of cows fixed. With higher average milk yield, higher depreciation costs (the replacement costs per cow per year as proportion of total fixed costs per cow per year) and lower average herd life, the economic value of herd life increases when keeping the economic value of yield constant (Allaire and Gibson, 1992). They used the 'normative approach' (using equations) and economic efficiency as perspective, because Van Arendonk and Brascamp (1990) had shown equivalence between perspectives when using this ratio. In terms of economic weights standardised by the genetic standard deviation, milk production is found to be twice as important as herd life, which is consistent with the conclusion of Burnside *et al.* (1984).

None of the studies estimating the economic value of longevity discussed thus far considered the advantage of having more opportunity of culling low producing cows when herd life is increased, as suggested by Rendel and Robertson (1950). Van Arendonk (1985) and Rogers *et al.* (1988) included this advantage, by using dynamic programming to determine the economic consequences of changes in involuntary culling rate, whilst optimising voluntary culling. They found that the economic weight for herd life was 50% higher than that derived when ignoring voluntary culling and variation in production between cows. Dekkers (1991) came to the same conclusion and showed that when omitting changes in voluntary culling (as a consequence of improved involuntary culling) economic values were 30% underestimated for involuntary culling. The economic values derived in this study are therefore close to the expected values from the literature. Economic weights expressed in genetic standard deviations were 1.0, 0.2, -0.2 and 0.8 for protein, fat, milk and longevity respectively.

Linear type traits: Currently there are no direct evaluations for longevity in the UK. In the present study, linear type traits were considered as indirect alternatives to direct evaluations of longevity. However even with national direct evaluations available, type traits may still contribute to the accuracy of evaluating longevity - particularly for younger bulls when the 'direct' evaluation will depend heavily on ancestors' records, until daughters are old enough to express differences in longevity. In this study, udder depth, angularity, teat length and foot angle were chosen for the prediction of survival up to lactation four. Although no direct biological explanations are available for the relation between these type traits and longevity, there is some evidence that udder characteristics are related to mastitis. For example, using a similar type classification system to that used in the UK, Rogers *et al.* (1991a) reported negative genetic correlations between somatic cell counts and (i) udder depth (-0.21 to -0.64), (ii) fore udder attachment (-0.09 to -0.47) and (iii) teat placement (0.00 to -0.51) and positive correlations between SCC and teat length (0.16 to 0.20). Also, udder depth had a consistent positive genetic correlation with longevity in most other studies (Boldman *et al.*, 1992; Short and Lawlor, 1992; Luijkx *et al.*, 1992). Although a negative relationship between longevity and udder depth was reported in a study by Rogers *et al.* (1990), a negative genetic correlation between survival till the end of the first lactation and udder depth was found (but a positive correlation between udder depth and survival till 54 months of age). This is probably due to culling on yield in the first lactation and the strong correlation between yield and udder depth. Reported values for the correlations between longevity and teat length (Luijkx *et al.*, 1992), and between longevity and angularity (Boldman *et al.*, 1992; Short and Lawlor, 1992) are in the same direction as the correlations used in this study. For foot angle, the correlations with longevity are less consistent, with values ranging from -0.16 to 0.35 (Rogers *et al.*, 1990; Brotherstone and Hill, 1991b; Boldman *et al.*, 1992; Short and Lawlor, 1992; Luijkx *et al.*, 1992). One of the possible explanations for different correlations between foot angle and longevity in different data sets could be genotype environment interaction. For example, in one study the regression of herd life on foot angle was stronger for cows in tie-stall housing than it was in loose housing (Burke and Funk, 1993). Differences in the method of assessment of foot angle and foot trimming practices between countries may also affect these results.

Furthermore, it can be questioned if a distinction should be made between pedigree registered and non pedigree cows. Dentine *et al.* (1987), Rogers *et al.* (1988) and Short and Lawlor (1992) found different relationships between type and measures of herd life in pedigree and grade cows. Brotherstone and Hill (1991b) found differences between pedigree and non pedigree herds in the relationship between survival and the type traits 'rear legs side view', 'teat position side view' and 'foot angle'. Nevertheless, they concluded that there was no evidence that regressions and correlations are substantially lower for the non-pedigree than for pedigree progeny. Some studies incorporate quadratic terms for the type traits because an intermediate economic optimum is perceived. Brotherstone and Hill (1991a) found no evidence for an intermediate optimum using genetic regressions, although most type traits showed a clear optimum when herd life was regressed on phenotypic measurements of type (Brotherstone and Hill, 1991a; Foster *et al.*, 1989).

Index derivation: In the calculation of the index weights, the Gig and G matrices were kept the same for all three indices even though the contribution of the yield traits to predicting genetic merit for longevity (as defined in this study) is small. The practical advantage was that index weights for PIN are the sum of weights for YIN and LIN, hence the three indices became additive. If the optimal PIN index was not used, but the sum of a yield index - with only the (co-) variances for milk, fat and protein yield included in the Gig and G matrix - plus an index based on only the four linear type traits, then a loss of 2% in the rate of genetic gain would be expected (results not shown).

The index appears robust to 50% changes in economic values for protein yield and longevity, but very sensitive to setting the value of protein at zero. Large changes in the economic value for milk or fat yield give efficiencies above 0.985, therefore allocation of quota costs entirely to fat yield does not seem critical (given the UK average quota situation, about 20-25% of the quota leasing costs could be attributed to milk yield). To illustrate the robustness to further changes in economic weights of milk, fat and protein, the consequences of selection on any one of the milk traits and on YIN and PIN are shown Table 2.7. As expected from the high correlations between the yield traits, the opportunities to change the composition of milk are restricted, and given the payment scheme assumed here, maintaining the current protein percentage is more profitable than increasing protein percentage.

Also, PIN appears to be robust when applied to measurements other than multivariate PTAs. When BLUP is used, PTAs are scaled progeny deviations and different heritabilities and different number of records available for each trait are already properly accounted for, although correlations between the index traits are still ignored in univariate analysis. This explains the difference in efficiency between Table 2.5a and Tables 2.5b and c. When only a few measurements for yield were available together with a large number of half sib records for type the large drop in efficiency was a result of a change of sign of the weighting for udder depth (results not shown). When PTAs for yield have low accuracy, there is greater emphasis on udder depth as a predictor of yield rather than longevity alone. As it is unlikely that animals will have a lot of type records on relatives and at the same time no records for yield on those sibs, this observation is not likely to have any practical implications. The reverse situation is more likely to occur (a lot of sibs with yield records, but no type records) and when applied to PTAs, the index appears to be robust in that situation.

Table 2.1: Heritabilities (diagonal), phenotypic (above the diagonal) and genetic correlations (below the diagonal) from Brotherstone and Hill (1991b) and S. Brotherstone (personal communication). Linear type score is scored from 1-9, with an approximately intermediate mean.

	Longevity	Milk	Fat	Prot.	ANG	FA	UD	TL
Standard deviation	49	895	35	27	1.34	1.17	1.64	1.24
Longevity[1] (%)	.06	-	-	-	-	-	-	-
Milk (kg)	.00	.47	.83	.94	.27	-.03	-.28	.05
Fat (kg)	.00	.77	.52	.87	.25	-.02	-.25	.02
Protein (kg)	.00	.93	.85	.45	.24	-.02	-.27	.05
Angularity[2] (ANG)	.11	.44	.42	.43	.26	-.04	.06	-.01
Foot angle (FA)	.09	.02	.05	.07	-.13	.27	.10	-.01
Udder depth (UD)	.21	-.48	-.40	-.44	.01	.03	.39	-.09
Teat length (TL)	-.19	.18	.12	.17	.08	-.09	-.21	.44

[1] Cows not involuntarily culled in the first 4 lactations, corrected for genetic differences in yield.

[2] A high score for ANG, FA, UD and TL means more angular, steeper, shallower and longer, respectively.

Table 2.2: Optimum index weightings for PIN, when the interest is in yield or longevity only or in profit (yield plus longevity).

Goal:	profit	yield	longevity	
Index:	PIN	YIN	LIN	direction
PTA for:				
Milk (kg)	-0.015	-0.030	0.015	
Fat (kg)	0.60	0.60	0.00	
Protein (kg)	3.84	4.04	-0.20	
Angularity (sd)	3.9	0.0	3.9	more angular
Foot angle (sd)	1.8	0.0	1.8	steeper
Udder depth (sd)	4.8	0.0	4.8	shallower
Teat length (sd)	-4.1	0.0	-4.1	shorter

Table 2.3: Consequences of a 0.22 standard deviation change in the index for (A) the production traits and (B) the linear type traits, when three different goals are assumed.

A:

Goal:	profit	yield	longevity
Index:	PIN	YIN	LIN
Response per annum in:			
H (£)	16.0	15.3	4.5
longevity[1] (%)	0.23	0.00	0.81
milk (kg)	114	119	0
fat (kg)	4.8	5.0	0.0
protein (kg)	3.8	3.9	0.0

[1] Percentage cows not involuntarily culled in the first 4 lactations, corrected for genetic differences in yield

B:

Goal:	Profit	Yield	Longevity		
Index:	PIN	YIN	LIN	1	9
Stature	0.07	0.05	0.07	125 cm	149 cm
Chest width	-0.03	-0.02	-0.05	Narrow	Wide
Body depth	0.04	0.04	-0.01	Shallow	Deep
Angularity	0.08	0.06	0.05	Coarse	Angular
Rump angle	-0.02	-0.02	-0.02	High	Low pins
Rump width	0.00	0.00	0.00	Narrow	Wide
Rear legs side	0.00	0.01	-0.01	Straight	Sickled
Foot angle	0.02	0.01	0.04	Low	Steep
Fore udder attachment	-0.02	-0.05	0.09	Loose	Strong
Udder support	0.02	0.02	0.00	Broken	Strong
Udder depth	-0.05	-0.10	0.15	Below	Above Hock
Teat placement rear view	0.01	0.00	0.05	Wide	Close
Teat placement side view	0.06	0.06	0.01	Close	Apart
Teat length	0.00	0.03	-0.11	Short	Long

Table 2.4: Efficiency of using PIN (weighting factors from the base situation), compared to the optimum PIN in situations where the true economic values for one of the goal traits (milk, fat and protein yield and longevity) differ by -100, -50, +50 and +100 percent from the base values, while keeping the other economic values at the base values.

	-100%	-50%	+50%	+100%
Longevity	.960[+]	.990	.992	.970
Milk	.994	.998	.997	.985
Fat	.992	.998	.999	.996
Protein	.140	.956	.994	.987

[+] e.g. the rate of genetic gain with PIN is 96% of the maximum genetic gain, when using the optimum index in the situation that the economic value of longevity is null (-100% of the base value) and all other economic values are at their base values.

Table 2.5: Efficiency of using PIN weights on (A) the phenotypic half sib mean, or (B) PTAs from univariate analysis, or (C) PTAs from two multivariate analysis, one for type and one for the yield traits, when different number of (half sib) records are available for type and yield.

A:

Number of progeny with yield records:	Number of progeny with type records:				
	10000	1000	50	5	1
10000	1.00	1.00	.999	.952	.770
1000	1.00	1.00	.999	.953	.772
50	.993	.994	.999	.962	.795
5	.831	.831	.876	.985	.900
1	.512	.515	.564	.795	.969

B:

Number of progeny with yield records:	Number of progeny with type records:				
	10000	1000	50	5	1
10000	1.00	1.00	1.00	.999	.999
1000	1.00	1.00	1.00	.999	.999
50	.993	.993	.999	.999	.999
5	.814	.816	.857	.985	.992
1	.457	.459	.498	.738	.971

C:

Number of progeny with yield records:	Number of progeny with type records:				
	10000	1000	50	5	1
10000	1.00	1.00	.999	.999	.999
1000	1.00	1.00	.999	.999	.999
50	.993	.993	.999	.999	.999
5	.816	.818	.856	.985	.994
1	.461	.462	.491	.719	.971

Table 2.6: Efficiency of using PIN (weighting factors from the base situation), compared to the optimum PIN in situations where the true genetic correlation between one of the type traits and longevity, differs by -100, -50, +50 and +100 percent from the base values, while keeping the other genetic correlations at the base values.

	-100%	-50%	+50%	+100%
Angularity	.993	.998	.998	.993
Foot angle	.996	.999	.999	.996
Udder depth	.973	.993	.994	.976
Teat Length	.984	.996	.996	.985

Table 2.7: Consequences of selecting the top 5% of the population using different selection indices. Returns are based on the assumed future milk prices and the margin is based on the calculated economic values.

Index:	average	milk	protein	fat	F+P	YIN	PIN
longevity (%)							+2.1
milk (kg)	5500	6726	6640	6444	6565	6577	6535
fat (kg)	226	264	268	276	275	271	269
protein (kg)	184	218	220	215	219	220	219
F%	4.10	3.93	4.04	4.28	4.18	4.12	4.12
P%	3.35	3.24	3.32	3.34	3.33	3.34	3.35
F / P	1.22	1.21	1.22	1.28	1.26	1.23	1.23
Returns (£)	1264	1483	1507	1511	1519	1515	1505
Margin (£)		+123	+138	+126	+136	+139	+146

CHAPTER 3

INTERACTIONS BETWEEN GENOTYPE AND FEEDING SYSTEM FOR MILK PRODUCTION, FEED INTAKE AND BODY TISSUE MOBILISATION IN DAIRY COWS

3.1 Introduction

There is a wide range in production circumstances both between and within countries. However, one of the major breeding goals of most dairy farmers, whatever the production circumstances, is to increase profitability. The introduction of quotas on milk production in the EC in 1984 has led to interest in reduced cost systems in some countries. For this reason, and because of the large influx of North American Holstein semen to most EU countries, and the introduction of new breeding schemes involving testing bulls in nucleus herds, investigating genotype x environment (G x E) interactions is particularly important at the present time.

Danell (1982) reviewed several studies in which interactions between feeding regime and sire, production level and sire, and housing system and sire were found to be of no importance. More recently, Van der Werf and Ten Napel (1991) found a genetic correlation for milk traits of 0.78 between high and low yielding herds, and the sire by herd interaction accounted for only 3% of the phenotypic variance. Most previous studies have focused primarily on milk production traits. In some studies G x E interaction for feed intake or efficiency of milk production has been considered when animals were fed according to yield (Richardson *et al.*, 1971; Lamb *et al.*, 1977; Wang *et al.*, 1992). However, feeding according to yield makes biological interpretation of the results difficult. Studies where animals were not fed according to production have been performed by Korver (1982) and Oldenbroek (1988), but together these studies present a rather confusing view of the positive existence and magnitude of genotype x feeding interactions in dairy cows.

Earlier studies at the Langhill Dairy Cattle Research Centre showed advantages to high genetic merit cows for milk solids production in a high input system of feeding (Persaud *et al.*, 1990; Simm *et al.*, 1994). More recently, research has been started to see whether these advantages are maintained under a lower input feeding regime. Indications that high genetic merit animals might not be able to maintain their advantage under a low input system (hence, a G X E interaction) come from other studies (e.g. Grieve *et al.*, 1976; Custodio *et al.*, 1983), which have indicated that the increase in gross energetic efficiency of high genetic merit cows is not due to better utilisation of feed, but rather to a higher degree of body tissue catabolism and to a simple dilution of maintenance. If there was a limit to the rate of tissue mobilisation or the amount of mobilisable tissue, high genetic merit cows might lose their advantage on a low input diet, i.e. there could be a genotype by feeding system interaction for production, or for efficiency or for body composition. Because tissue reserves in dairy cows in good condition are substantial (e.g. Gibb *et al.*, 1992; Butler-Hogg *et al.*, 1985) it is possible that the use of these reserves in one lactation might buffer high merit animals against nutritional adversity and so diminish interactions in the short term, with these only becoming evident in the longer term (i.e. in subsequent lactations). For these reasons a long-term study of genotype x feeding system interactions was established. In this experiment which started at Langhill in 1988, cows have been offered *ad libitum* two complete mixed diets, varying in the proportions of concentrate and grass silage.

The objective of this part of the study is to use preliminary records from the Langhill G x E experiment to estimate the effects of genotype by feeding system interaction, within a single lactation, on performance traits and body composition of heifers and cows.

3.2 Material and methods

Animals: Records were obtained from cows housed and managed at the Scottish Agricultural College/University of Edinburgh Langhill Dairy Cattle Research Centre. In each year calving began early in September and animals joining the trial all calved between September and January in any year. All cows involved in the study were Holstein-Friesians, kept indoors in conventional cubicle housing from calving to July and offered complete mixed diets *ad libitum*. Through the use of Calan Broadbent electronic gates the extended indoor period allowed measurement of feed offered to, and refused by, individual cows for four days a week, from calving to a minimum of 26 weeks and up to 38 weeks after calving (depending on the calving date of each cow). The data reported here are for performance over the first 26 weeks of lactation, recorded over four consecutive years from 1988-1992 inclusive. Cows were milked twice daily (0500 and 1500 hours) and 0.4 kg concentrates was fed in the parlour at each milking during the housed period.

Genetic groups: There were two genetic groups: a selection line (S) and a control line (C). Since 1973 S animals have been bred to bulls with the highest genetic merit for kg fat plus protein (F + P) available in the UK. Since 1976 the C animals have been bred to bulls of about national average genetic merit for F + P. For each line every year 4-5 bulls are selected solely on their predicted transmitting abilities (PTA). The bulls are then each used randomly over the cows and heifers in the relevant line. The only exceptions are that a bull is not mated to a close relative and bulls known to cause a high incidence of calving difficulties are not used on heifers. The S bulls were originally selected on their UK proofs, but during the last 15 years predicted transmitting abilities of foreign bulls have been converted to British proofs. In 1986 animals were re-allocated to S and C to balance these lines for average Holstein percentage. Allocation was based on genetic merit for F + P and Holstein percentage. Since the beginning of this experiment heifers were selected on pedigree index (predicted genetic merit, based on pedigree information) and allocated to either the high concentrate (HC) or low concentrate (LC) feeding system. Allocation to the feeding systems was random, except that offspring from the same bull were allocated equally to the two feeding systems (similarly in the first year multiparous cows were allocated equally to the two feeding systems). Cows have been maintained on the same feeding system in subsequent lactations and the objective is to record at least three lactations from each cow on a single feeding system. The mean PTAs (on the 1990 base) for fat + protein yield were 4.3 kg (s.d. = 7.7) for the C and 18.8 kg (s.d. = 9.9) for the S animals involved in the study reported here.

Diets: A complete diet based on grass silage, brewers grains and concentrates, was offered *ad libitum* to all animals. The feeding systems were designed to achieve, over a full lactation, proportions (in total DM) of concentrates, brewers grains and silage of 20:5:75 (LC) and 45:5:50 (HC). The animals on HC had an annual average concentrate intake of about 2.5 tonnes per cow. The LC animals ate about 1.0 tonnes of concentrate per annum. Animals were grouped according to stage of lactation and diet type. For both feeding systems the proportion of the dry matter from silage in the diet was altered when the group were 100 and 200 days from calving, on average, so that problems of underfeeding in early lactation were minimised but a substantial differential between feeding systems was maintained. Silage dry matter as a proportion of total DM in the diet was designed to average 0.40, 0.50, and 0.60 for HC and 0.65, 0.75 and 0.85 for LC in early, mid and late lactation respectively. Different compound balancer meals were included in HC and LC, with metabolisable energy and crude protein contents in the concentrate dry matter of about 13 MJ kg^{-1} and 180 g kg^{-1} respectively for HC and 12.6 MJ kg^{-1} and 310 g kg^{-1} for LC. This was done so that protein, mineral and micronutrient contents of both feed systems were not limiting performance (AFRC, 1991 and 1992), leaving forage:concentrate ratio as the key feed variable. The chemical composition of the diets used in the four years of study reported here is given in Table 3.1.

Milk yield and composition: Milk yields and milk composition analyses were recorded once every week, for a morning and afternoon milking separately. Fat, protein and lactose percentages were calculated as the average from the morning and afternoon sample, weighted by milk production. Average weekly milk, fat, protein and lactose yields for each cow were calculated as the sum of the morning and afternoon yields, multiplied by 7. The energy (MJ) in the milk was estimated from the morning and afternoon samples, using the formula of Tyrrell and Reid (1965):

$LE = (0.384\ F\% + 0.223\ P\% + 0.199\ L\% - 0.108)\ MY$

LE = milk energy (MJ); F%, P%; L% = fat, protein and lactose percentage and MY = milk yield (kg)

Feed intake and diet composition: Heifers were trained before calving to use individual electronic feeding gates. The complete diet was dispensed into individual feed bins, once daily. The weights of fresh diet offered and refused were recorded on 4 days consecutively each week. Daily samples from the different diets (early, mid and late lactation; HC and LC) and daily samples from refusals were analysed for dry matter. Each daily intake was calculated as:

$DMI = (FF \times DMFF) - (FR \times DMFR)$

DMI = dry matter intake (kg); FF, FR = Feed offered and feed refused; DMFF, DMFR = Dry matter proportion of feed offered and refused.

Daily samples of each diet were bulked to monthly samples and analysed to determine chemical composition. The estimated metabolisable energy content (ME MJ kg dry matter) was based on the summation of the estimated ME contents of the different dietary components (Thomas *et al.*, 1988b). The ME of silage was based on *in vitro* digestibility, and the ME contents of the balancer meal and brewers grains were estimated with neutral cellulase gammanase digestibility (NCGD) incubation techniques.

Live weight and condition score: Cows were weighed and condition scored within the 24 hours following calving and thereafter once a week after milking. Condition scoring was based on a system used by Russel *et al.* (1969) in sheep and further adapted for cattle by Lowman *et al.* (1976). This system defines 6 scores 0-5 (with increasing score indicating increasing fatness), and describes each score in terms of the amount of tissue cover over the transverse processes of the lumbar vertebrae and around the tail head (scoring was to ¼ unit).

Data handling: About 13,250 weekly records were available, on 391 lactations (210 cows). All lactations with fewer than 20 weekly records and all lactations with fewer than 7 weekly records in the first 15 weeks and no record after 23 weeks of lactation were discarded. Range checks were carried out before entering the data - a simple procedure was used to check for outliers, as follows. For each separate lactation a cubic polynomial was fitted through the weekly records for milk yield, fat %, protein %, lactose %, dry matter intake, ME intake, CP intake, live weight and condition score. Outliers were discarded on the basis of the estimated variance, within each separate lactation, about the fitted curve. When the observed value was more than 3.5 standard deviations different from the fitted value the observed value was rejected. In total 161 weekly milk yields were rejected, and from the other recorded traits the number of records discarded varied between 8 and 48. Given the fact that at least twenty weekly records were available in each lactation to estimate the curve, and that there was a low number of discarded records, it is unlikely that any strong bias was introduced by this method. Missing and discarded records were replaced by fitted values from a second polynomial, fitted without the outliers (fewer than 5% of the weekly records were finally estimated in this way). Records from the first 2 weeks of lactation were ignored throughout, because most missing values for yield and intake were in this period. Also previous studies at Langhill have shown that records from this period are of limited value.

Dependent variates: The weekly records were combined to form 12 traits of interest during the first 26 weeks of lactation: Milk yield (Milk), fat plus protein yield (F + P) and dry matter intake (DMI), were calculated as the average of the weekly records multiplied by 26. Fat (F%) and protein (P%) percentage, were calculated as the average of the weekly percentage weighted by the weekly milk yields. Gross energetic efficiency (ENEF) was calculated as 100 x LE (MJ)/ME intake (MJ). Gross protein efficiency (PROTEF) was calculated as 100 x protein yield (kg)/CP intake (kg). Average live weights (ALW) and condition scores (ACS), were calculated as the average weekly measurements.

Measured ALW is the aggregate of gut fill (GF), lipid (L) and lipid free empty body weight (LFEBW). ACS is an index of L/(ALW-GF). To evaluate changes in body composition an attempt was made here to estimate the different components contributing to ALW and ACS. The value of GF was estimated as (Emmans, personal communication): $GF = DMI\ (kg/day) * (11 - 7 * D)$ where D, the digestibility of feed, was estimated as diet ME density (MJ/kg)/15 (see Table 3.1). Based on data from Wright and Russel (1984) lipid (kg) per kg EBW was estimated as: $L/EBW = -0.0431 + 0.120 * ACS$ (Emmans, personal communication).

Analysis: Residual maximum likelihood (REML) (Patterson and Thompson, 1971) was used to estimate fixed effects. The Genstat REML (Genstat 5 Committee, 1989) option was used, with a random cow effect to account for covariance between subsequent lactations of the same cow. This REML routine approximates standard errors (s.e.) and standard errors of the differences (s.e.d.) for the effects included in the model. Two univariate models were used for the heifer and cow data separately:

Model 1:

$Y_{ijklm} = U + Y_i + M_j + LN_k + FS_l + LINE_m + FS_l \times LINE_m + b_1\ AC_{ijklm} + b_2\ H\%_{ijklm} + C_{ijklm} + E_{ijklm}$

Model 2:

$Y_{ijkl} = U + Y_i + M_j + LN_k + FS_l + b_1\ AC_{ijkl} + b_2\ H\%_{ijkl} + b_3\ PI_{ijkl} + b_4\ (FS_i \times PI_{ijkl}) + C_{ijkl} + E_{ijkl}$

where

Y_{ijklm} = Milk, F%, P%, FP, DMI, ENEF, PROTEF, ALW, ACS, GF, Lipid or LFEBW, aggregated over 26 weeks

U = overall mean

Y_i = year of calving (1988, 1989, 1990, 1991)

M_j = month of calving (Sept., Oct., Nov., Dec.)

LN_k = lactation number (2-3, >3 in cow data set only)

$b_1\ AC_{ijklm}$ = linear regression on age at calving in days

$b_2\ H\%_{ijklm}$ = linear regression on Holstein percentage

FS_i = effect of feed system (concentrate and forage)

$LINE_m$ = genetic line effect (selection or control)

$FS_i \times LINE_m$ = interaction between line and feeding system

$b_3\ PI_{ijklm}$= regression on pedigree index

$b_4\ (FS_i \times PI_{ijklm})$= regression on interaction between pedigree index and feeding system

C_{ijklm} = random cow effect (only in cow data set)

E_{ijklm} = residual effects

The pedigree index for F + P yield (PI) was calculated as 0.50 * sires' predicted transmitting ability (PTA) for F + P plus 0.25 * maternal grandsires' (MGS) PTA for F + P. PTAs of sires and MGS came from the August 1992 national animal model BLUP analysis (Wiggans *et al.*, 1988; Animal Data Centre, 1993), but no Langhill records were included in this particular run, since this evaluation was performed for England and Wales only. This made the regression coefficients of phenotypic values on PI equivalent to genetic regressions, because there is no environmental covariance between PI and the phenotypic measurement. Model 1 (without the random cow effect) was used to estimate least square means for the weekly performance in the 4 groups.

3.3 Results

The number of cows and records within each of the fixed effect classes for the data set is given in Table 3.2. Table 3.3 shows means corrected for fixed effects and for covariance between lactations of the same cow. Selected animals yielded more milk and fat + protein (kg) than control line animals ($P<0.01$). There was no line effect on milk composition of older cows, but in heifers milk protein concentration was slightly, but significantly ($P<0.05$) higher in control than selected animals. The numerically greater dry matter intake (DMI) in selected animals was not significantly different from the controls; the difference in mean DMI between lines was small compared with the differences in milk production. As a result, energetic and protein efficiency were both significantly ($P<0.05$) greater in selected animals than in controls. The pattern of change in gross efficiency was similar for heifers and cows in the same genetic groups (Figure 3.1).

Mean condition score (ACS) was significantly lower ($P<0.05$) in selected animals. As there were no feed system x line interactions this difference applied in each of the dietary treatments. Differences between the feeding systems were observed for DMI and calculated gut fill (GF), which were greater with HC than LC. In heifers only this was associated with a greater average live weight (ALW; $P<0.05$). The HC supported higher rates of milk, and fat + protein yield ($P<0.01$), a lower milk fat concentration ($P<0.05$) and, in cows only, a higher milk protein concentration ($P<0.05$) than LC. Protein efficiency was greater ($P<0.01$) with HC than LC. There was no significant feed system effect on energetic efficiency in the cows data, but significance is approached in the heifer data for energetic efficiency. Control heifers on HC produced a similar yield of fat plus protein to selected animals on LC, but with a lower fat concentration.

Differences in live weight and condition score during lactation are shown in Figure 3.2 and 3.3 for heifers and cows, respectively. Heifers from the C line on HC become heavier during lactation than the other three groups (Figure 3.2), probably through a combination of higher GF and, by calculation, more lipid stored. Most of the difference in condition score (Table 3.3), between control line animals and selection line animals, is created at the end of the lactation (Figure 3.3). In early lactation, condition scores on the two feeding systems were very similar within genetic line. However selection line cows on LC were clearly leanest by week 26 (Figure 3.3).

Regressions on PI showed correlated responses for most traits (Table 3.4), Milk, F + P, ENEF, PROTEF all showed positive regressions on PI. The regression of milk production on PI was significantly different between LC and HC diets. Figures 3.4 and 3.5 show these relationships graphically. For each PI point cows produced 18 kg and 47 kg more milk on LC and HC, respectively and 1.35 kg and 2.53 kg more F + P. The interaction between PI and feeding system was significant for milk yield (but not for F + P) which suggests a genotype x feed system interaction. High PI cows appear to be leaner than low PI cows, but this was primarily observed on the high concentrate system (Table 3.4).

3.4 Discussion

The aim of the long-term study at Langhill is to explore whether or not genotype x feeding system interactions exist and, if so, whether these are large enough to justify different selection decisions or testing systems for different feeding systems which might be employed in the UK or elsewhere. From the treatment means for single lactation records of 26 weeks which are reported here, there were no genotype x feeding system interactions detected (Table 3.3). However regression of performance measures on PI and the PI x feed system LC interaction indicated that interactions of potential importance may exist. The results are discussed against this background.

Milk yield: The decreasing effect of extra concentrate on F% has been found by several other authors (for a review see Sutton, 1989). The magnitude of the effect of feed system on fat % was relatively large given that the HC feed contained, on average, only 45% concentrate, and the LC feed 20% concentrate in diets based on grass silage. A wide range of concentrate allowances (with grass silage available *ad libitum*) spanning this range of concentrate:forage failed to yield any response in milk fat % in Gordon's (1984) work. Also, concentrate manipulation (in kind or amount) when concentrates form less than 0.6 of feed DM has generally promoted only small changes in milk fat content (Sutton, 1989). It has been held that dietary effects on milk fat concentration are less extreme with diets containing a large proportion of grass silage (than, for example, with diets based on hay or maize silage) because the characteristics of the silage have such a major influence on patterns of rumen fermentation (Chalmers *et al.*, 1978). Our data, collected over four years, show that feeding system effects on milk fat % can be substantial with complete mixed diets based on grass silage, and that the effects are in the direction expected from wider studies on forage:concentrate ratio and milk composition. In this study estimates for the feeding system effect on P% were just significant (Table 3.3) in the cows. Weekly records showed a clear decline in P% at peak lactation on LC for both S and C (results not shown), but there was no difference between LC and HC for P% during mid and late lactation.

Regression coefficients for complete lactation F + P yield on PI are expected to be 2 for both cows and heifers because PIs were estimated transmitting abilities. Higher regression coefficients were observed on HC and lower regression coefficients were observed on LC for the 26 week period included in this study. This might suggest that individuals of very high merit for milk solids production may have the expression of their potential compromised by inadequate nutrition, but the magnitude of this 'trend' was not sufficient to indicate a statistically significant interaction. In contrast to the regression coefficients for F + P, regressions of milk on PI were significantly different between the feeding systems. A log transformation and models with different combinations of feeding system, line and PI did not change this significant interaction between feeding system and genetic merit for milk yield (results not shown), suggesting that the interaction is not just a scale effect (mean related to the phenotypic variance). Lamb *et al.* (1977) found no genotype by diet interaction between daughters of USA Holstein Friesian bulls, but also concluded that regressions on index seem to have a stronger slope on high input diets. A possible explanation for the different slopes could be that heritabilities increase with increasing herd mean and increasing phenotypic variance (Hill *et al.*, 1983 and references therein). In Chapter 4 an attempt is made to estimate the variance components on both feeding systems separately, to investigate some of these issues further.

Also, the differences between regression lines on high and low input feeding systems suggest that continued selection for F + P in S is likely to make detection of any feed system x line interaction easier. There is obviously something of a conflict here between the interpretation of the comparison between group means - which show no genotype x environment interactions - and the indications from the regression analysis that an interaction exists, at least for milk. By way of explanation the group mean values for F + P (kg) are shown on Figure 3.5. From this figure it is readily seen that the means are fairly close together in comparison with the full spread of the data, and it is probably for this reason that the group mean contrasts failed to identify a significant interaction while the regression analysis did. A biological interpretation of this putative interaction should await a more definitive demonstration of its existence.

Intake and efficiencies: Both heifers and cows were able to eat more of the drier and less bulky HC diet than they did of LC. That there was a small (though non-significant) difference in DMI between lines (with selected animals eating more) poses the interesting question of why the control animals on LC failed to eat more than they did; selected animals on that feeding system ate a little more than the controls on LC - but not as much as controls on HC. Whatever the factor that limited intake of the LC system to less than that for HC, the intake difference between lines, though not statistically significant, might suggest that dietary factors alone could not account for this difference.

Although the diets used had been designed to exclude dietary protein concentration (or metabolisable protein yield, AFRC, 1992) as a constraint on performance, gross protein efficiencies are reported here - not least because of the rapidly increasing interest in management factors which can reduce dietary N wastage in intensive production systems (Tamminga, 1992). Higher gross protein efficiencies were observed on HC, which was a consequence of higher milk P% and a lower protein/energy ratio in the diet. In neither case, however, was the protein efficiency of a magnitude which would suggest that dietary protein was limiting performance. In energetic terms S were more efficient than C on both feeding systems. Although there was a large difference between LC and HC in condition score at the end of the lactation (Figure 3.3), this does not seem to have affected energetic efficiencies in the same period (Figure 3.1). Similarly, the cows on HC produced much more milk than those on LC and therefore diluted their maintenance costs over more output. Nevertheless, energetic efficiency was not different between the feeding systems (over 26 weeks), and the major component affecting gross efficiency in this study seems to have been genetic line. Even after correcting gross energetic efficiencies for maintenance, lactation and live weight change there was still a 3.5% advantage to the selection line (Veerkamp *et al.*, 1993). This suggests that there may be differences in energetic efficiency between the two lines which are not simply a reflection of different combinations of maintenance and 'performance' elements.

Live weights and body tissue: No significant feeding system effects were apparent for ACS or lipid, and from early to mid lactation, heifers and cows in the same genetic line had surprisingly similar condition scores (Figure 3.3), with S being slightly leaner than C. This suggests that cows 'seek' to reach a certain condition score in mid lactation, which is affected by genotype. It also supports the view presented by Emmans and Neilson (1984) that animals reduce their feed intake (or increase production) when more lipid is available for mobilisation, rather than the view that animals mobilise lipid because they produce more milk than they can support from intake alone. Regression of the interaction between PI and feeding system on ACS and LIPID indicate that for every kg reduction in PI for F + P, 0.9 kg LIPID is deposited during the first 26 weeks of lactation. Lamb *et al.* (1977) also concluded that daughters of high genetic merit bulls used less of their feed intake for increase of body tissue, although in their experiment cows were fed according to yield. Korver *et al.* (1985) found a clear influence of diet on 'stage of lactation at minimum live weight' and 'maximum live weight decrease'.

Conclusions: The objective of this study was to evaluate the extent of effects of genotype by feeding regime interaction within a single lactation, on performance and body tissue mobilisation. The results clearly showed that selection line animals were leaner after 26 weeks of lactation, but the interaction between feeding system and PI for ACS suggests that this is not due to extra body tissue mobilisation of selected animals, but rather to a relatively higher feed consumption of the control line animals at the end of the lactation. The line x feeding system interaction was not significant which would suggest that G x E is not expected to have a large impact for dairy herds in the UK, within the range of diets and PI examined here. However regressions of performance on PI did show an interaction which, though small, may have more substantial implications for the very highest PI animals if feeding is not adequate.

Table 3.1: Chemical composition of the early-, mid- and late lactation diets[+].

	HC			LC		
lactation period	early	mid	late	early	mid	late
(days):	0-100	100-200	200>	0-100	100-200	200>
DM (g/kg)	350	327	311	277	265	256
ME(MJ/KG DM)	11.96	11.82	11.56	11.60	11.45	11.15
CP (g/kg DM)	180	180	169	193	183	166
NH_3-N	78	88	90	102	89	97
ADF	218	240	265	254	276	308
NDF	370	412	445	405	450	493
AHEE	61	61	64	52	55	58
pH	4.3	4.4	4.4	4.3	4.2	4.2

[+] All values per kg DM unless otherwise indicated:
DM = g dry matter/kg diet
ME = metabolic energy (MJ) (see text for details)
CP = crude protein (g)
NH_3-N = ammonia N (g) per kg total N
ADF = acid detergent fibre
NDF = neutral detergent fibre
AHEE = acid hydrolysed ether extract

Table 3.2: Structure of the data set: data are the number of records for each category$^+$ (Number of cows is 204 and total number of records is 377)

Group*:		Month of calving:		Year of calving:		Lactation	
C-LC	74	Sept.	118	1988	83	1	128
S-LC	117	Oct.	94	1989	78	2-3	157
C-HC	84	Nov.	102	1990	110	>3	92
S-HC	102	Dec.	63	1991	106		

$^+$ 1 record = data for one cow in one lactation

* C and S are the control and selection line on the high and low concentrate feeding systems (HC and LC respectively)

Table 3.3: Estimates for the mean effects of genetic line and feeding system, corrected for fixed effects and the covariance of repeated lactations of the same cow (records are up to 26 weeks of lactation).

Cows only	S-HC^{+}	C-HC	S-LC	C-LC		Diet	Line	Line*Diet
(N =249)	mean	mean	mean	mean	s.e.d.$^{\pm}$			
Milk (kg)	6123	5425	5031	4533	166	**	**	-
F%	4.10	4.11	4.50	4.37	0.13	*	-	-
P%	3.05	3.12	3.02	3.01	0.05	*	-	-
F + P (kg)	436	391	375	334	12	**	**	-
DMI (kg)	3648	3474	3232	3099	87	**	-	-
ENEF (%)	43.6	40.9	43.9	40.6	1.2	-	*	-
PROTEF (%)	28.1	26.7	24.7	23.2	0.7	**	*	-
ALW (kg)	633	614	622	612	11	-	-	-
ACS	2.43	2.56	2.35	2.52	0.08	-	*	-
GF (kg)	109	104	100	96	3	**	-	-
Lipid (kg)	132	136	126	135	7	-	-	-
LFEBW (kg)	393	374	396	381	6	-	*	-
Heifers only	S-HC	C-HC	S-LC	C-LC		Diet	Line	Line*Diet
(N = 128)	mean	mean	mean	mean	s.e.d.			
Milk (kg)	4769	3962	3924	3234	147	**	**	-
F%	4.09	4.06	4.42	4.33	0.13	*	-	-
P%	3.11	3.22	3.01	3.14	0.05	-	*	-
F + P (kg)	343	286	290	240	10	**	**	-
DMI (kg)	3096	3044	2614	2512	72	**	-	-
ENEF (%)	40.6	34.3	42.6	36.3	1.3	-	**	-
PROTEF (%)	26.5	22.9	23.8	21.3	0.8	*	**	-
ALW (kg)	537	552	535	530	10	*	-	-
ACS	2.52	2.65	2.48	2.60	0.06	-	*	-
GF (kg)	93	91	81	78	2	**	-	-
Lipid (kg)	116	127	116	123	5	-	-	-
LFEBW (kg)	329	334	338	330	6	-	-	-

[+] C and S are the control and selection line on the high and low concentrate feeding systems (HC and LC respectively)

[±] Standard error of the differences (s.e.d.) is the average of the 6 approximate s.e.d.'s. Approximated significance levels for Line, Diet and Line x Diet effects are specified as: * < 0.05; ** < 0.01

Table 3.4: Estimates for the regression coefficients of a range of traits on pedigree index for kg fat + protein (on the high concentrate system) and regression coefficients for the interaction between PI x DIET (the difference between the regression coefficient on HC and LC).

	Cows only			
	PI		PIxDiet LC	
	b_{HC}	se[+]	b_{HC}-b_{LC}	se
Milk (kg)	47 **	8	-29 **	11
F%	-0.007	0.006	0.016	0.009
P%	-0.005 *	0.002	0.003	0.003
F + P (kg)	2.53 **	0.64	-1.18	0.86
DMI (kg)	11 **	4	-8	6
ENEF (%)	0.16 **	0.06	-0.03	0.09
PROTEF (%)	0.10 *	0.04	-0.06	0.05
ALW (kg)	0.3	0.6	-0.1	0.8
ACS	-0.014 **	0.004	0.010 *	0.005
GF (kg)	0.3 **	0.1	-0.3	0.2
Lipid (kg)	-0.9 *	0.4	0.6	0.5
LFEBW (kg)	0.8 **	0.3	-0.5	0.4
Heifers only	PI		PI x Diet LC	
	b	se	b	se
Milk (kg)	34 **	6	-8	8
F%	0.002	0.005	-0.002	0.007
P%	0.005 *	0.002	-0.003	0.003
F + P (kg)	2.35 **	0.42	-0.67	0.58
DMI (kg)	1	3	0	4
ENEF (%)	0.28 **	0.05	-0.03	0.070
PROTEF (%)	0.15 **	0.03	-0.05	0.04
ALW (kg)	-0.7	0.4	0.9	0.6
ACS	-0.007 **	0.002	0.001	0.003
GF (kg)	0.0	0.1	0.0	0.1
Lipid (kg)	-0.6 **	0.2	0.3	0.3
LFEBW (kg)	-0.2	0.2	0.6 *	0.3

[+] Standard errors are approximates given by REML function (*$p<0.05$; **$p<0.01$:$H_0 = 0$).

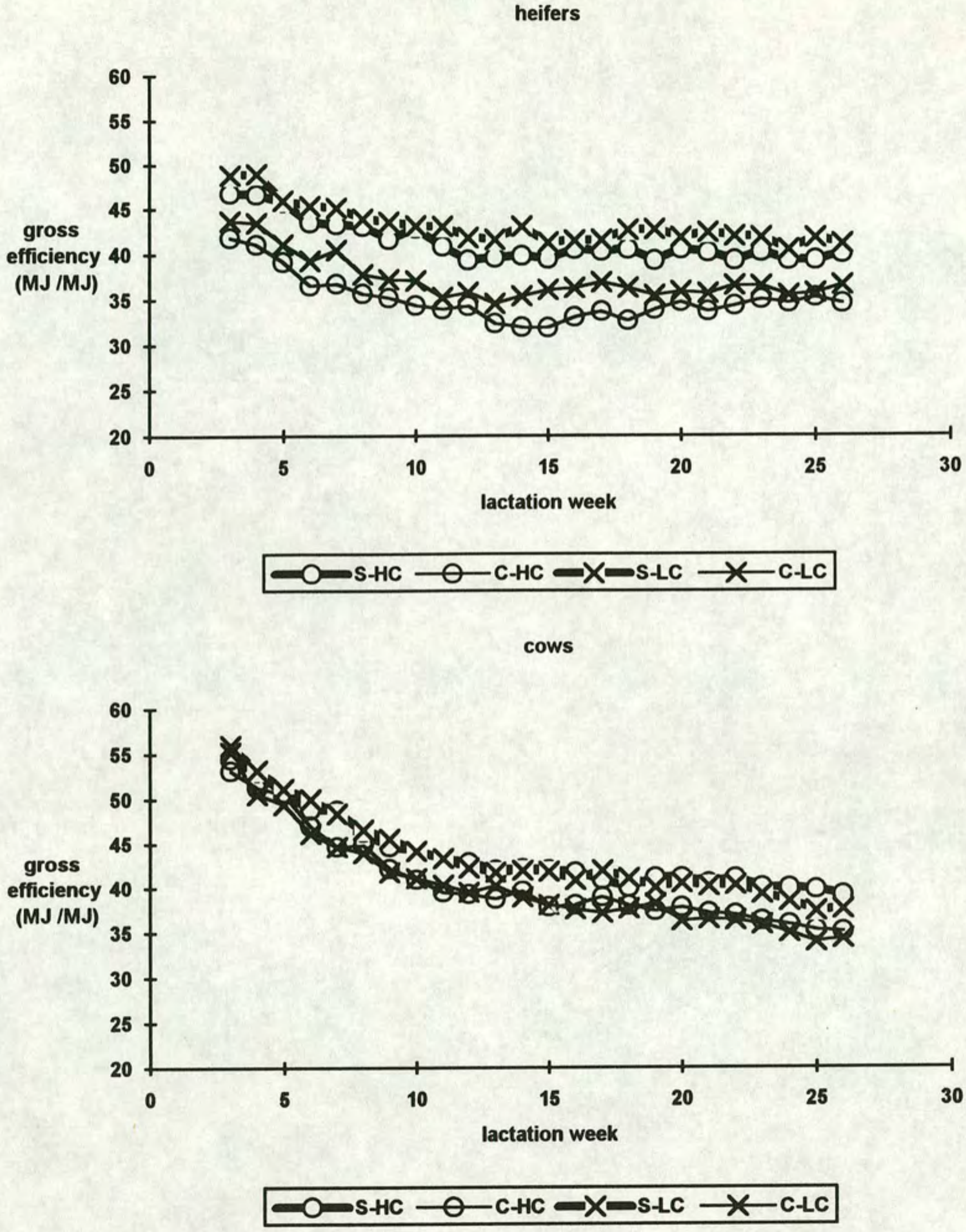


Figure 3.1: Mean gross energetic efficiency during lactation, for selection (S) and control (C) line heifers and cows, on high- and low concentrate feeding systems (HC and LC, respectively).

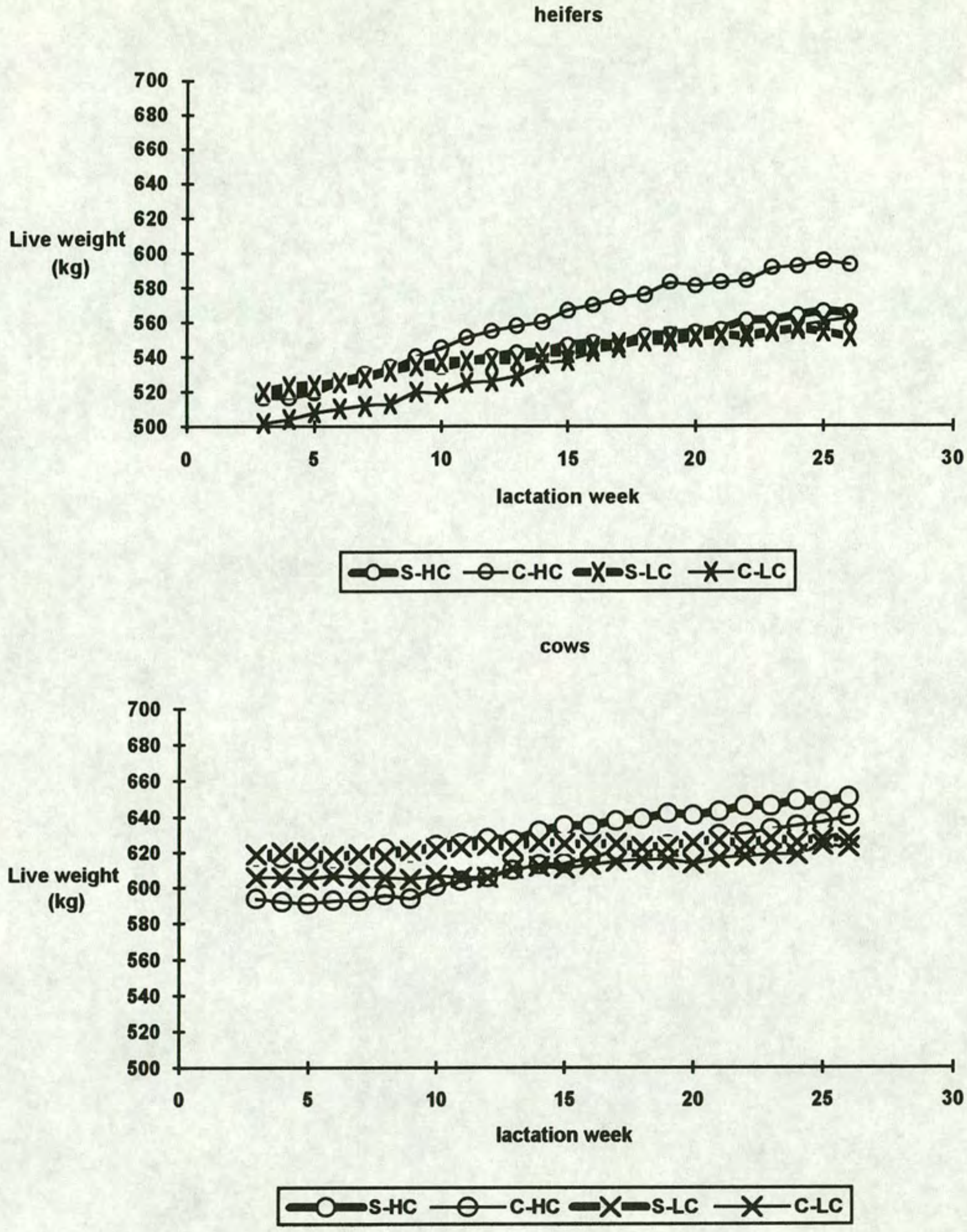


Figure 3.2: Mean live weight during lactation, for selection (S) and control (C) line heifers and cows, on high- and low concentrate feeding systems (HC and LC, respectively).

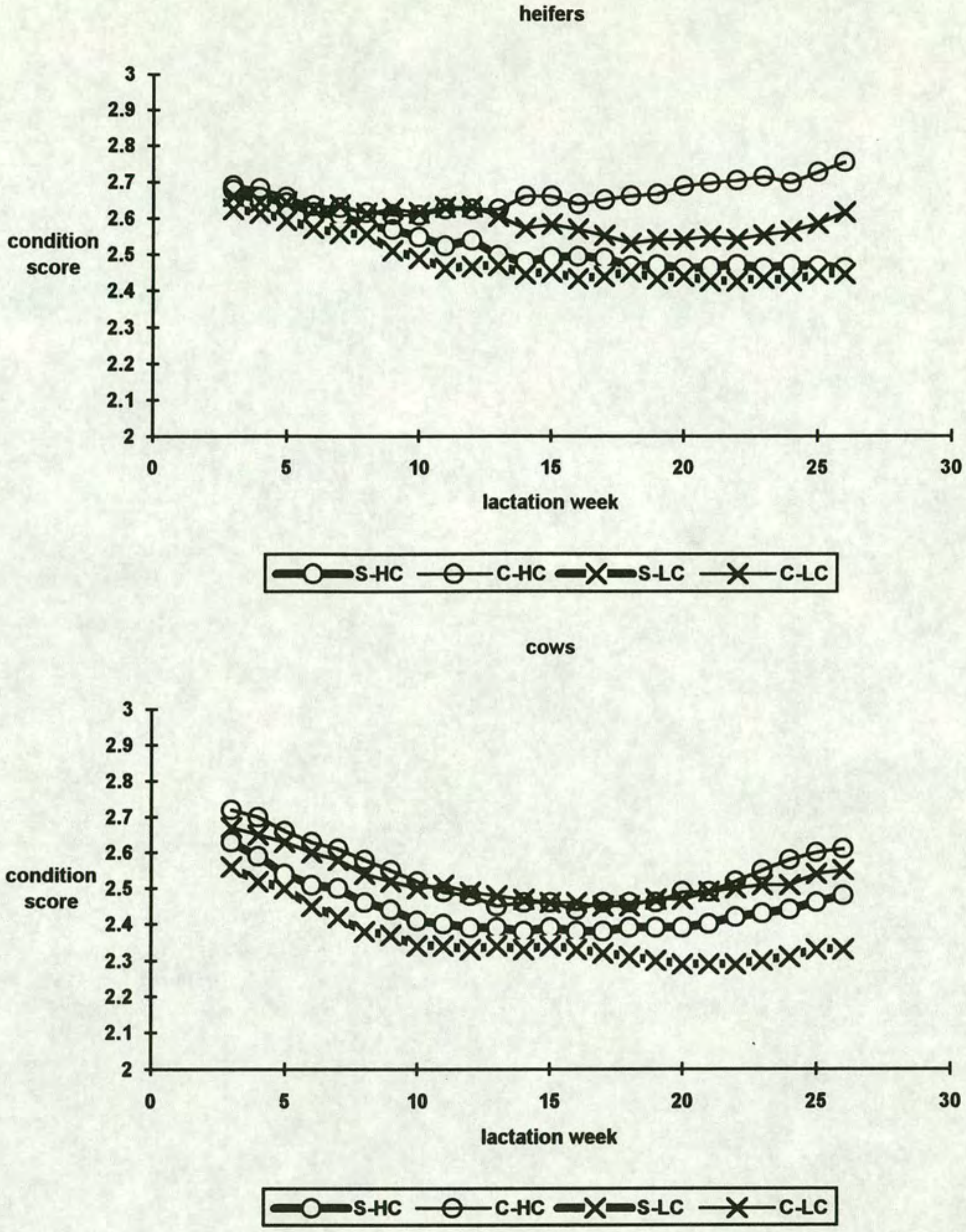
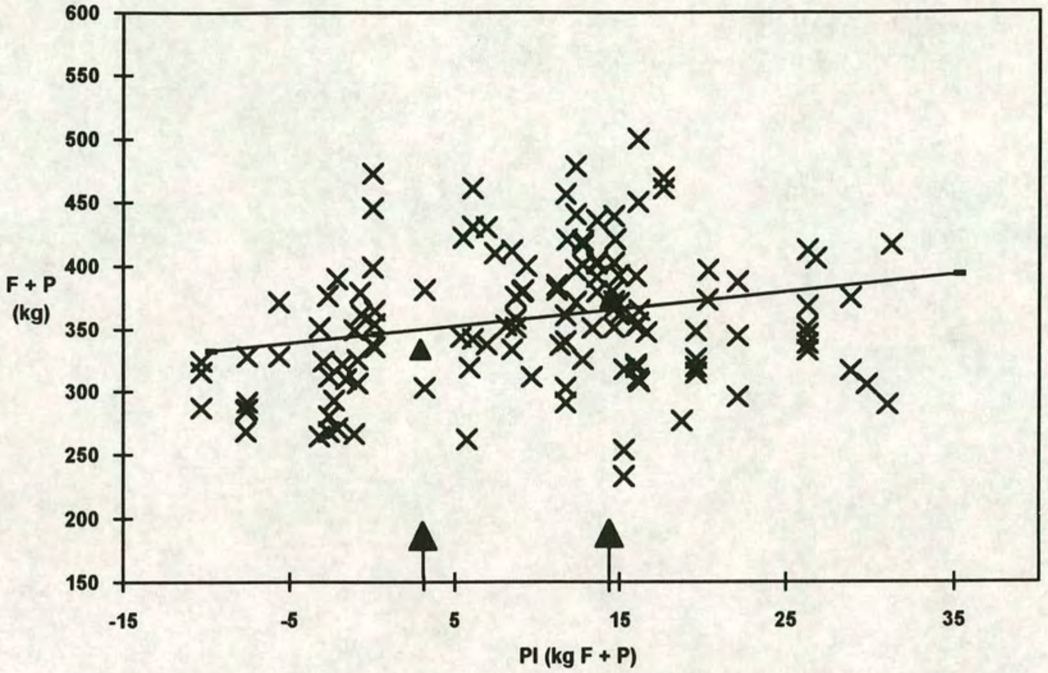
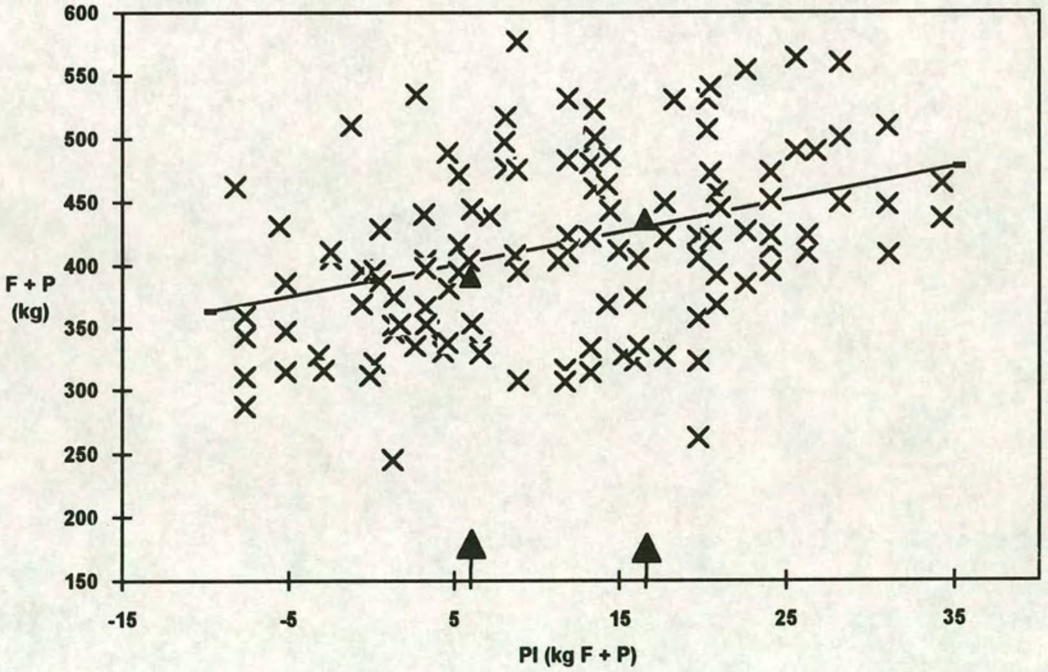


Figure 3.3: Mean condition score during lactation, for selection (S) and control (C) line heifers and cows, on high- and low concentrate feeding systems (HC and LC, respectively).

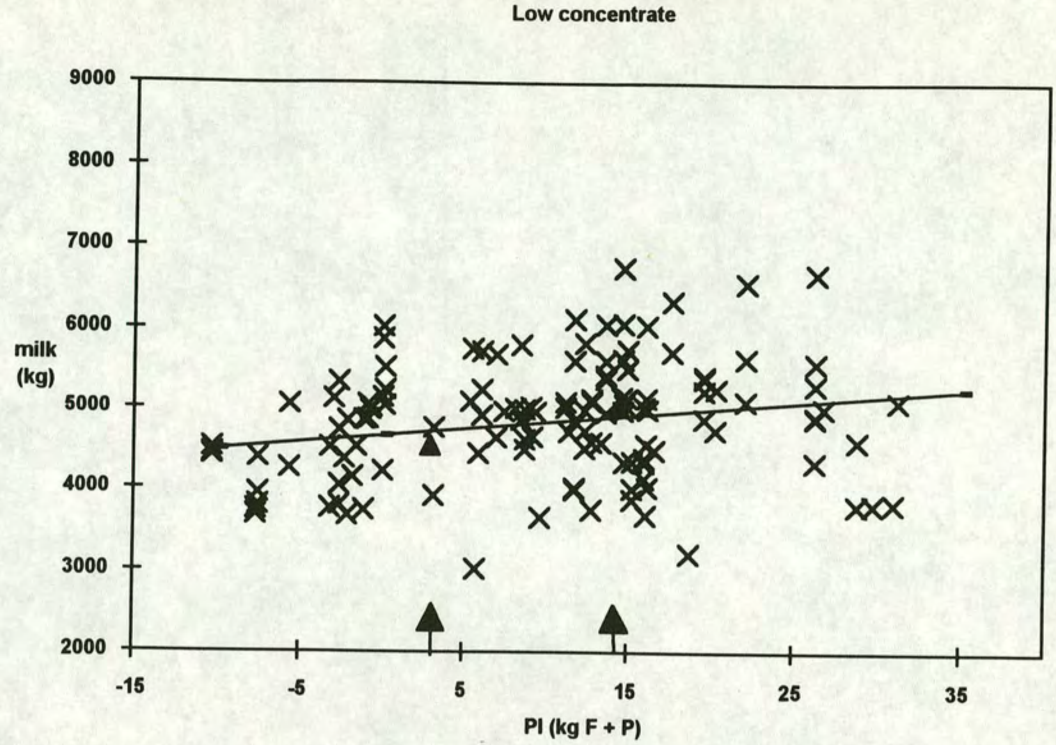


Low concentrate



High concentrate

Figure 3.4: Relationship between pedigree index (PI) for F + P and F + P yield during the first 26 weeks of the lactation, on both low and high concentrates feeding systems (no heifers included). Arrows indicate the means for S and C.



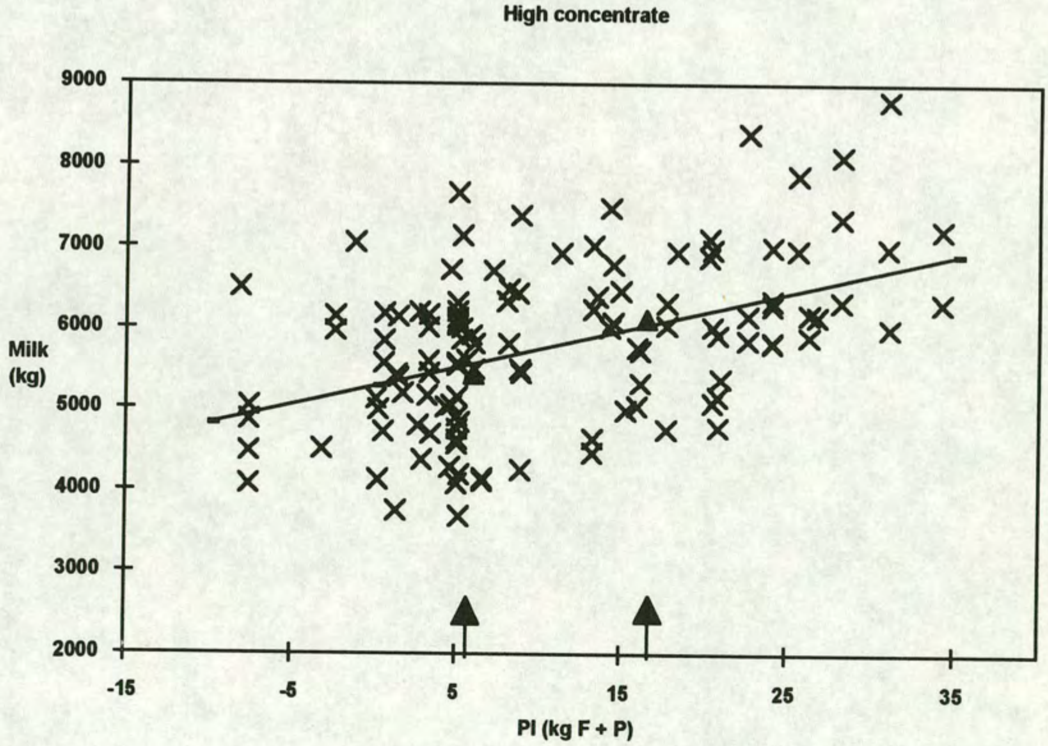


Figure 3.5: Relationship between pedigree index (PI) for F + P and milk yield during the first 26 weeks of the lactation, on both low and high concentrate feeding systems (no heifers included). Arrows indicate the means for S and C.

CHAPTER 4

VARIANCE COMPONENTS FOR THE SAME TRAIT EXPRESSED ON DIFFERENT FEEDING SYSTEMS

4.1 Introduction

In Chapter 3 phenotypic records, measured on two feeding systems differing in concentrate to forage ratio, were regressed on pedigree index for fat plus protein yield and different genetic relationships with milk yield on the two feeding systems at Langhill were observed. This showed a possible existence of genotype by environment interaction.

Generally three different explanations can be given for observed G x E interactions: (i) animals rank differently across environments (Falconer, 1952 and 1990), (ii) an environmental covariance exists between genotype and environment (e.g. animals fed according to yield) and (iii) genetic variance depends on the environment - "environmental sensitivity" (Falconer, 1952) or "pseudo-interaction" (Dickerson, 1962). Only true ranking differences give rise to a departure from unit genetic correlations between traits in different environment and are of concern for the selection of breeding animals. However existence of G x E interaction violates some of the assumptions of most prediction (BLUP) and estimation (REML) models. For example these methodologies assume that, (i) there is no remaining covariance between the random effects and the other effects in the model and (ii) that the additive genetic effect and residual affect are normally distributed with homogenous variance across levels of fixed effects and random effects (Visscher, 1991).

For these reasons the objectives of this chapter are (i) to estimate variance components for a range of traits on the two complete mixed diets, offered *ad libitum*, and (ii) estimate the genetic correlation between the same trait on both Langhill feeding systems (Chapter 3), using an individual animal model with unequal design matrix and finally, (iii) investigate the accuracy of the estimated correlations.

4.2 Material and methods

Data: The same data treatment procedures were used as in Chapter 4. However, in this Chapter data prior to 1988 and data collected in the season 1992 -1993 were included. In those years the recording procedures were similar to those described in

Chapter 4, with the only major differences being that (i) no low concentrate feeding system (LC) was used from 1980-1981 till 1987-1988 and (ii) in the years 1980-1981 to 1987-1988 only fortnightly protein and fat percentages were available. Table 4.1 describes the size of the data set and the raw means and CVs for the different traits are given in Table 4.2.

Univariate analysis: The total data set was split between the HC and LC groups and each data set was analysed using the univariate option from a Derivative-Free REML package (Meyer, 1989). This package allows simultaneous estimation of an additive random genetic effect and a common environmental effect between lactations on the same cow. The model used was:

$$Y_{ijklmnop} = U + A_i + C_j + Y_k + M_l + LN_m + LINE_n + b_1\, AC_{ijklmno} + b_2\, H\%_{ijklmnp} + E_{ijklmnop}$$

where

$Y_{ijklmnop}$ = Milk, F%, P%, FY, PY, DMI, LW, CS, during 26 weeks of lactation

U = overall mean

A_i = random additive genetic effect of ith individual.

C_j = random effect of jth repeated lactation .

Y_k = year of calving (1980 - 1992)

M_l = month of calving (Sept., Oct., Nov., Dec.)

LN_m = lactation number (1, 2, 3, >3)

$LINE_n$ = genetic line effect (selection or control)

$b_1\, AC_{ijklmno}$ = linear regression on age at calving in days

$b_2\, H\%_{ijklmnp}$ = linear regression on Holstein percentage

$E_{ijklmnop}$ = residual effects

A full relationship matrix was included in the model. The expectations of the additive direct genetic (A_i), common environmental (C_j) and residual error effects are zero and their variance are σ^2_a, σ^2_c and σ^2_e respectively. Covariances between the random effects are assumed zero.

Bivariate analyses: Secondly a bivariate analysis was conducted. The model fitted was like fitting the two univariate models (as described previously), but now a genetic co-variance was estimated between the same trait on the two feeding systems.

Hence the estimates of the fixed effects and the covariates were separate for each feeding system. Both the original data and log transformed data were analysed, the latter to homogenise the variances. A version of DFREML previously described by Crump (1992) which could cope with this unequal design animal model was used. The variance-covariance structure was:

$$V(u) = \quad G = \begin{bmatrix} A\sigma^2_{a1} & A\sigma_{a12} & 0 & 0 \\ A\sigma_{a12} & A\sigma^2_{a2} & 0 & 0 \\ 0 & 0 & I_c\sigma^2_{c1} & 0 \\ 0 & 0 & 0 & I_c\sigma^2_{c2} \end{bmatrix}$$

$$V(E) = \quad R = \begin{bmatrix} I\sigma^2_{e1} & 0 \\ 0 & I\sigma^2_{e2} \end{bmatrix}$$

$$\begin{aligned} \mathrm{cov}(u,e) &= 0 \\ V(Y) &= ZGZ' + R \end{aligned}$$

Where:

A = the numerator relationship matrix;
Z = incidence matrix relating random effects to records.
I_c = identity matrix with rank equal to the number of cows
I = identity matrix with rank equal to the number of lactations
u = vector with random effects
G = matrix with (co-) variances between random effects
Y = vector of observations
$\sigma^2_c, \sigma^2_a, \sigma^2_e$ = variances for permanent environmental, additive direct effect and residual error effect for trait 1 and 2.
σ_{a12} = covariance between trait 1 and 2 for additive direct effect

The permanent environmental effect was fitted for lactations on the same feeding system only. Because there was a small number of animals (n = 21) with records on both feeding systems, possible environmental co-variances between the feeding systems have been assumed to be negligible.

Accuracy of estimated genetic correlations was approximated by fixing the genetic correlation around its maximum value, and re-maximising the likelihood function with respect to all remaining parameters (Cameron and Bracken, 1992), to create the profile likelihood. To achieve this some small additions were made to DFREML. The difference of the log likelihood from two different models can be tested as a Chi^2 (Wilks, 1938) and when fixing one parameter (genetic correlation) the number of degrees of freedom is 1. Effectively, if the difference between two log-likelihoods (for the two models with optimum and fixed genetic correlation) is 3.841 / 2 = 1.92, than there is a significant ($\alpha = 0.05$) difference between the two genetic correlations.

Simulation: Monte Carlo simulation was used to investigate sampling correlations and possible Type II errors (concluding that there is no G x E where actually there is one). A simplified hierarchical structure, similar to the structure of the data set used here, was chosen in which N bulls and n dams produced n offspring ($N < n$). Each offspring had ℓ lactation records available on either trait 1 or 2 (e.g. HC and LC feeding systems). An additive infinitesimal model was assumed with phenotypic variances of unity, means of zero and heritabilities h^2_c and h^2_f for traits 1 and 2. Genotypes for the sires and dams were created randomly, using the Cholesky decomposition (Toro and Silio, 1991) to simulate the genetic correlation (r_{gcf}) between traits 1 and 2. An additional selection line effect (S) for half of the sire genotypes could be included, shifting the mean for trait 1 by S phenotypic standard deviation units. Lactation records for both traits for each of the offspring were created from the sire's and dam's genotype plus (i) a Mendelian sampling component (mean zero and variance one half of the genetic variance, and correlation between trait 1 and 2 based on the Cholesky decomposition), (ii) an uncorrelated permanent environmental effect for each animal (variances c^2_c and c^2_f), plus (iii) a random environmental effect for each lactation. In the base situation the following parameter values were used: $N = 50$, $n = 4, \ell = 2$; $h^2_c = h^2_f = 0.45$; $r_{gcf} = 0.80$; $c^2_c = c^2_f = 0.10$; $S = 0$.

4.3 Results

Estimated variances and variance components are given in Table 4.3 for the univariate analysis. The phenotypic variances for milk, fat and protein yield are nearly a factor two higher on the concentrate feeding system than on the forage system. Permanent environment effects appear to be higher on the forage system than on the concentrate system and, especially for milk and protein yield, dry matter intake and live weight h^2 is much smaller and c^2 is much larger on LC than HC.

Estimates for the variance components from the bivariate analysis (Table 4.4) are comparable with the univariate analysis. A decrease in h^2 (e.g. milk) coincides with an increase in c^2. Genetic correlations are close to unity except for milk and fat yield and fat percentage. Similar results were obtained for the transformed data, although genetic correlations were slightly lower, and heritabilities were slightly higher. Figure 4.1 shows the likelihood surface for fixed values of r_g when optimising the other variance components in the model for all the traits. The flat surface infers that only precarious conclusions can be drawn from the estimated genetic correlations in this study, even for the highly heritable traits (F% and P%).

Simulation of a data set (base situation in Table 4.5) showed that on average in 50 replicates the genetic variance (and the h^2) are underestimated and the c^2 is overestimated. The error variance and phenotypic variance are close to the simulated values (0.45 and 1.0, respectively). The average estimated genetic correlation is lower than the simulated value and the variation in estimated r_g is large (s.d. = 0.41). If mean differences between selection and control line sires were ignored in the model than genetic variances and covariances would have been overestimated for both traits. Obviously, when the selection effects were accounted for in the model, no differences from the base estimates were observed.

Figures 4.2 a, b, and c give an indication of the sampling correlation in the base situation between the estimated heritability for the first trait and (a) the estimated heritability for the second trait, (b) the genetic correlation between traits one and two and (c) the permanent environment effect on trait 1. As also expected from the results in Table 4.3 and 4.4 the sampling correlation between estimated h^2 and c^2 was large and negative (Figure 4.2c).

4.4 Discussion

Variance components were estimated for cows fed one of two feeding systems differing in the proportion of forage to concentrate. In absolute values there were remarkable differences in both the phenotypic and additive genetic variance for the milk yield traits, the variances on the high concentrate feeding system being twice as high as the variance on the low concentrate feeding system. There is ample evidence from national data sets which show heterogeneous variances among herds in the UK (Hill *et al.*, 1983; Brotherstone and Hill, 1986; Meyer, 1987; Visscher, 1991). The higher variances at higher means could be explained partly by a scale effect - the variances simply being related to the mean. However the fact that the coefficients of variation differ across the feeding systems (after correcting the variance for the fixed effects these were 0.135 and 0.163 for milk yield on HC and LC respectively) and that the log transformation had hardly any effect on the ratio of genetic variances on HC and LC (Table 4.4 B), suggest that this can not be the full explanation. In analysis of large national data sets several other factors contributing to heterogeneous variance of yield have been suggested, in addition to the scale effect. For example Brotherstone and Hill (1986) and Vinson (1987) suggested that heterogeneity of variances in yield could be explained due to differential management, nutritional and feeding systems (e.g. feeding according to yield or fixed amounts of concentrate) or due to more reliable pedigree recording in some herds (Hill *et al.*, 1983). Some of these arguments however seem not to be a relevant explanation for the results in this study, because the forage to concentrate ratio in the feeding system was the only key variable to be different between the two feeding systems. Another often quoted explanation for heterogeneous variances is (i) that some gene effects are restricted in poor environments or (ii) that average gene effects are reduced in herd environments with less opportunity (Hammond, 1947). Under this hypothesis it is expected that the heritability is lower on the LC, which would be consistent with results from Hill *et al.* (1983) and references therein. Hill *et al.* (1983) concluded that heritabilities for the yield traits increase with increasing herd means. Also in this study, between the two feeding systems, there appear to be large differences in the h^2 for some of the traits, with generally those on the HC being higher. However these observed differences for the h^2 between the feeding systems are most likely the consequence of the small data set and the fact that it is intrinsically difficult to separate additive genetic variance and permanent environmental variance in this data set (Figure 4.2). The similar repeatabilities across the feeding systems might support the conclusion that the genetic control of traits is not very different between the two feeding systems, although the data set is too limited to fully test this hypothesis.

The latter is consistent with the conclusion that for fat yield heterogeneous phenotypic variances but homogeneous heritabilities were observed, when estimating variance components for 26 large pedigree herds separately (Visscher, 1991). Nonetheless, a proper biological explanation for heterogeneous variance across the feeding systems is still lacking. It might be that some of the higher variances on the HC feeding system could be explained by the longer time period that records were collected, because preliminary analysis on a subset of the data used here (the data set used in Chapter 3) showed that variances of yield were increased to a lesser extent than they were in this study.

There has been a long running interest in the possibility of genotype x environment interactions in dairy cattle and Danell (1982) reviewed several studies in which interactions between feeding regime and sire, production level and sire, and housing system and sire were not found to be of importance. More recently, Van der Werf and Ten Napel (1991) found a genetic correlation for milk traits of 0.78 between high and low yielding herds, and the sire by herd interaction accounted for only 3% of the phenotypic variance. However, these studies focused primarily on milk production traits and not many studies have investigated the combined effect of feeding system and genotype on feed intake, efficiency and tissue mobilisation. Richardson *et al.* (1971) performed an experiment with 228 Jerseys heifers sired by 13 different bulls and found a significant interaction between ration and sire for gross efficiency, measured over the whole lactation. Lamb *et al.* (1977) found evidence for a sire by ration interaction for milk energy production, gross efficiency over 305 days and fat yield. In their analysis, the estimate of the variance components for interaction of sire with ration ranged in relative magnitude from 15% to 99% of the sire variance component. However, most of the interaction was accounted for by a single bull from New Zealand. Wang *et al.* (1992) reported a breed by concentrate feeding interaction for milk production (56- and 112 days milk) and feed efficiency measured in Ayrshire and Holstein cows. These authors also observed a re-ranking of sires on different concentrate feeding levels. However, in all of these studies (Richardson *et al.*, 1971; Lamb *et al.*, 1977; Wang *et al.*, 1992) animals were fed concentrates according to production, which makes biological interpretation of the results difficult.

Studies where animals were not fed according to production have been performed by (Korver, 1982 and Oldenbroek, 1988). Korver (1982) compared Dutch Friesians and crossbreeds between Holstein- and Dutch Friesians for several feed intake, milk production and live weight traits and did not observe a significant feeding system x breed interaction. In his experiment two fixed amounts of concentrates were fed and cows had *ad libitum* access to roughage. Oldenbroek (1988) reported breed by diet interactions for intake (over 39 weeks of lactation) and production characteristics for a group of Jersey heifers compared with a group Holstein Friesian, Dutch Friesian, and Dutch Red and White heifers.

Genetic correlations in this study ranged from 0.64 to 1.00 on the normal scale and were slightly lower on the transformed scale (0.53 to 1.00), suggesting that animals might rank differently on the two feeding systems for milk and fat yield and fat percentage, but standard errors were to large too draw any strong conclusions.

The simulation results showed that including line in the model accounted for the shift in the mean between control and selection line animals. Of course this is a simplified situation and in practice variances might have changed as a consequence of selection. However in the Langhill project, both in the control and selection line, selected young bulls or selected proven bulls have been used. Therefore it is difficult to anticipate any effect of selection on variances in the control and selection line separately. The circular argument here is that if we were able to simulate the selection effect properly, we would also have been able to properly account for it in the analysis. Further inaccuracies in the model might be the assumption of a repeatability model. This model assumes homogeneous variances across lactations and unit genetic correlation between the same trait in different lactations. This might not be appropriate, for example heifers grow which affects their live weight and in later lactations they become fat which also affects live weight. Therefore the r_g for live weight between lactations might not be unity. However, separating the variance in a permanent environmental and additive genetic effect in this data set proved to be difficult enough, and for that reason no further parameters were added to the model.

The average estimated variance components in the simulation differed from the original population values. However this is no evidence for a possible bias, because boundaries were set for h^2, c^2 and r_g within the REML program. Therefore it was expected that the average value for the genetic correlation (r_g) is lower than the population value and also it was expected that the standard deviations were underestimated. Nonetheless standard error were still high, even with an increase in the data set up to 3200 records. The pattern of change in the standard error of the genetic correlation (Figure 4.3) shows that resources will be used most efficiently when the number of heifers entering the trial each year will be increased. Either increasing the number of heifers from each bull or using more bulls each year (with the same number of heifers per bull) are two similar possibilities. It is, however, clear that increasing the number of lactations recorded per animal does not add very much to the accuracy of the estimated genetic correlation.

Conclusions: The objective of this study was to evaluate the extent that variance components vary across two feeding systems differing in forage to concentrate ratio. Large differences were observed in the phenotypic and genetic variances between the two feeding systems, and these differences were not explained fully by the difference in mean performance. Also, differences were observed for the heritabilities, but repeatabilities were similar across the two feeding systems. None of the genetic correlations between the two diets was significantly smaller than 0.80, and so, formally, the relative ranking of genotypes was the same in both feeding systems. However, the genetic correlation for fat yield in particular was low (0.64) and results from a simulation study showed that separating all the variance components was difficult, and that the power of the experiment was low. For this reason, the null hypothesis - that genetic control for the range of traits examined is the same across the two feeding systems - can not be maintained more confidently, and for this purpose these analysis needs to be repeated when more records from Langhill are available.

Table 4.1: Structure of the data set used for the two feeding systems (high concentrate and low concentrate, HC and LC respectively).

	HC	LC
# records	672	251
# animals with records	328	128
# dams	235	112
# sires	100	45
	# records LC	# records HC
Year of calving		
1980	34	0
1981	35	0
1982	36	0
1983	38	0
1984	83	0
1985	82	0
1986	83	0
1987	37	0
1988	40	44
1989	37	42
1990	58	55
1991	53	55
1992	56	55
Month of calving:		
September	233	80
October	214	56
November	174	62
December	51	53
Lactation:		
1	229	88
2	147	63
3	117	40
>3	179	60
Control line	256	108
Selection line	416	143

Table 4.2: Raw mean and CV for 8 different traits, on two different feeding systems (high concentrate and low concentrate, HC and LC respectively).

	HC		LC	
	mean	CV	mean	CV
MILK (kg /day)	28.08	0.20	24.04	0.20
FY (kg/day)	1.14	0.21	1.06	0.21
PY (kg/day)	0.90	0.20	0.73	0.19
F% (%)	4.09	0.11	4.41	0.12
P% (%)	3.23	0.08	3.04	0.07
DMI (kg/day)	17.8	0.13	15.3	0.17
LW (kg)	606	0.11	586	0.11
CS (units 0-5)	2.62	0.16	2.38	0.17

FY, PY, F% and P% are fat and protein yield and percentage respectively

DMI is dry matter intake, LW is average live weight, CS is condition score

Table 4.3: Univariate variance component estimates for 8 different traits, on two different feeding systems (high concentrate and low concentrate, HC and LC respectively).

	HC					LC				
	σ^2_{ac}	σ^2_{ec}	σ^2_{pc}	h^2_{c}	c^2_{c}	σ^2_{af}	σ^2_{ef}	σ^2_{pf}	h^2_{f}	c^2_{f}
MILK (kg /day)	9.3	8.8	21.3	0.43	0.16	2.7	4.3	10.7	0.25	0.34
FY (kg/day)	0.023	0.016	0.047	0.51	0.14	0.011	0.011	0.024	0.46	0.08
PY (kg/day)	0.009	0.007	0.019	0.47	0.14	0.002	0.003	0.008	0.21	0.42
F% (%)	0.18	0.03	0.23	0.79	0.07	0.21	0.04	0.28	0.76	0.11
P% (%)	0.033	0.099	0.043	0.76	0.01	0.031	0.011	0.046	0.70	0.07
DMI (kg/day)	1.8	1.1	3.1	0.56	0.09	1.2	1.2	3.8	0.33	0.35
LW (kg)	2190	610	3139	0.70	0.11	1042	369	2679	0.39	0.47
CS (units 0-5)	0.06	0.06	0.15	0.43	0.17	0.05	0.06	0.13	0.41	0.13

$\sigma^2_{a.}$, $\sigma^2_{e.}$ and $\sigma^2_{p.}$ are the genetic, environmental and phenotypic variance, respectively.
$h^2_{.}$ and $c^2_{.}$ are the heritability and the permanent environmental effect, respectively.
The underscores f and c indicate low and high concentrate diet, respectively.

FY, PY, F% and P% are fat and protein yield and percentage respectively
DMI is dry matter intake, LW is average live weight, CS is condition score

Table 4.4: Bivariate variance component estimates for 9 different traits, on two different feeding systems (high concentrate and low concentrate, HC and LC respectively). On the normal scale (A) and scaled and log transformed values (B).

A:

	HC							LC				
	σ^2_{ac}	σ^2_{ec}	σ^2_{pc}	h^2_c	c^2_c	σ_{acf}	r_{gcf}	σ^2_{af}	σ^2_{ef}	σ^2_{pf}	h^2_f	c^2_f
MILK	9.2	8.8	21.0	0.44	0.14	4.9	0.87	3.4	4.3	10.5	0.33	0.27
FY	0.022	0.016	0.045	0.49	0.15	0.011	0.64	0.012	0.011	0.025	0.50	0.05
PY	0.0086	0.0075	0.0184	0.50	0.12	0.0047	1.00	0.0026	0.0031	0.0085	0.30	0.33
F%	0.18	0.03	0.23	0.79	0.06	0.17	0.84	0.23	0.037	0.27	0.86	0.00
P%	0.034	0.010	0.044	0.78	0.00	0.032	0.95	0.034	0.011	0.046	0.75	0.00
DMI	1.7	1.0	3.1	0.55	0.11	1.9	0.93	2.5	1.2	3.7	0.67	0.00
LW	2094	606	2998	0.70	0.10	1418	1.00	1418	356	2806	0.51	0.40
CS	0.065	0.056	0.15	0.45	0.16	0.063	1.00	0.062	0.058	0.14	0.44	0.15

B:

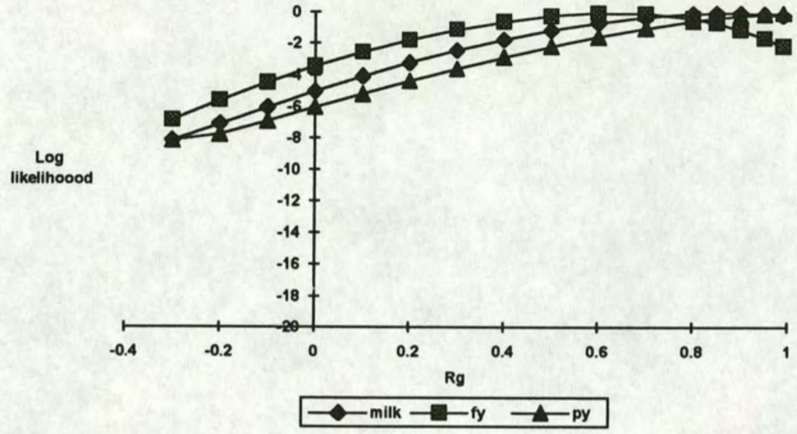
	HC							LC				
	σ^2_{ac}	σ^2_{ec}	σ^2_{pc}	h^2_c	c^2_c	σ_{acf}	r_{gcf}	σ^2_{af}	σ^2_{ef}	σ^2_{pf}	h^2_f	c^2_f
MILK	16480	11782	28819	0.57	0.02	8904	0.72	9413	7196	18490	0.51	0.10
FY	20661	12878	35084	0.59	0.04	8377	0.53	11875	10183	22062	0.54	0.00
PY	14354	9441	24220	0.59	0.02	8872	0.81	8321	5086	16134	0.52	0.17
F%	10370	2089	12461	0.83	0.00	7837	0.72	11422	1889	13313	0.72	0.00
P%	3095	939	4034	0.77	0.00	3330	1.00	3582	1159	4742	0.76	0.00
DMI	6044	3108	9352	0.65	0.02	6758	0.83	10947	4364	15325	0.71	0.00
LW	5675	1612	7287	0.79	0.00	6201	1.00	6785	991	8177	0.83	0.05
CS	5050	14158	26589	0.19	0.28	7824	1.00	12121	14708	29966	0.40	0.10

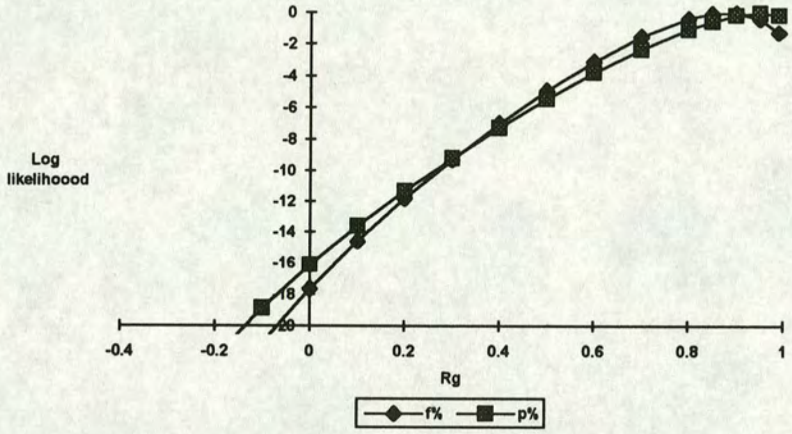
σ_{acf} and r_{gcf} are the genetic covariance and genetic correlation respectively. For units and other abbreviations see Table 4.2.

Table 4.5: Mean estimated parameters (abbreviations in Table 4.3) from simulated data for 50 replicates (with standard deviation).

	trait 1							trait 2				
	σ^2_{ac}	σ^2_{ec}	σ^2_{pc}	h^2_c	c^2_c	σ_{acf}	r_{gcf}	σ^2_{af}	σ^2_{ef}	σ^2_{pf}	h^2_f	c^2_f
population	**.45**	**.45**	**1.00**	**.45**	**.10**	**.28**	**.80**	**.45**	**.45**	**1.00**	**.45**	**.10**
base	.43 (.21)	.46 (.07)	1.02 (.11)	.41 (.18)	.13 (.14)	.29 (.19)	.68 (.41)	.44 (.20)	.46 (.06)	1.01 (.13)	.42 (.16)	.12 (.14)
S = 1	.50 (.19)	.46 (.07)	1.04 (.12)	.47 (.15)	.08 (.11)	.36 (.19)	.80 (.27)	.46 (.21)	.46 (.06)	1.03 (.13)	.44 (.17)	.11 (.14)
S = 2	.62 (.17)	.45 (.07)	1.12 (.12)	.55 (.12)	.04 (.07)	.52 (.14)	.91 (.14)	.55 (.17)	.45 (.06)	1.08 (.13)	.50 (.12)	.08 (.09)
Line in model:												
S = 2	.43 (.19)	.46 (.07)	1.02 (.11)	.42 (.17)	.13 (.12)	.28 (.19)	.68 (.42)	.43 (.21)	.45 (.06)	1.01 (.13)	.41 (.18)	.14 (.16)
N x n x ℓ = 800												
N = 100	.43 (.13)	.44 (.04)	.99 (.08)	.44 (.12)	.11 (.11)	.29 (.13)	.74 (.30)	.41 (.16)	.45 (.05)	.99 (.09)	.42 (.15)	.14 (.15)
n = 8	.40 (.18)	45 (.04)	1.00 (.09)	.40 (.17)	.15 (.15)	30 (.14)	.78 (.27)	41 (.14)	45 (.04)	1.00 (.08)	.41 (.13)	.14 (.13)
ℓ = 4	.39 (.16)	.45 (.03)	.99 (.09)	.40 (.16)	.15 (.15)	.28 (.18)	.75 (.37)	.42 (.18)	.44 (.04)	1.00 (.12)	.41 (.16)	.14 (.15)
N x n x ℓ = 1600												
N = 200	.45 (.13)	.45 (.03)	.99 (.05)	.46 (.12)	.09 (.11)	.36 (.12)	.84 (.20)	.43 (.12)	.44 (.03)	.99 (.07)	.43 (.12)	.12 (.11)
n = 16	.41 (.11)	.45 (.03)	1.00 (.06)	.41 (.10)	.14 (.09)	.33 (.11)	.79 (.18)	.43 (.12)	.45 (.03)	.99 (.06)	.43 (.11)	.12 (.10)
ℓ = 8	.41 (.15)	.45 (.02)	.99 (.09)	.41 (.13)	.13 (.13)	.31 (.17)	.71 (.36)	.46 (.15)	.45 (.02)	1.01 (.09)	.45 (.13)	.10 (.11)
N x n x ℓ = 3200												
N = 400	.43 (.10)	.45 (.02)	1.00 (.04)	.43 (.10)	.12 (.10)	.34 (.08)	.79 (.17)	.44 (.10)	.45 (.02)	.99 (.04)	.45 (.10)	.10 (.10)
n = 32	.45 (.10)	.45 (.02)	1.00 (.04)	.45 (.09)	.10 (.08)	.35 (.09)	.81 (.10)	.41 (.11)	.45 (.02)	1.00 (.05)	.41 (.10)	.14 (.08)
ℓ = 16	.43 (.14)	.45 (.02)	.99 (.09)	.43 (.13)	.11 (.12)	.33 (.14)	.81 (.26)	.42 (.14)	.45 (.02)	1.00 (.08)	.42 (.13)	.13 (.12)

S is differences between selection and control line in s.d., N, n and ℓ are the number of sires, offspring per sire and lactations per animal.





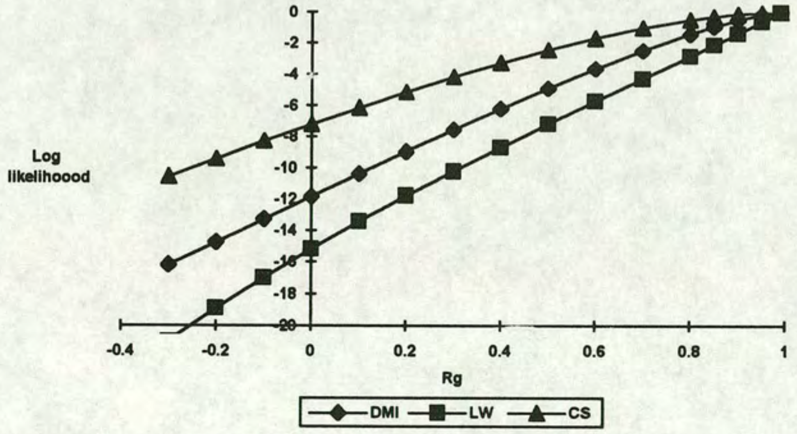


Figure 4.1: Log likelihood for different fixed values for r_{gcf}, when other parameters in model are optimised.

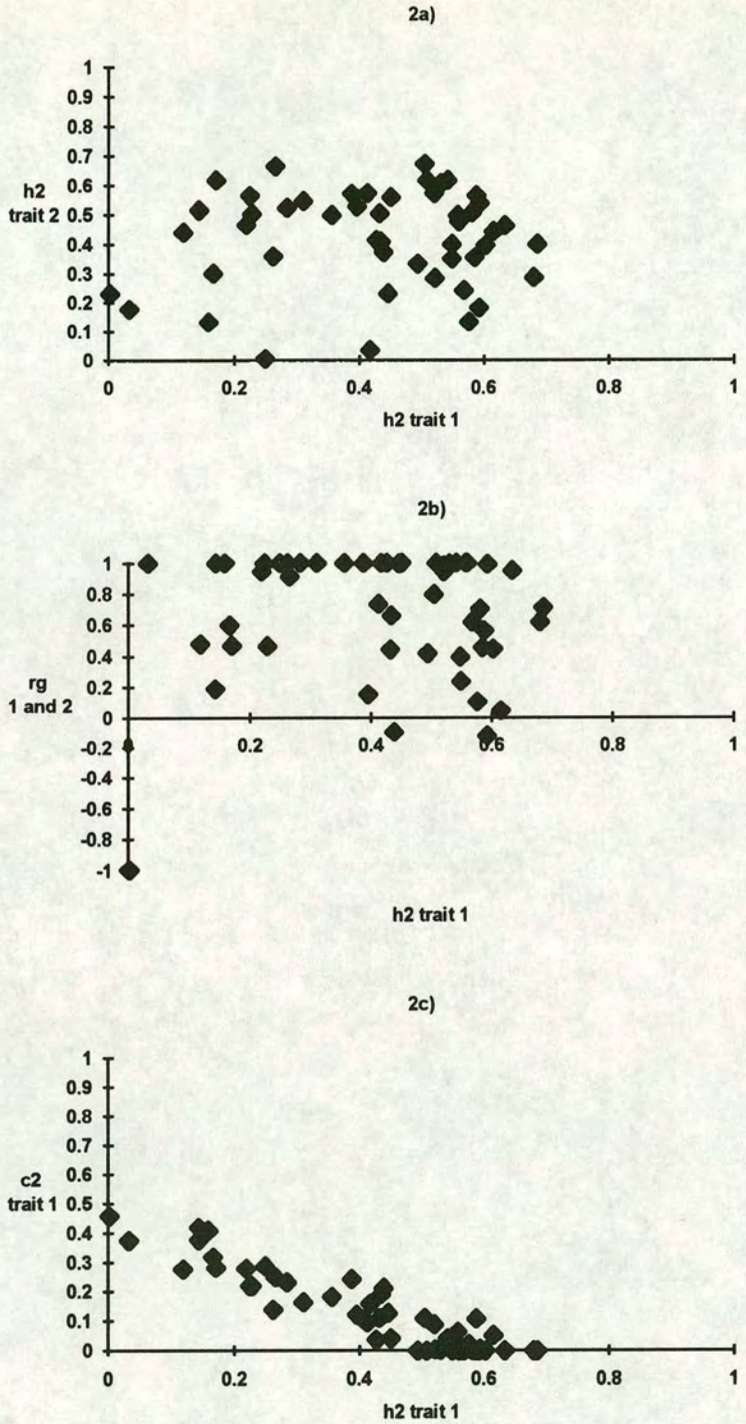


Figure 4.2: Association between estimated heritability for trait 1 (simulated value = 0.45) and estimated values for (a) heritability of trait 2 (h^2_f), (b) genetic correlation (r_{gcf}) between trait 1 and 2 and (c) permanent environment effect for trait 1 (c^2_c). Each point indicates the results of one of the 50 replicates.

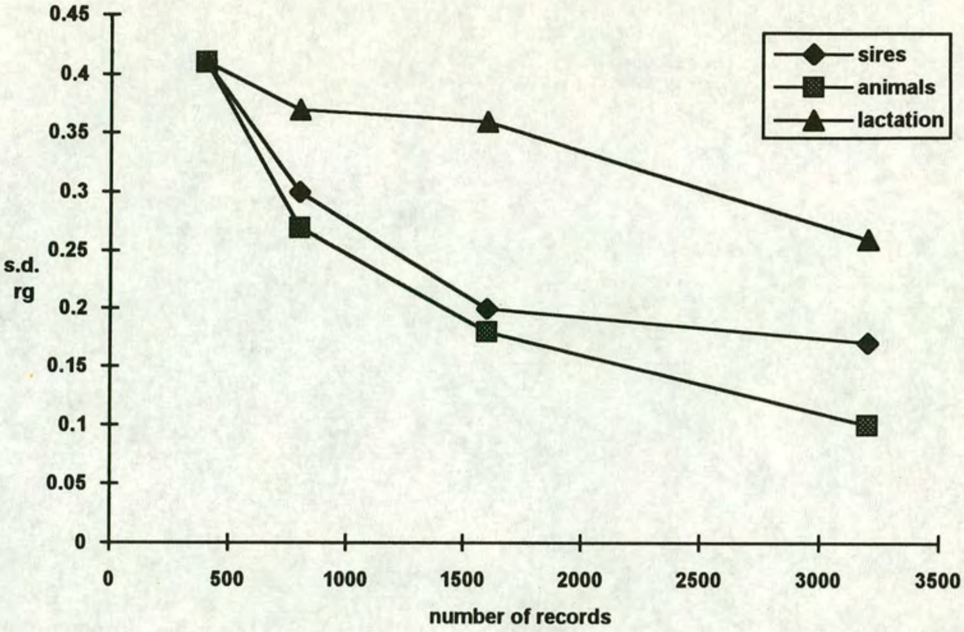


Figure 4.3: Effect of increasing the number of records on the standard deviation of the genetic correlation. Three different possibilities have been simulated: (i) increasing number of sires from which offspring are measured (100, 200 or 400), (ii) increasing number of animals per sire (8, 16 or 32) or (ii) increasing number of lactations per animal (4, 8 or 16).

CHAPTER 5

VARIANCE COMPONENTS FOR RESIDUAL FEED INTAKE IN DAIRY COWS

5.1 Introduction

The breeding goal of many dairy farmers is to maximise profitability. Because feed costs account for about 0.80 of the total variable costs associated with milk production (MMB, 1990) possible genetic differences between cows in feed intake are of considerable importance. A widely used, and sensible, measure of the efficiency with which the cow uses feed is the gross energetic efficiency, which is defined as the energy in the milk produced divided by the energy intake (Brody, 1945). The energy intake is now usually expressed as the metabolisable energy (ME) intake to reduce, but not eliminate, differences in efficiencies between diets.

A problem with the gross efficiency is that it is a ratio of two quantities, or traits (problems with ratio traits for breeding are described, for example, in Simm *et al.*, 1987), and that it does not distinguish between the ME used for the separate functions of maintenance, lactation and body tissue gain which can be seen as having partial efficiencies of k_m, k_l and k_f respectively. Because tissue reserves in dairy cows may be substantial (e.g. Butler-Hogg *et al.*, 1985; Gibb *et al.*, 1992) it is possible that the use of reserves in a part of one lactation, or over one whole lactation, might buffer some animals against the effects of a temporary nutritional adversity. Consequently, variation in gross efficiency which becomes apparent during part of the life span, might diminish in the longer term i.e. in the dry period or in subsequent lactations.

To try to overcome the two problems arising from the use of gross efficiency, an alternative measure of a partial efficiency can be expressed as a 'residual feed intake', RFI, (Koch *et al.*, 1963; Luiting, 1991). RFI is the actual energy intake of an animal after correction for the energy calculated to be needed for maintenance, production and body condition change. It reflects differences, which may be real or only apparent, in the utilisation of feed energy by that animal compared with the population mean and, hence, possible differences in some combination of the partial efficiencies k_m, k_l and k_f.

In lactating dairy cows, Kennedy *et al.* (1993) and Van Arendonk *et al.* (1991) reported heritability estimates of 0.14 and 0.19 for RFI, respectively. Ngwerume and Mao (1992) and Svendsen *et al.* (1993) found no evidence for any additive genetic variation in RFI. Veerkamp *et al.* (1993, Appendix) found a difference in RFI between two lines of cows selected for either high or average fat plus protein yield with the higher yielding line apparently being more efficient. Kennedy *et al.* (1993) discussed the statistical and genetic properties of residual feed intake, and how the apparent genetic variation in it can be illusory because the phenotypic RFI is not genetically independent of the component traits.

The objective of this study was to investigate if any genetic variation for RFI, and hence in partial efficiencies, exists in cows fed *ad libitum* on complete mixed diets and, if present, whether this is purely a reflection of genetic correlations between energy intake and the components traits, or not.

5.2 Material and methods

Animals and recording: The data set used was that described in Chapter 3, where it was used to investigate possible effects of genotype by environment interaction. Only a brief description is given here. The data-set contained 128 heifer and 249 cow lactations up to 26 weeks of lactation, recorded on 204 animals. Records were obtained from cows housed and managed at the Scottish Agricultural College/University of Edinburgh Langhill Dairy Cattle Research Centre. All cows involved in the study were Holstein-Friesians which were kept indoors in conventional cubicle housing from calving to July and offered complete mixed diets *ad libitum*. In each of the 4 years calving began early in September and all of the animals used calved between September and January in any one year.

The herd comprises two genetic groups - a selection line S and a control line C. Since 1973 the selection line has been bred to bulls with the highest genetic merit for combined fat and protein yield (F + P) available in the UK. The control animals have been bred to bulls of about national average genetic merit for F + P since 1976. The selection line is in the top 1% of herds in the UK, ranked on average genetic merit for F + P. The genetic merit of the control line has increased only slightly since 1976.

Two complete diets were offered *ad libitum*. The diets were designed to achieve, over a full lactation, proportions (in the total dry matter) of concentrates, brewers grains and silage of 0.20:0.05:0.75 (LC) and 0.45:0.05:0.50 (HC), with annual average concentrate intakes of about 1.0 and 2.5 tonnes per cow, respectively. Animals were grouped according to stage of lactation and diet type, and for both diet types the proportion of the dry matter in the diet from silage was altered when the group had on average completed 100 and 200 days of lactation. Different compound balancer meals were included in HC and LC, with metabolisable energy and crude protein contents respectively in the concentrate dry matter of about 13.0 MJ kg^{-1} and 180 g kg^{-1} for HC and 12.6 MJ kg^{-1} and 310 g kg^{-1} for LC. Both LC and HC are relevant representations of feeding systems used by commercial farmers in the UK.

The complete diets were dispensed into individual feed bins, once daily. The weights of fresh feed offered and refused were recorded on 4 days consecutively each week. Daily samples from the different diets (early, mid and late for both LC and HC) and refusals were analysed for dry matter. Daily samples of each diet were bulked to monthly samples and analysed to determine chemical composition. The complete LC and HC diets averaged calculated ME contents of 11.55 MJ kg^{-1} and 11.90 MJ kg^{-1} and crude protein contents of 190 g kg^{-1} and 182 g kg^{-1} (DM basis) respectively.

Cows were weighed and scored for body condition once a week after milking. Condition scoring was based on the scale proposed by Lowman *et al.* (1976). The scale runs from 0 (very thin) to 5(very fat) with each score described in terms of the amount of tissue cover over the transverse processes of the lumbar vertebrae and around the tail head. Each score was made to the nearest 1/4 of a unit. The weekly weight records of individual cows varied quite widely and it was therefore decided to estimate the weekly weight and condition score changes from the first derivative of a cubic polynomial fitted for the live weight and condition score data of each recorded lactation.

Milk yield, (MILK, kg/d), fat plus protein yield (F + P, kg/d) and dry matter intake (DMI, kg/d), were calculated as the average of the weekly records. The contents of fat (F%) and protein (P%) in the milk were calculated as the average of the weekly percentages weighted by the weekly milk yields. The milk energy yielded as milk was calculated from the formula of Tyrrell and Reid (1965): $LE = (0.384\ F\% + 0.223\ P\% + 0.199\ L\% - 0.108) \times MY$, where LE is milk energy (MJ/d), MY is milk yield, kg/d, and F%, P% and L% are the fat, protein and lactose percentages in the milk. Mean live weights (LW, kg), live weight changes (LWC, kg/d), condition score changes (CSC, units/d) and condition scores (CS, units), were calculated as the averages of the 26 weekly measurements.

The estimates of energy requirements were based on those proposed by AFRC (1991) and were $((0.53 \times (LW/1.08)^{0.67}) + (0.0091 \times LW)) = MN$ MJ/d for maintenance and $(27.36 \times LWC) = SC$ MJ/d for state change. Table 5.1 gives the corrected treatment means for the 2 lines on the 2 feeding systems.

Residual feed intake : Phenotypic residual feed intake was defined in terms of ME as RFI = (actual ME intake, MEIN) - (estimated ME requirement, MERQ). Three different methods were used to estimate MERQ: (i) For the calculation of

RFI_1, MEIN was regressed on LE and live weight change (all expressed per unit metabolic body size defined as $LW^{0.75}$) and the fitted values taken as MERQ. (ii) RFI_2 was based on MN, LE and SC and AFRC (1991) values for the partial efficiencies k_m, k_l and k_f, respectively, and (iii) MEIN was regressed on all yield and component traits and on the two way interactions between LW and CS and between LWC and CSC (RFI_3); in this third model no further constant was fitted. No other fixed effects were included in the model.

An alternative way of computing RFI is presented by Kennedy *et al.* (1993). The estimated phenotypic and genetic variance-covariance matrices (P and G) between MEIN, LE, $LW^{0.75}$ and LWC were used to calculate (i) phenotypic and genetic partial efficiencies (i.e. partial regressions of MEIN on the component traits) and (ii) genetic and phenotypic parameters for both phenotypic and genetic residual feed intake (RFI_p and RFI_g, respectively). RFI_p should be virtually the same as RFI_1, but possible difference might appear as a consequence of different estimation procedures (for example, accounting for fixed effects).

Analysis: Least squares analysis was used to investigate if lactation (1, 2, 3 and >3), year (1988, 1989, 1990, 1991), month of calving (Sept., Oct., Nov. and Dec.), line (selection and control) and feeding system (HC and LC) and the covariates, Holstein percentage and age of calving, had significant effects on RFI. None of the two way interactions between the effects was important and so these were not considered any further.

Multivariate analyses were performed to estimate the variances and co-variances. An individual animal model, with the numerator relationship matrix, was fitted using the Hill-Thompson algorithm (Thompson and Hill, 1990) in DFREML (Meyer, 1989). This package allows simultaneous estimation of an additive random genetic effect and a permanent environmental effect. The permanent environmental effect is included to take account of the covariance between lactations on the same cow. The fitted model was:

$$Y_{ijklmnop} = \mu + A_i + C_j + Y_k + M_l + LN_m + GROUP_n + b_1\, AC_{ijklmnop} + b_2\, H\%_{ijklmnop} + E_{ijklmnop}$$

where

$Y_{ijklmnop}$ = observation

μ = overall mean

A_i = random additive genetic effect of ith individual.

C_j = random effect of jth repeated lactation .

Y_k = year of calving (1988, 1989, 1990, 1991)

M_l = month of calving (Sept., Oct., Nov., Dec.)

LN_m = lactation number (1, 2, 3 and 3 >)

$GROUP_n$ = line by feed group effect (S-HC, C-HC, S-LC, C-LC)

$b_1\ AC_{ijklmnop}$ = linear regression on age at calving in days

$b_2\ H\%_{ijklmnop}$ = linear regression on Holstein percentage

$E_{ijklmnop}$ = residual effects

A full relationship matrix was included in the model. The expectations of the additive direct genetic (A_i), common environmental (C_j) and residual error effects are zero and their variances are σ^2_a, σ^2_c and σ^2_e respectively. Covariances between the random effects are assumed to be zero. For simplicity of illustration only the variance-covariance structure for a bivariate model (trait_1 and trait_2) is given, although multivariate models with 3 or 4 traits were used in further analysis:

$$V(u) = \quad G = \begin{bmatrix} A\sigma^2_{a1} & A\sigma_{a12} & 0 & 0 \\ A\sigma_{a12} & A\sigma^2_{a2} & 0 & 0 \\ 0 & 0 & I_c\sigma^2_{c1} & I_c\sigma_{c12} \\ 0 & 0 & I_c\sigma_{c12} & I_c\sigma^2_{c2} \end{bmatrix}$$

$$V(E) = \quad R = \begin{bmatrix} I\sigma^2_{e1} & I\sigma_{e12} \\ I\sigma_{e12} & I\sigma^2_{e2} \end{bmatrix}$$

$$\text{cov}(u,e) = 0$$
$$V(Y) = ZGZ' + R$$

Where:

A = the numerator relationship matrix;

Z = incidence matrix relating random effects to records.

I_c = identity matrix with rank equal to the number of cows

I = identity matrix with rank equal to the number of lactations

u = vector with random effects

G = matrix with (co-) variances between random effects

Y = vector of observations

σ^2_c, σ^2_a, σ^2_e = variances for permanent environmental, additive direct effect and residual error effect.

σ_{a12}, σ_{c12} = covariance between trait 1 and 2 for additive direct effect and permanent environmental effect.

5.3 Results

Selection line animals on the low concentrate feeding system (S-LC) had the lowest residual feed intake (Table 5.1). In Figure 5.1, ME intake and energy output for maintenance, lactation and live weight change are shown for the four groups of animals. These graphs show how selected cows on the low concentrate (LC) diet produced similar amounts of milk energy as the control cows on the high concentrate diet (HC). However, between these two groups, ME intake is higher for the controls and energy put into live weight is lower for the selection line animals. Based on live weight measurements during lactation and AFRC (1991), the requirements for maintenance are indistinguishable between the four groups. Figure 5.2 shows the residual feed intake (RFI_2) during lactation for the Langhill selection and control line cows fed two diets as was described above. The selection line and the low concentrate diet clearly have lower mean values for RFI. This shows that non-random deviations from the AFRC equations occur for the apparent overall efficiency of energy use, with the line difference suggesting that there may be a genetic component to RFI. For all four groups, ME intakes were higher than the requirements based on the AFRC k values and the calculated requirements for maintenance, lactation and live weight change (based on measured milk component yield, live weight and live weight change).

Residual feed intake based on AFRC predictions, RFI_2, had a mean value of 8 MJ per day, so that the actual ME intake was on average 8 MJ/d higher than that predicted (Table 5.2). This could have been due, at least in part, to physical wastage, as the values in AFRC (1991) are from experiments in calorimeters with no physical feed wastage rather than from feeding trials where some wastage is unavoidable.

Obviously the means for RFI_1 and RFI_3 were close to zero, as these were based on least squares estimates for the k-values from within the data. Estimates for the regressions were compared with those of AFRC. Each unit of $LW^{0.75}$ day, and each kg live weight change, required 0.68 MJ ME (s.e. = 0.06) and 26.0 MJ ME (s.e. = 4.4), respectively; the AFRC values are approximately 0.48 and 44.9 MJ ME. The partial efficiency for LE was estimated as 0.71 as the reciprocal of the regression coefficient of 1.41 (s.e. = 0.07) which is slightly higher than the value of 0.64 given by AFRC (1991).

Heritability estimates for the three measures of residual feed intake ranged from 0.30 to 0.38 with the correlations between them larger than 0.90 (Table 5.2).

As expected, the phenotypic correlations between RFI and the component traits used to calculate (or estimate) RFI were close to zero (Table 5.3). Condition score and live weight change were still genetically correlated with all three measures of residual feed intake, suggesting different environmental and genetic relationships between these two traits and ME intake. Estimates for phenotypic and genetic correlations between feed intake and residual feed intake were similar at around 0.68.

Estimates for both phenotypic and genetic correlations for the major traits used to estimate residual feed intake are shown in Table 5.4. Genetically a large live weight change was associated with a higher MEIN, though the phenotypic correlation was estimated at close to zero (-0.05). This suggests that the environmental correlation between LWC and MEIN was in the other direction. Heritability estimates for phenotypic and genetic residual feed intake, based on the estimated variance-covariance matrix for MEIN, LE, $LW^{0.75}$ and LWC, were 0.34 and 0.05, respectively. Genetic correlations between RFI_g and the components and phenotypic correlations between the RFI_p and the components were zero, because that is how they were defined.

Similar partial regressions could be calculated (Table 5.5). Partial energetic efficiencies (1 / b) for LE ranged from 0.58 for the genetic regression to 0.86 for the regression to calculate RFIp. Partial genetic regression coefficients for MEIN on metabolic live weight and live weight change differed appreciably from the phenotypic regression coefficients.

5.4 Discussion

Even though Kennedy *et al.* (1993) clearly showed that the effects of selection on residual feed intake (RFI) can be virtually the same as those of selection on an index which combines feed intake and the separate component traits, RFI might still be of interest. It reflects a difference, or differences, in the utilisation of energy by an animal compared with the population mean and, hence, possible differences in (i) some combination of the partial efficiencies k_m, k_l and k_f or (ii) some differences in the equations used to calculate the energy needed for maintenance, lactation (LE) or body condition change (LWC) (e.g. deviation from normality or additivity) ,or (iii) variation in traits other than those in the model (Luiting and Urf, 1987; Luiting, 1991).

Although RFI is expected to be statistically unrelated to the component traits, it is possible to think of reasons why RFI would not be biologically independent of all of the component traits in this study. For example, the ME needed for the output of energy in milk (LE) has been calculated as the heat of combustion value of that milk divided by a single k-value. It may not be appropriate to assume that the same k-value applies to all three of the chemical components - fat, lactose and protein - which contribute to the energy content of milk. Within feeding systems the effect of differences in the k-values of the different components might be small, because there was no significant difference in F% and P% observed (Chapter 3). However, the assumption of a homogeneous composition of the LE between feeding systems is more hazardous; F% is much higher and P% is significantly lower on the low concentrate feeding system. This could be an explanation for the relatively high phenotypic correlations between RFI_1 and RFI_2 and the milk components (Table 5.3). Likewise, significant differences in dry matter intake between the feeding systems will result in different gut fill values, and therefore it might not be appropriate to assume homogeneous live weights and live weight changes between the feeding systems. Other important inaccuracies which might affect the relations with RFI come from errors in the estimation of ME. Inaccurate estimation of ME in, for example, the silages fed might bias differences between the two feeding systems fed at Langhill. So, there are good reasons why it is difficult to correctly include in the models all of the component traits and therefore it might be misleading to assume that RFI is biologically independent of the component traits.

For these reasons the properties of RFI might differ under different environmental circumstances or as a consequence of the definition of RFI. Table 5.6 reviews some studies on RFI. When fixed amounts of concentrates are fed with *ad libitum* roughage, the diets of individual cows will contain different proportions of roughage. The distinction between our results and others is probably due to feeding the cows *ad libitum* total mixed rations. In studies (1) to (4) in Table 5.6, fixed amounts of concentrates were fed or cows were fed according to yield. In studies (5) and (6) feeding was *ad libitum*. Of course, because of the costs of measuring the feed intake of individual dairy cows, only relatively small data sets are generally available to estimate genetic parameters and therefore large sampling errors are likely to occur.

As shown by Kennedy *et al.* (1993) RFI is genetically independent of the component traits only when the genetic partial regressions are used (as is done for RFI_g). The observed values of > 0.30 for the h^2 of RFI_1, RFI_2 and RFI_3 may be misleading as they are a consequence of the large genetic covariances with some of the component traits, because the h^2 for RFI_g is only 0.05. The large genetic correlation between live weight change (and presumably the same could be argued for average condition score) and RFI can be explained as a consequence of the environmental and genetic correlations between ME intake and LWC (Table 5.4) being of opposite sign. This implies that cows with high genetic merit for LWC (gain in weight) are also the cows with the highest intake capacity, but also that the cows which ate most also lost more weight than average. This in turn suggests that the cows with the highest intake capacity (the high producing cows, given the r_g of 0.44 between MEIN and LE) were not able to support their higher production sufficiently when fed the complete mixed diets used here, without using body reserves. When comparing animals as if they were giving the same milk yield at the same metabolic live weight (the basis for the partial regressions in Table 5.5), then both the phenotypic, and the genetic, regression coefficients of MEIN on live weight change are positive. This lends support to the hypothesis that even the high intake capacity cows were not able to support their higher milk yields due to environmental restrictions.

It is an interesting observation that equations of the kind proposed by AFRC (1991) are unable to deal correctly with genetic differences because of antagonistic genetic and environmental relationships between traits. It poses the interesting question of whether such equations are suitable for predicting the economic consequences of selection, a purpose for which they are often used in so-called bio-economic models. Economic values for breeding purposes (Hazel, 1943) should be the partial genetic regression coefficients and therefore it seems not to be appropriate to use equations of the kind which reflect phenotypic effects.

There is a continuing debate about the value of measuring feed intake in breeding programs. Initially, responses in efficiency from selection on milk yield were predicted to be high enough so that feed intake measurement could be ignored in selection (Freeman, 1975). However, as pointed out by several authors (see Persaud *et al.*, 1991), these estimates were expected to be too high, because they were derived from data where cows were fed according to yield. Recent estimates of genetic correlations under *ad libitum* feeding (Persaud *et al.*, 1991) seem to suggest that the correlated response from indirect selection for efficiency, by selection on fat plus protein yield, is expected to be only 47-75% of that from direct selection for efficiency. However, based on data from Moore *et al.* (1992), Kennedy *et al.* (1993) concluded that the measurement of feed intake is not worthwhile, as it provides no information over and above that provided by milk production and body weight at calving. Unfortunately, the data set of Moore *et al.* (1992) is based on test day records for individual cows. In their data set the amounts of grain and protein fed were calculated according to yield, and cows were not fed *ad libitum*. In addition, the estimation of the forage intakes of individual cows was based on group feeding with individual intakes predicted from live weight. For these reasons it is not surprising that they concluded that the measurement of feed intake does not provide any additional information when live weight and milk yield are measured. When the conclusion of Kennedy *et al.* (1993) is tested using the estimated correlations in Table 5.4 between MEIN, LE and LW, a heritability for RFI_g of 0.35 is estimated (results not shown). Therefore, results from this study certainly suggest that measurement of feed intake provides information over and above that provided by live weight and LE. However, the results in this study also showed that when live weight change is accounted for, together with live weight and yield, the heritability for RFI_g is only 0.05. This suggest that any true genetic variation in the partial efficiencies is small. Consequently, one could conclude that by measuring yield, live weight and live weight changes, nearly all of the genetic variation in energy intake is accounted for.

However, the large amount of genetic variation in feed intake accounted for by live weight change seemed unrealistic. Additionally Hill and Thompson (1978) showed the increased chance that large canonical heritabilities are biased upwards and small canonical heritabilities are biased downwards as the number of variables in multivariate analysis increases or the number of records decreases. Visscher (1994) showed that a similar bias occurred for the accuracy of selection (genetic R^2) when one trait was predicted from several other traits. Therefore it was decided to simulate a simple data structure and analyse this data set with REMLPK to test possible biases in the heritability of genetic residual feed intake (50 replicates). For simplicity a hierarchical design was assumed with n sires (50, 100, 200, 400, 800 and 1600), 8 offspring per sire and 1 record per offspring. Four traits were simulated (which could be seen as feed intake, yield, live weight and live weight change) and h^2 was assumed to be 0.36, 0.45, 0.71 and 0.16, respectively. All genetic correlations were assumed to be 0.25 and all environmental correlations were assumed to be zero. This gives population values for the h^2 for phenotypic and genetic RFI of 0.34 and 0.30, respectively. There was considerable bias in the small data sets in the estimate of the

h^2 for genetic residual feed intake, Table 5.7, with h^2 being underestimated. Therefore the estimate of h^2 for the genetic residual feed intake of 0.05 found in this study is expected to be strongly biased downwards. The bias is most likely due to the fact that when calculating RFI, the variance explained by the components is maximised (least squares) and hence the residual variance is minimised. It is the same argument as that of Visscher (1994) who found that the genetic R^2 is biased upwards.

Conclusions: The objective of this study was to investigate if any genetic variation in RFI exists, and, if present, whether this is a reflection of genetic correlations between feed intake and the component traits. When energy requirement for each cow was estimated from phenotypic regressions then the h^2 for residual feed intake was estimated to be from 0.30 to 0.38, depending on the way of calculating the energy requirements. Estimates for the genetic correlation between residual feed intake and several other traits showed that this relatively high h^2 came from high genetic correlations of residual feed intake with live weight change and condition score. When energy requirements were estimated using coefficients based on partial genetic regressions of energy intake on milk energy yield, metabolic live weight and live weight change then the heritability of residual feed intake was only 0.05. The difference between the estimates of heritability for 'genetic' residual feed intake and phenotypic residual feed intake was a consequence of (i) the antagonistic genetic and environmental correlations between live weight change and energy intake and (ii) a strong bias downwards in the estimation of the h^2 for genetic residual feed intake. From this indirect evidence, it was concluded that 0.05 is probably the lower boundary for h^2 of genetic RFI and therefore, that it is likely that the residual variation of feed intake, after accounting genetically for lactational energy, metabolic live weight and live weight change, has a heritable component to it and therefore measuring feed intake on dairy cows still gives information of value.

Table 5.1: Corrected mean values for several traits (abbreviations in text) for LINE (S is selection and C is control) and DIET (HC and LC, high and low concentrate). The average standard error of the differences (S.E.D.) is an approximation given by REML.

	S-HC	C-HC	S-LC	C-LC	
N =	102	84	117	74	
	mean	mean	mean	mean	S.E.D.
Milk (kg/d)	31.6	27.6	26.3	23.0	0.7
Fat (%)	4.12	4.12	4.46	4.43	0.11
Protein (%)	3.07	3.15	3.00	3.07	0.04
DMI (kg/d)	19.2	18.7	16.8	16.3	0.4
LW (kg)	609	606	601	597	9
CS (0-5)	2.47	2.59	2.40	2.56	0.06
LWC (kg/d)	0.17	0.32	0.04	0.15	0.04
CSC (units/d * 100)	-0.12	-0.02	-0.13	-0.07	0.04
MEIN (MJ/d)	228	222	194	188	4
MN (MJ/d)	42.4	42.3	42.1	41.8	0.5
LE (MJ/d)	98.1	86.1	84.5	73.8	2.2
SC (MJ/d)	4.62	8.62	1.18	4.12	1.02
RFI_1 (MJ $lw^{-.75}day^{-1}$)	0.021	0.077	-0.072	-0.019	0.039
RFI_2 (MJ day^{-1})	9.7	15.3	2.7	8.6	3.5
RFI_3 (MJ day^{-1})	2.36	8.06	-6.73	-0.17	3.5

Table 5.2: Mean, phenotypic variance (σ^2_p), heritability (h^2) and permanent environmental (c^2) effect for three different measures of residual feed intake, and their correlations[1].

	mean	σ^2_p	h^2	c^2	RFI_1	RFI_2	RFI_3
RFI_1 (MJ $lw^{-.75}day^{-1}$)	0.00	267	0.38	0.15	-	0.98	0.95
RFI_2 (MJ day^{-1})	8.23	406	0.32	0.18	0.99	-	0.93
RFI_3 (MJ day^{-1})	0.01	394	0.30	0.29	0.93	0.91	-

[1] Genetic correlation below diagonal and phenotypic correlation above diagonal.

Table 5.3: Multivariate (RFI_1, RFI_2 and RFI_3 together with each component trait) estimates for genetic and phenotypic correlations between three different measures of RFI and several component traits.

	RFI_1		RFI_2		RFI_3	
	r_g	r_p	r_g	r_p	r_g	r_p
milk yield	0.07	-0.09	0.04	-0.09	-0.11	-0.09
fat yield [1]						
protein yield	-0.02	-0.11	-0.06	-0.13	-0.11	-0.13
lactose yield	-0.05	-0.06	-0.08	-0.06	-0.19	-0.04
fat (%)	-0.32	-0.12	-0.31	-0.10	0.01	0.10
protein (%)	-0.02	-0.02	0.01	-0.05	0.04	-0.05
LE	-0.16	-0.13	-0.21	-0.13	-0.00	-0.02
LW	0.00	-0.06	0.09	-0.03	0.12	-0.05
CS	0.26	-0.06	0.33	-0.03	0.36	-0.06
LWC	0.49	-0.05	0.52	-0.19	0.35	-0.07
CSC [1]						
DMI	0.64	0.73	0.63	0.68	0.69	0.76
MEIN	0.62	0.73	0.60	0.69	0.68	0.77
CPIN	0.51	0.73	0.45	0.69	0.60	0.77

[1] Negative variance estimate for permanent environmental effect on CSC.

Table 5.4: Parameters[1] for ME intake, lactational energy, metabolic live weight and live weight change from multivariate REML and parameters for phenotypic and genetic residual feed intake calculated from these parameters.

	h^2	c^2	MEIN	LE	$LW^{0.75}$	LWC	RFI_p	RFI_g
MEIN	0.36	0.26	-	0.48	0.14	-0.05	0.89	0.42
LE	0.45	0.07	0.44	-	-0.18	-0.47	0.00	0.23
$LW^{0.75}$	0.71	0.14	0.30	-0.10	-	0.30	0.00	-0.13
LWC	0.10	0.16	0.23	-0.65	0.42	-	0.00	-0.81
RFI_p	0.34	-	0.75	-0.18	0.06	0.57	-	-
RFI_g	0.05	-	0.59	0.00	0.00	0.00	-	-

[1] Genetic correlation below diagonal and phenotypic correlation above diagonal.

Table 5.5: Partial, regression coefficients of MEIN on LE, $LW^{0.75}$ and LWC from four different sources (in MJ / unit).

Source:	LE	$LW^{0.75}$	LWC
RFI_1 (fitted regression)	1.41	0.68	26.0
RFI_2 (AFRC)	1.56[1]	0.48[2]	44.9[3]
RFI_p (from estimated P)	1.16	0.59	17.7
RFI_g (from estimated G)	1.72	0.07	166

[1] 1 / k_l and $k_l = 0.64$

[2] approximation from MN.

[3] 27.38 MJ kg^{-1} / k_f and $k_f = 0.61$

Table 5.6: Overview of heritabilities for RFI reported in the literature.

Source[1]	h^2	# records:	period:	feeding[2]:	RFI calculation:	
			(days)		traits	method[3]
Phenotypically calculated RFI:						
(1)	0.19	360 heifers	0 - 120	fixed conc., ad lib. roughage, 2 random conc. groups	FCM, LWC, $LW^{.75}$	est. b's
(2)	0.02	247 cows	0 - 300	TMR, 3 conc. groups according to yield	FCM, LWC, $LW^{.75}$	est. b's
(3)	0.04	353 cows	7 - 84	fixed conc., ad lib. roughage, 2 random groups	FCM, LWC, $LW^{.75}$	fixed b's
	0.00		85 - 168			
(4)	0.14	> 80000 cows	1 - 305	conc. according to yield, not ad lib., several groups, no indiv. intake	FCM, LW	est. var.
(5)	0.69	295 cows	1 - 250	TMR ad lib. 1 group	FCM, LWC, $LW^{.75}$	fixed b's
(6)	0.38	377 lactations	1 - 182	TMR ad lib. 2 random conc. groups	LE, LWC, $LW^{.75}$	est. b's
	0.32				LE, LWC, $LW^{.75}$	fixed b's
	0.30				several	est. b's
	0.34				LE, LWC, $LW^{.75}$	est. var.
Genetically calculated RFI:						
(4)	0.01	> 80000 cows	1 - 305	conc. according to yield, not ad lib., several groups, no indiv. intake	FCM, LW	est. var.
(6)	0.05	377 lactations	1 - 182	TMR ad lib. 2 random conc. groups	LE, LWC, $LW^{.75}$	est. var.

[1] 1. Van Arendonk *et al.*, 1991; 2. Ngwerume and Mao, 1993; 3. Svendsen *et al.*, 1993; 4. Kennedy *et al.*, 1993; 5. Jensen *et al.*, 1991; 6. this study.

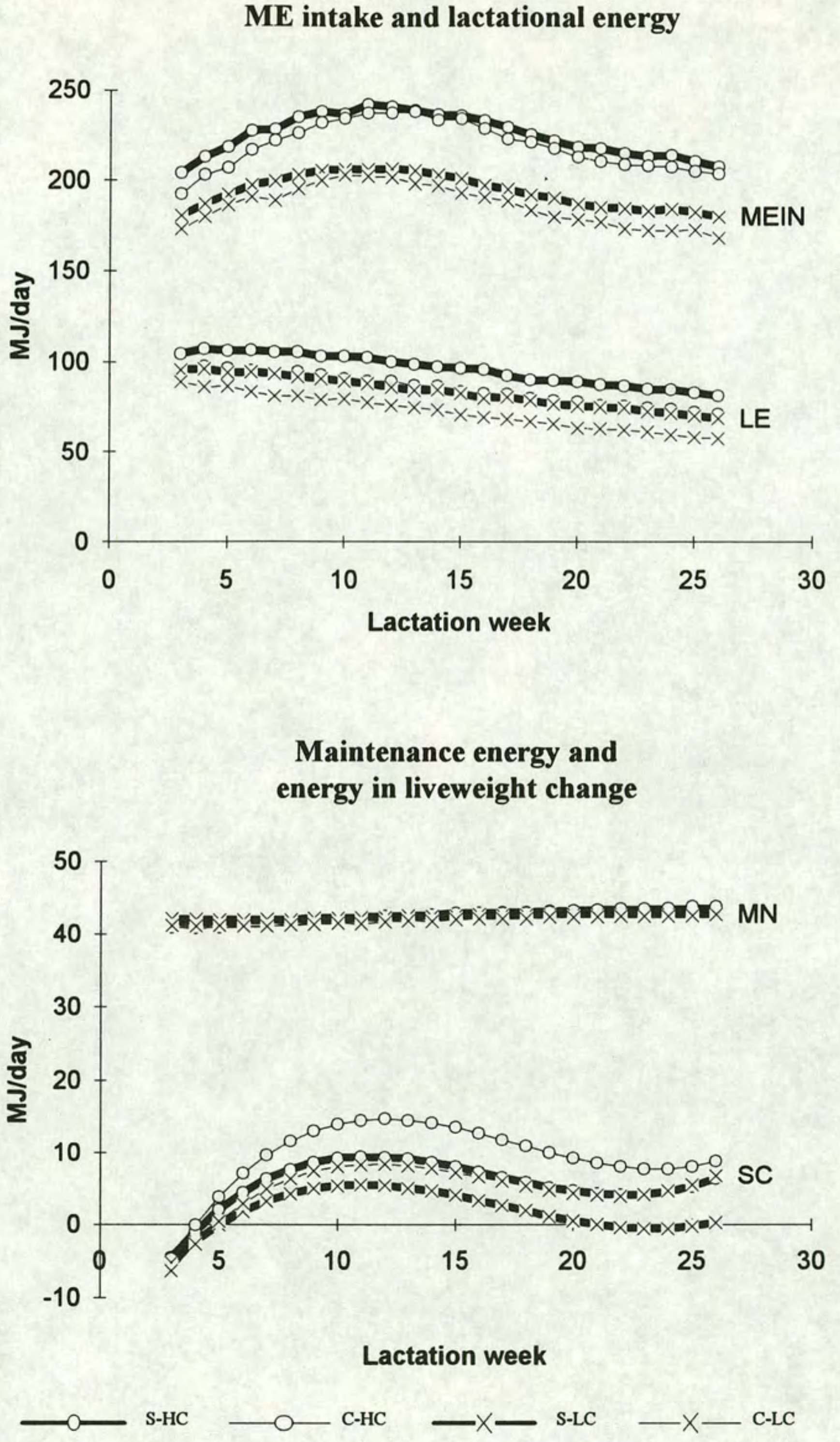
[2] TMR = total mixed ration; conc. = concentrate.

[3] est. b's = partial efficiencies estimated as partial regression from data.
fixed b's = partial efficiencies from literature.
est. var. = partial efficiencies from estimated variance and covariance matrix.

Table 5.7: Average estimates for the h^2 of phenotypic and genetic RFI (± s.d. of the 50 replicates) from simulated data, using n sires with 8 offspring and 1 record per offspring. The number of zero estimates is the number of h^2 for genetic RFI < 0.001.

	RFI$_p$	RFI$_g$	
population:	0.34	0.30	# zero estimates
n:			
50 [1]	0.35 ±0.16	0.09 ±0.14	27
100	0.32 ±0.07	0.09 ±0.08	14
200	0.34 ±0.07	0.17 ±0.13	6
400	0.34 ±0.06	0.23 ±0.11	2
800	0.34 ±0.04	0.28 ±0.06	0
1600	0.34 ±0.03	0.28 ±0.06	0

[1] Two replicates did not converge.


ME intake and lactational energy

Maintenance energy and energy in liveweight change

Figure 5.1: Metabolisable energy intake and energy in lactation, energy for maintenance and live weight change, for selection and control line cows (S and C) on a high and low concentrate feeding system (HC and LC, respectively).

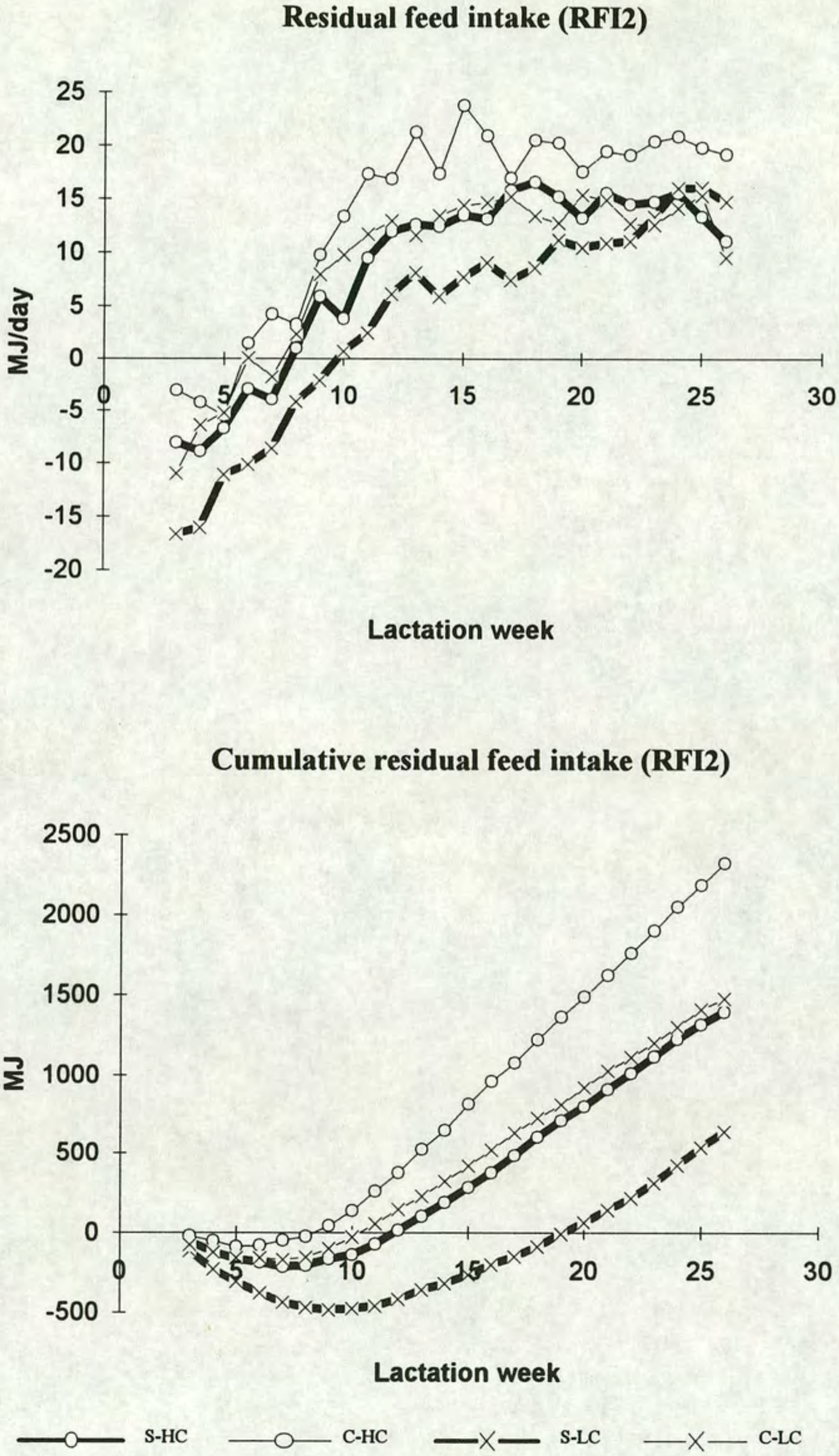


Figure 5.2: Residual feed intake (RFI_2) and cumulative residual feed intake during lactation, for selection and control line cows (S and C) on a high and low concentrate feeding system (HC and LC, respectively).

CHAPTER 6

GENERAL DISCUSSION.

6.1 Sources of variation in feed utilisation

It was reported in Chapter 3 that gross efficiency was higher for selected heifers and cows on both a high and low input feeding system. Furthermore, there is abundant evidence of genetic variability in feed efficiency (for reviews see Blake and Custodio, 1984; Korver, 1988; Persaud, 1990), and thus in gross energetic efficiency, measured as between breed (Gibson, 1986; Oldenbroek, 1988) or selection line/group differences (Persaud *et al.*, 1990; Chapter 3) or expressed as heritabilities (Persaud *et al.*, 1991; Van Arendonk *et al.*, 1991; Jensen *et al.*, 1991; Svendsen *et al.*, 1993). Published heritabilities for gross efficiency are moderately large and often very similar to the heritability of milk yield (Persaud, 1990). The problem with gross efficiency is that it does not distinguish between the energy used for the separate functions of maintenance, lactation and body tissue gain, or loss. Therefore, the evidence of genetic variation in gross efficiency indicates some genetic component in the whole complex function of intake, maintenance, body tissue mobilisation and yield and it seems desirable to know if the increase in efficiency is due to a change in the net efficiencies or due to a change in partitioning of feed between these components.

In Chapter 5 residual feed intake was used to investigate if there were any additional sources of variation in feed efficiency after adjusting for variation in some of the components of feed utilisation: lactation, maintenance and live weight change. Adjustment was first made phenotypically and secondly genetically, and it was concluded that some genetic variation in partial efficiencies exist, on the basis of (i) a difference in residual feed intake between selection and control line animals and (ii) the likelihood that there is still genetic variation in feed intake, after genetic correction for yield, maintenance and body tissue change. However, the exact source(s) of genetic variation are still unclear. For this reason the literature was reviewed to investigate possible evidence for the existence of genetic variation in digestion and metabolisation of food and the possible existence of genetic variation in energy used for the separate functions of maintenance, lactation and body tissue gain, or loss, which can be seen as having different partial efficiencies. (Where metabolisable energy, ME, is used as the input scale these three efficiencies are conventionally called k_m, k_l and k_f respectively).

Van Es (1961) showed that little between animal variation exists in the ability to digest a given diet. Grieve *et al.* (1976) found no relationship between genetic merit for milk yield and apparent digestibilities of ration components in 24 Canadian Holstein heifers. This agreed with the results from Davey *et al.* (1983), who compared high and low genetic merit Friesians. Similarly, Grainger *et al.* (1985) found no difference between high and low merit genotypes in their ability to metabolise the gross energy of the feed, or in the individual losses of energy in the faeces, urine and methane. Also, Custodio *et al.* (1983) suggested that cows of different genetic merit for milk did not differ in their ability to digest fibre and starch for milk secretion. No differences in partitioning of gross energy into digestible or metabolisable energy were found by L'Huillier *et al.* (1988) and Tyrrel *et al.* (1990) in experiments comparing Holstein and Jersey cows. In contrast, Freeman (1975) indicated that large differences in digestibility have been observed among cows and Trigg and Parr (1981) found that high genetic merit animals digested a (slightly) higher amount of the gross energy intake.

Traditionally, energy chambers are used to estimate the partial efficiencies with which ME is converted to different products. Sources of variation in the partial efficiencies, k_m, k_l and k_f, (for maintenance, lactation and body tissue mobilisation respectively) are known to exist (for a review see Moe, 1981). For example, typical values for k_l range from 0.54 to 0.74. Most of this variation, however, comes from experiments where the same cow (or group of cows) were fed different diets. Hence the observed variation in k-values is mainly environmental. Some experiments have focused on between animal variation. For example, Van Es (1961) found a between animal coefficient of variation of 5-10% for the amount of energy needed per kg metabolic body weight for maintenance but was not persuaded that there were real differences between cows. There were large time effects which were apparently 'seasonal'.

Grainger *et al.* (1985) reported that differences between high and low genetic merit cows in the use of ME (measured as heat production at a common ME intake) did not exist or were very small. Also, Bauman *et al.* (1985) indicated on the basis of a literature review that little variation exists among animals in the partial efficiency with which ME is utilised. Nevertheless, 34 Holsteins converted relatively more energy into milk than 29 Jerseys in the second third of the lactation; there was no significant difference in the first third of the lactation (Blake *et al.*, 1986). These authors attributed this difference to the Jerseys laying down more adipose tissue and concluded that there were no notable differences in energy utilisation between the breeds. No differences were observed in the energy utilisation of 6 Holstein and 6

Jersey cows in early lactation (Tyrrel *et al.*, 1990). Contrasting results were obtained by L'Huillier *et al.* (1988) who reported the efficiency of utilisation of ME for milk and tissue to be 0.58 and 0.48 in Jerseys and Holsteins respectively.

Walter and Mao (1989) used eighteen different models to estimate partial efficiencies from data collected under practical farming conditions. These authors were able to obtain partial efficiencies which were very similar to those efficiencies coming from energy chambers. Saama *et al.* (1991) compared gross efficiency and net efficiency of 30 pluriparious cows using two different methods. Estimates came from field records for 4 weekly periods and, in alternate weeks, from energy chambers. Field gross and net efficiency closely approximated the values in the energy chambers.

Using genetic size scaling rules Taylor *et al.* (1986) compared maintenance efficiency of mature Hereford, Aberdeen Angus, Dexter, British Friesian and Jersey cows and concluded that maintenance increased with increasing milk yield (expressed per kg mature weight). Coupled with an extensive discussion of the literature, these authors attributed this difference in maintenance requirements to large genetic differences in k_m. In contrast, Veerkamp *et al.* (1993, Appendix) estimated partial energetic efficiencies for maintenance, lactation and live weight changes, for selection line and control line cows on high and low concentrate feeding systems. Non-significant interactions between the line or feeding system and k-values were backwards eliminated. Estimates for k_m were higher for the low concentrate feeding system and for the selection line and estimates for k_l were higher on the high concentrate feeding system. However, estimates for k_f were greater than one and therefore not realistic.

Variance components for partial efficiencies have been estimated by Butazonni and Mao (1989) and Svendsen and Mao (1989). They estimated k-values from several measurements within a lactation for an individual animal. Heritabilities of around 0.4 were estimated for those k-values. Also, Walter and Mao (1989) estimated a genetic correlation of 0.56 between milk yield and k_l, which would suggest that selection for milk yield will result in a higher efficiency of converting ME into milk energy. Although this method of identifying genetic variation in partial efficiency and genetic covariances between the partial efficiencies is appealing - because large data sets can be used - it is unclear if these genetic parameters are biased by, for example, the amount of information available for each individual animal. Measurements of the k-values are not independent and for that reason the estimated correlation between the k-values might be partly a consequence of the sampling covariance between them. More justification of the technique might be needed here.

Conclusions: From the literature it is unclear if there is any genetic variation in the ability to digest or metabolise a given feed or in the partial efficiencies, k_m, k_l and k_f. Most studies investigating sources of variation in feed efficiency can be classified as being: (i) based on analyses of very large data sets from field records, but with individual cow feed intakes predicted from herd averages (sometimes adjusted for yield and live weight, or both), (ii) studies based on analyses of a much smaller number of individual feed intake records from experimental herds, or (iii) studies on very few animals of uncertain genetic background in calorimeters which allow the components of the energy balance to be measured. Results from energy chambers suggest no breed differences, whereas estimates from field data suggest that there is some genetic variation in the apparent net efficiencies.

Some factors might have influenced the identification of possible sources of variation in partial efficiencies. For example, in lactating cows it is difficult to account properly for maintenance and body tissue mobilisation. Often live weight and live weight changes are used to infer requirements for maintenance and body tissue mobilisation. However, it is well known that live weight is a bad predictor of body tissue composition (Benedict, 1927 quoted in Moe *et al.*, 1971). Body weight can be seen as a complex of gut fill, lipid and lipid-free empty body weight and these components can vary independently. For example, during the first weeks of lactation cows lose lipid, but gut fill increases as a consequence of higher intakes. Figures 3.2 and 3.3 also illustrate the different patterns of change for live weight and condition score during lactation. Possible correlations with yield, might further compound the difficulties of estimating partial efficiencies.

Overall, it can be concluded that there is no strong evidence to assume genetic differences in *partial* efficiencies and that the most important sources of genetic variation in *gross* energetic efficiency are yield, the capacity for feed intake, the extent to which body tissue is mobilised and any differences in partitioning between these components. The consequence is that high genetic merit animals are more efficient, because they partition the available energy different from low genetic merit cows and not because the processes used to transform consumed feed into valuable product have become more efficient. More reliable evidence (than that in Chapter 5) needs to be collected before any true genetic variation in partial efficiencies can be assumed.

6.2 Selection for feed intake, live weight and feed utilisation.

If it is assumed that there is no selection effect on the partial efficiencies, then all the genetic changes come from a change in partitioning of feed. Consequently, whether selection should be for increased or decreased ME intake is not easy to determine, because it depends on whether the extra intake is partitioned into yield or into body tissue and vice versa. Additional complications are the opportunity to increase the energy density in a diet and the opportunity of dairy cows to use body tissue reserves to buffer against (temporary) nutritional adversity and subsequently replenish these body reserves in other parts of the lactation or in the dry period. The parameter estimates from Chapter 5 can be used to illustrate this point, because all the component traits can be expressed in the same units (MJ/day), using the regression coefficients in Table 5.5.

For example, Table 6.1 shows that 1 s.d. selection on yield (or lactational energy) increases intake (within the same 26 weeks period) by only 6.2 MJ /day, whereas the milk output is expected to increase by 12.8 MJ /day. Hence, the rate of genetic progress in milk yield is faster than can be supported by the increase in ME intake (in the same 26 week period) alone. If the energy density of the diet can be increased, or animals can use extra body tissue as a buffer and subsequently increase intake outside the measured period, this is not a problem. However, when none of these options is possible (or desirable for economic reasons), the gap between energy required and energy intake will increase as a consequence of selection on yield only, which might not be acceptable for reasons of animal welfare and sustaining fertility and health.

If liveweight change is ignored, the goal weights based on 'economic' considerations are then -1 : 1 : -1 for ME intake, lactation and maintenance. The selection effects of applying these values on multivariate PTAs for LE, MN and LWC are given in Table 6.1 (Index 1). Intake and weight are decreased, whereas milk yield and liveweight loss are expected to increase. The gap between ME intake and energy required is expected to increase by 9.6 MJ / day for each s.d. selection on this index.

Often in practice, no feed intake measurements are available and hence several authors (Groen *et al.*, 1994, and references therein) calculated economic values for live weight only, and suggested that live weight should be weighted negatively compared to the yield traits in an index. Using such an index (Index 2) is expected to reduce the rate of increase in ME intake considerably compared with selection on yield only, and lead to some extra energy becoming available from the reduced amount of energy needed for maintenance. However, selection on this index is still expected to increase the gap between yield and intake and hence an increase in the dependency on body tissue mobilisation during early lactation.

Selection for positive intake whilst selecting for positive yield and negative weight at the same time (Index 3), is expected to increase both yield and intake. However, the rate of change in intake is higher than needed for the extra yield alone, and selected animals are expected to put more energy in body condition during the first weeks. Hence relatively fat animals will be selected.

These results illustrate the difficulty of finding appropriate weighting factors for feed intake, liveweight and yield in dairy cattle breeding goals. The difficulty is primarily in how to account for the buffering capacity of body tissue mobilisation and related effects on health and fertility. For this reason, as an alternative to the indices discussed thus far, it could be argued that an increase in milk yield (during early lactation) should be accompanied by a sufficient increase in intake capacity to accommodate the extra energy required. Hence, selection should be for increased lactational energy and decreased maintenance cost (weights are 1 : -1 respectively), conditional on ME intake increasing by 1 x (LE - MN). Brascamp (1984) reviewed the derivation of selection indices with constraints and the mixed index (desired gains and economic weights) discussed by him, needs to be adapted so that the response of one trait is restricted to be relative to the sum of responses in the two other traits.

6.3 Genotype by environment interaction

Chapter 3 and Chapter 4 are both concerned with genotype by feeding system interaction. In Chapter 3 the mean selection and control line performances were compared and genetic regressions of several traits on fat plus protein yield (in the national data set) were estimated. The results from these studies, suggested that animals did not rank differently across the two feeding systems for a range of traits (with the possible exception of fat yield), but that genetic variation for most traits was affected by the feeding systems. This is not surprising because there is ample evidence from national data sets of heterogeneous variances among herds in the UK (Hill *et al.*, 1983; Brotherstone and Hill, 1986; Meyer, 1987; Visscher, 1991). However, the problem has always been to find a proper biological interpretation for this phenomenon.

The results in this study suggest that a possible explanation could be that with a higher percentage forage in the diet, the high genetic merit animals are not capable of eating much more than the control line animals <u>during the first 26 weeks of lactation</u>, whereas on high concentrate diets high genetic merit animals have the advantages of higher intake and more body tissue mobilisation. Hence, differences in yield between cows were smaller on low input systems and variation in milk yield was reduced because intake was limited, largely by constraining factors in the diet, whilst with the more digestible feed (HC) intake was more a function of the cow and it potential to yield. This concern about the feed intake capacity of dairy cows during early lactation is supported by comparing the trends from year to year in the Langhill experiment

(Figure 6.1). Difference between the selection and control line increased with time for milk yield and dry matter intake on the high concentrate feeding system, but for dry matter intake the difference between the selection and control group hardly increased at all on the low concentrate feeding system.

Nonetheless, the high heritabilities for DMI (Chapter 4) suggested that there is a genetic component to variation in dry matter intake on both feeding systems. Also, the absolute genetic variance for DMI was higher on LC than on HC, but the high genetic correlation for DMI on both HC and LC suggest similar sources of genetic variation on both diets. This greater genetic variance for DMI with a 'limiting diet' might reflect the expression of the genetic differences in 'capacity' which are revealed with 'limiting' diet, but which are subdued when diets of higher digestibility are used. It is however unclear which of the several genetic factors affecting dry matter intake (e.g. appetite, rumen capacity or digestion) expression was limited on LC.

In Chapter 4 genetic correlations were estimated between the same trait on the two feeding systems at Langhill. In the latter analysis, line was included in the model to account for mean differences between selection and control line animals. If this line difference was ignored, it was expected that the genetic variances and the genetic correlation would have been overestimated. These expectations were confirmed by the simulation results in Chapter 4 (Table 4.5). However, it is obvious that the line effect does not adjust fully for the selection of bulls in the national data set.

An alternative way of adjusting for differences in genetic merit between the control and selection line animals would have been to include the pedigree index (PI) for fat plus protein yield in the model. However the expectation was that the genetic variances would be underestimated, whereas the effect on the genetic correlation was unclear. To investigate the consequences of including PI (0.5 sire's PTA + 0.25 maternal grandsire's PTA for F + P), the same bi-variate analyses as in Chapter 4 were performed on a subset of the data (all animals having a PI easily available, n = 776), but without PI or line in the model. Then the same analysis was repeated, but now with (i) PI as covariate or (ii) line as a fixed effect. Results in Table 6.2 show that there is hardly any effect on the genetic correlation between the diet if either PI or line is included in the model. The absolute variance estimates were more different. For example, the genetic (co-) variances for milk yield (kg /d) on HC and LC were for the models without line or PI, with line, and with PI, respectively:

$$G0 := \begin{pmatrix} 11.50 & 7.16 \\ 7.16 & 4.75 \end{pmatrix} \qquad Gline := \begin{pmatrix} 9.37 & 3.60 \\ 3.60 & 2.54 \end{pmatrix} \qquad Gpi := \begin{pmatrix} 7.93 & 2.87 \\ 2.87 & 2.14 \end{pmatrix}$$

It is unclear which of these variances should be taken as the population values. G0 is obviously an overestimation whereas Gpi underestimates the genetic variation, because all animals are compared as if they have the same genetic merit for fat plus protein yield. The problem here is that most of the selection has taken place on data from outside the experiment and hence REML does not adjust for this selection effect. It is unclear which is the most appropriate way of adjusting for this effect and some additional work needs to be done to solve this problem. Furthermore, the genetic correlation between the traits on HC and LC and fat plus protein yield in the national data set was not estimated. Answering this question in future analysis appears to be important, because it clarifies if different bulls should be selected in the national data set for different feeding systems.

6.4 Further research

In Chapter 2 linear type traits were used to predict longevity. Although the index was robust to errors in the genetic correlation between type and longevity, it seems sensible to work towards a method for direct evaluation of longevity. It is, however, unlikely that these direct measurements of longevity replace the index based on type traits fully, because type traits have a higher heritability and are available earlier in life. Further research should focus on direct measurements for longevity and how these direct measurements can be complimented by linear type traits.

It was concluded that the complex of intake, yield and body tissue mobilisation should be included in the breeding goal. However, there is a practical problem that no direct measurements of feed intake or live weight are available for daughters of bulls being progeny tested. A possible solution for this problem might be to use linear type traits as predictors for some of the goal traits. Linear type traits are measured on a relatively large scale in the national population, and represent (subjective) measurements of a range of characteristics. Sieber *et al.* (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 and Veerkamp *et al.* (1994, Appendix) concluded that linear type traits help to predict margin over feed costs of individual cows. So there might be benefits from including type traits in a selection index for improving the profitability of dairy cows. Hence, for these reasons, estimating genetic correlations between measurements of size (stature, chest width and body depth) and live weight and feed intake is suggested as further study. Additional, there is evidence of genetic correlations between linear type traits and reproduction, health and fertility (Chapter 1). This might be another possibility to use linear type traits in a selection index, to select towards a more comprehensive breeding goal.

A large part of this thesis is concerned with understanding the consequences of selection for yield on feed intake and body tissue mobilisation. For this purpose accurate genetic parameters (from a larger data set) are needed which describe the complex relationships between intake, yield and body tissue mobilisation, not only over complete lactations but from within lactation periods as well. Most of the genetic parameters available currently, including those estimated in this thesis, however, come from data sets which are too limited in size. Persaud and Simm (1991) and Van Elzakker and Van Arendonk (1994) published genetic correlations between part lactation measurements of feed intake and complete lactation measurements and Svendsen *et al.* (1994) published an extensive set of estimates of the parameters describing the genetic and phenotypic relationships between several traits contributing to the composite trait, feed efficiency. A method to evaluate the lactation period as a continuous trait instead of, for example, three distinct trimesters, is suggested by Kirkpatrick *et al.* (1994). It may be possible to extend this approach to include not only the lactation curve for yield, but also relationships with other traits which vary over time (e.g. dry matter intake, body tissue mobilisation and liveweight) and hence work towards a better genetic description (or model) of the 'infinite dimensional dairy cow' (Kirkpatrick *et al.*, 1994). Such an (imaginary) model should be the ultimate tool to predict consequences of selection and be used to calculate economic values of traits.

Finally, it is likely that continued increases in production will be achieved as a consequence of 'single' trait selection of dairy cows for increased yield components. The results in this thesis show that these benefits in yield are likely to be maintained across different feeding systems. However, the biological consequences of selection are not fully understood and, for example, it is not fully clear as yet why selected animals eat (sometimes) more and mobilise more tissue compared with control animals, when offered the same diet *ad libitum*. This might be one of the major reasons why it is difficult to predict the future sustainability of current selection goals and the performance of selected animals in different environments. However, if as much effort will be spent on understanding the consequences of selection as has been spent on methods to accelerate the rate of genetic progress, then negative consequences of single trait selection, as has been observed in other species, need to be compensated for by more comprehensive and sustainable selection criteria.

Table 6.1: Genetic gains of a 1 s.d. selection on any one of the four traits or three indices. The residual increase is the rate of change in the energy deficit during the measured period (26 weeks of lactation). All traits are expressed in metabolisable energy (MJ) per day (partial efficiencies from AFRC, Chapter 5).

Selection on:	MEIN	LEc	MNc	LWCc	Index1	Index2	Index3
ME intake (MEIN)	14.2	6.2	-4.2	3.2	-8.5	4.9	11.7
lactation (LEc)	5.6	12.8	1.3	-8.3	5.6	12.4	10.9
$LW^{0.75}$ (MNc)	0.9	-0.3	-3.2	1.3	-1.7	-1.0	-0.0
live weight change (LWCc)	0.8	-2.1	-1.4	3.3	-2.7	-2.3	-0.9
Residual increase	6.8	-4.1	-0.9	6.9	-9.6	-4.1	1.8

Index 1: - MEIN + LEc - MNc

Index 2: LEc - MNc

Index 3: MEIN + LEc - MNc

Table 6.2: Genetic correlation between the same trait on the high concentrate or low concentrate diet at Langhill. When compared with the model in Chapter 4, line is excluded from the model or line is replaced by pedigree index for fat and protein yield.

	no line	line	PI
milk yield	0.97	0.74	0.70
fat yield	0.66	0.41	0.39
protein yield	1.00	0.84	0.84
fat %	0.76	0.77	0.75
protein %	1.00	1.00	1.00
DMI	0.95	0.98	0.96
LW	1.00	1.00	1.00
CS	1.00	1.00	1.00

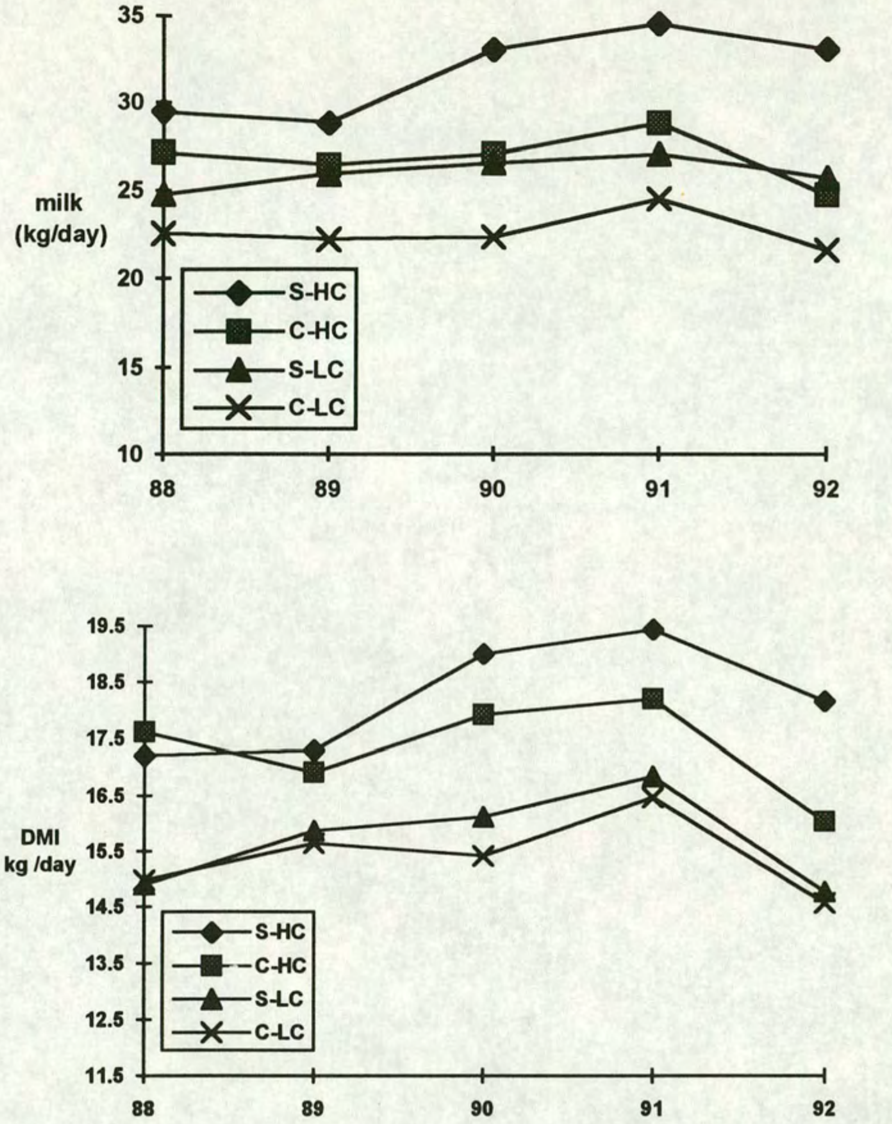


Figure 6.1: Mean milk production and dry matter intake for the four groups over the five years of the trial.

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APPENDIX
PUBLISHED PAPERS

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The economic performance of dairy cows of different predicted genetic merit for milk solids production

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Abstract

The aim of this study was to examine the relationship between pedigree index for kg fat plus protein and the financial margins between milk returns and food, health and reproduction costs in individual lactations. Records of milk and milk component production, food intake, health and reproduction were obtained for individual Holstein-Friesian cows over 38 weeks of lactation over a 7-year period, at the University of Edinburgh/Scottish Agricultural College Langhill dairy cattle research centre. Records for a total of 302 lactations were collected. Milk prices, input costs and margins were calculated for individual animals, using 1989/90 values. Regressions of margin over food costs (MF) and margin over food, health and reproduction costs (MFHR) on pedigree index (PI) for kg fat plus protein were all positive and ranged from £2·50 ± 3·00 per kg PI for MFHR for heifers, to £6·50 ± 2·10 per kg PI for MFHR for all animals. The lower regression for heifers was attributed to higher reproduction costs in animals of higher genetic merit, though the standard error for the regression estimated in this smaller data set was high. Sensitivity analyses showed that the regression coefficients remained very similar, even with ±50% changes in food, health or reproduction costs. It was concluded that selection on PI for kg fat plus protein is likely to lead to increased margin over food, health and reproduction costs.

Keywords: *dairy cows, economic margins, food intake, genetic merit.*

Introduction

The breeding goal of many dairy farmers is to maximize profitability, consistent with the health and welfare of their animals. The major financial returns in dairying are from sales of milk and its components and sales of surplus calves and cull cows. The major variable costs are associated with growing or purchasing food, and with health and reproduction and cow replacement. Despite this, to date, most breeding programmes worldwide have concentrated on outputs alone. This is partly because of the difficulty of measuring most of the inputs in large-scale progeny testing schemes, which involve recording the daughters of bulls under evaluation in many dispersed herds. There are also a number of studies which either show that selection for increased production generally leads to correlated increases in food intake and gross energetic efficiency or estimate positive genetic correlations amongst these traits (e.g. Hickman and Bowden, 1971 (in one of the two breeds); Freeman, 1975; Gibson, 1986; Korver, 1988; Andersen, 1989; Persaud, Simm, Parkinson and Hill, 1990; Persaud, Simm and Hill, 1991; van Arendonk, Vos and van der Werf, 1991). However, there is also evidence that, at least under *ad libitum* feeding, direct selection on gross efficiency or some function of inputs and outputs, may be more efficient than relying on correlated responses to selection for yield (Persaud *et al.*, 1991).

In studies of the phenotypic and genetic associations between production, health and reproduction in dairy cows, there is general agreement that the heritabilities of these traits are low, and that there are antagonistic genetic correlations between production and the incidence of some common diseases such as mastitis (see review of Emanuelson, 1988), and between production and reproductive success. In some cases these correlations are moderately low (e.g. Christensen, 1989 a and b; Solbu and Lie, 1990; Eriksson, 1991); In other studies they are higher (e.g. Wilton, van Vleck, Everett, Guthrie and Roberts, 1972; Simianer, Solbu and Schaeffer, 1991). To reduce or reverse the expected unfavourable correlated responses to selection for production alone, dairy cattle breeding programmes in several Scandinavian countries include selection on health and fertility.

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There is an urgent need for more comprehensive studies of breeding goals and criteria in dairy cattle to guide future selection strategies. However, because of the scarcity of reliable genetic parameters for many of the 'traits other than production' it will be several years before such studies can be completed. In the meantime, there is considerable value in examining populations of animals selected on output alone, to assess the consequences of past selection strategies, and to provide interim guidelines for selection programmes. This is the aim of the present study, using data collected over a 7-year period from the University of Edinburgh's Langhill dairy herd, where selection has been for increased milk solids production since 1973.

Material and methods

A dairy cattle breeding experiment was initiated by the University of Edinburgh, the predecessors of the Scottish Agricultural College and the Roslin Institute (Edinburgh) at the University's Langhill Farm in 1973. Since the outset, pedigree Holstein-Friesian artificial insemination (AI) bulls with reliable progeny tests have been selected for use at Langhill, on their estimated transmitting abilities for kg fat plus protein. Bulls have been selected either on the basis of a United Kingdom proof, or on the basis of a foreign proof where conversion factors were available. In 1976 a control herd was established at Langhill and, up to 1986, cows in this herd were bred at random using semen from one of 50 bulls which entered the studs of either the Milk Marketing Board of England and Wales (MMB) or the Scottish Milk Marketing Board (SMMB) progeny tests in 1976. In 1986 the original control bull panel was replaced by one comprising pure Holstein bulls of about national average genetic merit for kg fat plus protein, to reflect changes in the breed composition of the selection herd.

This study is based on records of milk production, food intake, health and reproduction collected since 1983. Full details of the recording procedures and methods of replacing missing data are given by Simm, Persaud, Neilson, Parkinson and McGuirk (1991). A summary of these procedures is given below.

Feeding and food intake recording

During the housed period cows were offered *ad libitum* a complete diet containing grass silage, wet brewers' grains and a compound balancer meal. Until 1988 all animals were given a relatively high concentrate diet with an annual average concentrate usage of about 2·5 t per cow. From 1988 onwards a proportion of the herd received a lower concentrate diet, with about 1·0 t concentrates fed per cow per annum. Animals were grouped according to stage of lactation and diet type, and for both diet types the ratio of silage to concentrates in the diet was altered when the group had, on average, completed 100 and then 200 days of lactation. Silage dry-matter (DM) proportions averaged about 400, 500 and 600 g/kg for the high concentrate diet and about 650, 750 and 850 g/kg for the low concentrate diet in early, mid and late lactation respectively. Different compound balancer meals were offered in the high and low concentrate diets, with metabolizable energy and crude protein contents in the DM of about 13·0 MJ/kg and 180 g/kg for the high concentrate diet, and 12·6 MJ/kg and 310 g/kg for the low concentrate diet.

Individual animal food intake measurements up to week 38 of lactation were obtained on up to 120 animals per annum, using Calan Broadbent electronic gates. The complete diet was dispensed into individual food bins once daily. The weight of fresh diet offered and refused was recorded on 4 days consecutively each week. Mean daily DM intakes for each week of the study were calculated from the DM analyses on the food offered and the refusals. In addition to the complete diet, a fixed amount of concentrate (0·8 or 1 kg per head per day) was given in the parlour to encourage entry of the cows.

Milk yield and fat and protein concentrations

Cows were milked twice daily. Milk yields were recorded weekly, as the sum of Tuesday afternoon and Wednesday morning yields. Concentrations of fat and protein in the milk were measured fortnightly until 1987/88 after which they were measured weekly.

Calculation of milk returns and input costs

For each animal in each week of lactation, milk returns were calculated and then accumulated over the whole recording period. Similarly total food costs, health costs and reproduction costs were calculated weekly and then accumulated. Although the data were collected over a 7-year period, 1989/90 milk prices and input costs were used throughout. Milk returns were calculated from the individual animal's yield and the average pool price received at Langhill from the SMMB, including a hygienic quality payment. Penalties and premiums for lower or higher butterfat and protein contents were calculated on a weekly basis for individual animals. Seasonality payments for individual cows were not considered in this study.

Food costs were also calculated on a weekly basis for individual animals based on their average weekly DM intake, the composition of the diet in that

Table 1 *Food costs used in calculating margins*

	Cost fresh (£/t)	Dry matter content assumed (g/kg)
Silage	15·00	(actual)
Brewers' grains	15·00	268
Sugar beet pellets/pulp	118·00	884
Chopped treated straw	55·00	(actual)
Molassine meal	153·00	770
Balancer meal		
High forage (1988 onwards)	188·00	870
Low forage (1979-1990)	156·00	870
Parlour concentrates		
pre-1988	115·00	890
1988/89 (malt culms)	88·00	878
1989/90	100·00	867

particular week of the study, and the cost of the diet ingredients as shown in Table 1. The cost of the fixed allocation of parlour concentrates was also included.

Since the start of the Langhill project detailed health records have been kept for all cows. Individual cow health costs were calculated over the food intake recording period and items included were as follows: (i) A call-out charge where a vet was involved. (These were provided by the University of Edinburgh Large Animal Practice and took into account the typical time needed to attend to a particular health event. A standard call-out charge of £14 was assumed for most events.) (ii) The cost of drugs or materials used, by the vet or farm staff. (Values were obtained from the Index of Veterinary Specialities (Anonymous, 1990), plus a 100% mark-up.) (iii) The lost revenue on milk withdrawn as a result of drug treatment. (In each case the milk yield and composition of the affected cow in the appropriate week were used to calculate the value of milk withdrawn for the relevant time period.)

As for health costs, there were several components to reproduction costs. (i) A service cost of £7 for the first service and £6 for repeat services (based on actual SMMB charges in 1989/90). (ii) Semen costs of £20 for the first and second services, and £17 for subsequent services. (It could be argued that lower costs should have been assumed for lower genetic merit cows. However, the aim of this study was to examine the economic effects of *biological* differences between cows of different genetic merit including differences in fertility, and not the effects of different *management* decisions for these different cows. The purpose of including a semen charge was to account for the variable *number* of services required, and hence the assumption of standard semen prices seems most appropriate. A semen storage charge of £0·12 was added for all second inseminations, and £0·28 for third and later inseminations.) (iii) A pregnancy diagnosis (PD) charge of £2 per PD was included, based on the actual number of PDs performed on the individual cow. (iv) A cost for prolonged calving intervals of £3 per day in excess of 365 days from the calving at which food intake recording commenced. (This figure was based on the results of Esslemont and Peeler (1993) from extensive 'Daisy' herd health and fertility recording service data, and includes the net effect of reduced annual milk and calf income and savings in concentrate costs.) Analyses of reproduction costs excluded those animals used as embryo transfer donors or recipients and those which did not have a subsequent calving record (e.g. cows previously designated as culls and not served).

From these returns and costs individual cow margins over food costs (MF), margins over food and health costs (MFH), and margins over food, health and reproduction costs (MFHR) were calculated.

Statistical methods

The main purpose of this study was to estimate the change in economic performance of animals with increasing predicted genetic merit for milk solids production. This was done using residual maximum likelihood (REML; Patterson and Thompson, 1971) in the GENSTAT computer program (version 5.2, GENSTAT 5 Committee, 1989). The statistical model used was:

$$Y_{ijklm} = \mu + a_i + C_j + M_k + L_l + F_m + b_1A + b_2H + b_3PI + e_{ijklm}$$

where Y_{ijklm} = record with effects as follows: μ = overall mean; a_i = random effect of cow; C_j = fixed effect of year of calving (1983 to 1989); M_k = fixed effect of month of calving (September, October, November); L_l = fixed effect of lactation number (1, 2, 3 to 5 and 6 to 9); F_m = fixed effect of feeding system (high or low concentrate); b_1A = linear regression on age at calving; b_2H = linear regression on % Holstein; b_3PI = linear regression on pedigree index (PI) for kg fat plus protein; e_{ijklm} = random error term.

Preliminary analysis showed that genetic line (selection or control) was not significant after fitting PI, so line was not included in the model. Since some cows had more than one lactation included in the data, cow identity was fitted as a random effect in appropriate REML analyses.

The records considered in this study were: (i) margin over food costs (MF) for 38 weeks of lactation (milk returns – food costs); (ii) margin over food and health costs (MFH) for 38 weeks of lactation (milk returns – food and health costs); and (iii) margin over food, health and reproduction costs (MFHR) for 38 weeks of lactation (milk returns – food, health and reproduction costs for the relevant time period).

PIs in this study were calculated from sires' and maternal grandsires' estimated transmitting abilities (directly from UK national evaluations or from converted foreign proofs) as:

½ (sire's Improved Contemporary Comparison
(ICC) for kg fat + protein)
+ ¼ (maternal grandsire's ICC for kg fat + protein).

PIs have two advantages over some other estimates of genetic merit. Firstly, they are virtually independent of production information collected within the individual herd, and hence problems of autocorrelation are avoided. Secondly, they can be calculated for animals of both sexes from conception onwards, and provide a valuable early selection tool.

Results

Table 2 shows the means, standard deviations and ranges for milk returns and the main costs of production. A very wide range in costs and margins is apparent. All distributions appeared normal, except those for health and reproduction costs which were approximately hyperbolic. Transformation of these two components was not attempted since MFHR was normally distributed.

Table 2 *Means, standard deviations and ranges of pedigree indexes, milk returns, food, health and reproduction costs and margins over these costs*

	Mean	s.d.	Min.	Max
Heifers (no.=94)				
Pedigree index (kg fat + protein)	15·0	10·1	−14·4	+31·4
Milk returns (£)	1179·0	200·7	785·6	1667·0
Food costs (£)	533·7	60·0	353·1	650·7
Health costs (£)	17·4	30·2	0·0	163·2
Reproduction costs (£)	169·8	150·7	29·0	665·8
Margin over food costs (£)	645·1	181·2	232·1	1078·0
Margin over food health and reproduction costs (£)	457·8	223·1	−165·8	959·0
All animals (no.=302)				
Pedigree index	11·1	10·1	−14·4	+31·4
Milk returns (£)	1331·0	252·2	763·9	2078·0
Food costs (£)	577·1	74·8	353·1	776·4
Health costs (£)	33·3	44·2	0·0	253·4
Reproduction costs (£)	140·0	143·2	29·0	969·8
Margin over food costs (£)	754·2	218·5	138·5	1438·2
Margin over food health and reproduction costs (£)	580·9	249·3	−165·8	1283·9

Table 3 *Repeatabilities of milk returns, food, health and reproduction costs, and margins over these costs*

	Repeatability
Milk returns	0·63
Food costs	0·67
Health costs	0·21
Reproduction costs	0·31
Margin over food costs	0·61
Margin over food and health costs	0·54
Margin over food, health and reproduction costs	0·37

Table 3 shows the repeatabilities of the main returns, costs and margins. Repeatabilities were highest for milk returns, food costs and the margin between them. These estimates of repeatabilities may be slightly biased as a result of including PI as a covariate in the statistical model. However estimates of repeatabilities from a model excluding PI were all within 0·03 of the values shown.

Table 4 shows the regressions of returns, costs and margins on PI. Regression coefficients did not differ significantly between feeding systems. Regressions of milk returns on PI were positive and significantly

Table 4 *Regression coefficients (b) and standard errors (s.e.) for regressions of milk returns, food, health and reproduction costs and margins over these costs on pedigree index (PI) for kg fat plus protein*

	b†	s.e.
Heifers		
No. of animals	94	
Milk returns	6·58	2·47
Food costs	1·23	0·49
Health costs	−0·14	0·39
Reproduction costs	2·99	2·01
Margin over food costs	5·37	2·30
Margin over food and health costs	5·51	2·29
Margin over food, health and reproduction costs	2·52	3·03
All animals		
No. of lactations	302	
Milk returns	8·10	2·08
Food costs	1·32	0·48
Health costs	0·27	0·36
Reproduction costs	−0·13	1·30
Margin over food costs	6·78	1·87
Margin over food and health costs	6·48	1·85
Margin over food, health and reproduction costs	6·47	2·08

† All regression coefficients are expressed in £ per kg PI for fat + protein.

Table 5 *Sensitivity of regressions of margin over food, health and reproduction costs (MFHR) on pedigree index (PI) to changes in food, health and reproduction costs (all animals)*

	Regression coefficient (£ per kg PI) for percentage change in costs (0 is 1989/90 value)				
	−50%	−25%	0	+25%	+50%
Costs changed					
Food costs	7·1	6·8	6·5	6·2	5·9
Health costs	6·6	6·5	6·5	6·4	6·4
Reproduction costs	6·4	6·4	6·5	6·5	6·6

different from zero in all data sets ($P < 0{\cdot}01$ to $P < 0{\cdot}001$). Regressions of food costs on PI were positive, and significantly different from zero ($P < 0{\cdot}05$ to $P < 0{\cdot}01$), but were much smaller than those for milk returns (0·16 to 0·18 of the corresponding milk returns coefficient). Regressions of health costs on PI were all close to zero. However, that for reproduction costs was positive and approaching statistical significance in the heifer data set. In the pooled data, the regression of reproduction costs on PI was negative, (but not significantly different from zero). Regressions of MF and MFH on PI were positive and significantly different from zero in all cases ($P < 0{\cdot}05$ to $P < 0{\cdot}01$). The same was true for MFHR in the pooled data.

It is important to know how sensitive these results are to changes in the relative value of returns and the various components of overall costs. Therefore the analyses described above were repeated with ±0·25 and ±0·50 changes in food, health or reproduction costs, with milk returns held constant. The results are shown in Table 5. Regression coefficients changed by only £0.10 per PI point with 0·50 proportional changes in health or reproduction costs, and by only £0·60 with 0·50 proportional changes in food costs.

Discussion

There is a need for research on more comprehensive breeding goals and criteria in dairy cattle because of the restriction on ouput in many western countries, which makes cost reduction a more important route for improving overall profitability. Such research is also needed because of the renewed interest in centralized breeding schemes which facilitate more comprehensive recording, and because of increasing concern for the health and welfare of farm animals.

Most studies of more comprehensive breeding goals and criteria in dairy cattle can be classified as being (i) theoretical or modelling studies (e.g. Rogers, van Arendonk and McDaniel, 1988; Keller and Allaire, 1990), or (ii) based on analyses of very large data sets from field records, but with a limited number of traits (e.g. Balaine, Pearson and Miller, 1981; Tigges, Pearson and Vinson, 1986) or (iii) based on analysis of a much smaller number of records, from experimental herds, but with a more comprehensive set of traits recorded (as in the present study), or a combination of (i) to (iii). Most studies of the second type have been based primarily on production and herdlife, with food costs accounted for as a function of milk or component production (e.g. Tigges *et al.*, 1986) or of milk and component production and live weight (e.g. Balaine *et al.*, 1981). In contrast, the present study was based on actual measures of food intake and costs derived from these.

In most studies milk or milk solids production was usually the most important predictor of overall profitability (e.g. Andrus and McGilliard, 1975; Balaine *et al.*, 1981 and other studies reviewed by Allaire and Thraen, 1985). However in the first two of these studies mastitis treatment costs were also important predictors of profitability. Herdlife is usually an important predictor of profitability also (Allaire and Thraen, 1985). However the value of herdlife may be over-emphasized as a result of the positive correlation between production and herdlife (see for example the review of Burnside, McClintock and Hammond, 1984) or as a result of ignoring more rapid genetic improvement resulting from shorter generation intervals (van Arendonk, 1991). In the present study herdlife was not accounted for explicitly — some animals had several lactations represented, but margins were calculated as the difference between milk returns and major costs in single lactations. However, this positive correlation between production and herdlife, the relatively high repeatabilities for margins reported here, and the high repeatabilities of milk production traits and food intake (e.g. 0·63 to 0·67, Persaud, 1990) — the two most important components of margins in this study — mean that similar results are expected when herdlife is accounted for. In the present study some returns and costs, such as calf value, cull values, culling costs, lost opportunity costs (van Arendonk, 1991) and rearing costs were not included in calculation of margins. This implied that these costs and returns do not differ amongst cows of different genetic merit. This is probably not true across strains of black and white dairy cattle (for example, some aspects of the growth and carcass quality of British Friesian *v.* Holstein Friesian animals differ — see Hitchings, 1983; Baber, Rowlinson, Willis and Chalmers, 1984) but evidence on relationships with genetic merit within strains of high-yielding dairy cattle is scarce.

In contrast to most earlier studies, this study used individual food intake records, rather than predicted values (and animals were given food *ad libitum*). Using predicted intake does not allow for variation between animals in the relationship between intake and milk production (or other independent variables), nor does it allow for different patterns of depletion and repletion of body reserves. The present approach allows for such variations, albeit only in the 38-week period recorded. The relationships between intake or body state change and genetic merit are implicitly assumed to be constant in the unrecorded period. Tissue catabolism makes an important contribution to energy requirements for milk production, and appears to be particularly important in genetically higher yielding cows (e.g. Custodio, Blake, Dahm, Cartwright, Schelling and Coppock, 1983; Grainger, Davey and Holmes, 1985). It is therefore important to check whether any bias has been introduced into the comparison of cows of different genetic merit, because of the use of part lactation records. Persaud (1990) examined the relationships between body weight or body-weight change and PI in a subset of the data used here. He reported a regression coefficient of –0·13 (±0·09) kg live-weight gain between weeks 1 and 38 of lactation per kg PI for fat plus protein. This was not significantly different from zero and probably reflects the opportunity for most cows in his study to replenish catabolized tissue by week 30 of lactation, because of *ad libitum* feeding of a high concentrate diet. However, it is still worth examining the implications of small differences in body size or state at the end of the 38-week recording period. The most direct approach is to estimate the cost of food required for higher merit cows to replenish the assumed 0·13 kg difference in weight change per kg PI for fat plus protein. (Recent unpublished results from Langhill show that higher genetic merit cows, especially those on a low concentrate diet, maintain slightly lower condition scores throughout the production cycle, over successive years. Hence, accounting for the cost of attaining similar body state may be a hypothetical exercise.) The difference in mean PI of cows in the selection and control lines in this study was around 20 kg fat plus protein. Hence, a difference of about 2·6 kg live weight would be expected at 38 weeks of lactation, based on Persaud's regression coefficient. To replenish this live weight would require approximately 10·6 kg DM (Agricultural Research Council, 1980) around 0·2% of the total intake over the whole recorded period. Accounting for this predicted difference in live weight would reduce the regression coefficients presented earlier by £0·06 per kg PI (about 1%) — insufficient to affect any of the conclusions drawn.

As expected from the results of farm surveys (e.g. Milk Marketing Board, 1990) food costs were the major variable costs in the present study. On average they accounted for proportionately 0·77 of the total costs considered, with reproduction and health costs accounting for the remaining 0·19 and 0·04 respectively. The very wide range between animals in these costs and MF, and MFH and MFHR was surprising. Since these margins are linear combinations of traits, the most important of which are moderately heritable, then the margins themselves are expected to be moderately heritable (with the repeatabilities estimated here being an upper limit for the heritabilities). This, together with the high variation, suggests considerable scope for genetic improvement. In a related study to the present one, we examined PI, live weight and linear type traits as predictors of these margins (Veerkamp, Simm and Persaud, 1994) and concluded that live weight and linear type traits are of potential value as selection criteria in future breeding programmes to improve margins.

Table 4 shows regression of MF, MFH and MFHR on pedigree index. In general for the pooled data, which is more reliable because of the higher number of animals, the financial advantage to high PI animals remains fairly constant, even when health and reproduction costs are included. For heifers, the picture appears to be a little different, with the financial advantage diminishing when reproduction costs are included. In these data the higher reproduction costs are mainly a consequence of longer calving intervals in the high pedigree index heifers. Similar observations have been made by Hageman, Shook and Tyler (1991) and by Bonczek, Richardson, Moore, Miller, Owen, Dowlen and Bell (1992). As more records on health are accumulated, greater emphasis will be given to studying possible relationships between genetic merit and incidence of specific diseases. However, at this stage, there appears to be no overall difference in total health costs. Similar conclusions were reached in a large US study (White, Miller and Wilcox, 1977) but this is in contrast to the results of Shanks, Freeman, Berger and Kelley (1978), and some of the studies mentioned earlier which report positive genetic correlations between the incidence of mastitis and production. The results in the present study may be a consequence of (i) a counterbalancing effect of other diseases occurring less frequently in high genetic merit animals, or more likely (ii) a result of the relatively small sample size in this study, or (iii) true differences between the populations of animals studied here and in some other reports, or an interaction with the particular management systems employed.

The results of the sensitivity analysis indicate that even with quite wide variations in the relative costs of food, health and reproduction, the relationship between genetic merit and margins is expected to remain very stable. Similar conclusions, though in a different context, were reported by Balaine *et al.* (1981), who showed high correlations amongst various indexes of profitability when using three different sets of costings spanning a 15-year period. Also, Beard (1987) reported that the efficiency of index selection exceeded 95% when food costs were varied in the range –100% to +37·5% of their original value. However in that study efficiency of selection dropped more markedly as the food costs increased by more than 37·5%. In practice it is relatively easy to alter the relative economic values of traits in the selection goal, in the light of new information on likely future trends; it is the genetic relationships amongst components of profitability, and predictors of it, which are more difficult to estimate. More work is needed in this area before more comprehensive and reliable indexes of overall profitability can be constructed. However, the results in the present study indicate that, within the range of genetic merit currently available in the UK, selection for higher PI for kg fat plus protein, (or closely related measures) is likely to lead to improved margins over food, health and reproduction costs.

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Biological basis of sustainable animal production

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Energy and protein utilization of cows of high and low genetic merit for milk solids production on a high and low input diet

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Summary

More efficient energy and protein utilization by dairy cows will contribute to more sustainable dairy production systems. This study compared the energy and protein efficiencies of cows of genetic control and selection lines - for fat plus protein yield - on two diets with different proportions of concentrate. Comparisons of diet effects on efficiency were problematic. There were clear differences between lines in gross energetic and protein efficiencies, with the selection line being more efficient on both diets. Apparent differences in net energetic efficiencies were in favour of the selection line.

Keywords: dairy cows, gross efficiency, residual feed intake, selection lines, food intake

Introduction

An increase in energy efficiency and protein efficiency (output/input) of dairy cows results in less waste (e.g. heat and manure) per unit output and less cost per unit output. Therefore, more efficient energy and protein utilization of dairy cows will contribute to more sustainable dairy production systems.

Gross efficiency is defined as energy in milk divided by energy intake (Brody, 1945) and is most commonly used to express energetic efficiency of animals. Korver (1988) discussed the limitations of gross efficiency for selection and reviewed variation in several biological components of gross efficiency. Hence, it is normally assumed that the metabolizable energy intake (ME) is split between maintenance, lactation and body tissue, with net efficiencies km, kl and kf, respectively.

Taylor et al. (1986) proposed the hypothesis, on the basis of presumed inter-breed relationships, that selection for milk yield will lead to increased gross efficiency, but also to more ME being needed for maintenance (decrease km). As a consequence, the advantage in gross efficiency of high-genetic-merit cows would decrease when such animals are not yielding their full potential.

Other studies (e.g. Grieve et al., 1976; Custodio et al., 1983) have indicated that the increase in gross energetic efficiency during (part) lactations of high-genetic-merit cows is not due to better utilization of food, but rather to a higher degree of body tissue catabolism and to a simple dilution of maintenance. This suggests that observed advantages in gross efficiency for high-genetic-merit animals could disappear (i) when gross efficiency was measured over the whole lifetime of a cow or (ii) when part lactation measurements of gross efficiency were corrected for body tissue catabolism (or residual food intake was used). Also, under more extensive systems, the rate of body tissue mobilization and the amount of mobilizable body tissue might become critical and high-genetic-merit animals might not be able to maintain their advantages in gross efficiency.

The aim of this study was to compare energy and protein utilization of cows of high and low genetic merit on two diets with different proportions of concentrate.

Material and methods

Animals and recording

Records were obtained from cows housed and managed at the Scottish Agricultural College/University of Edinburgh Langhill Dairy Cattle Research Centre. All cows involved in the study were Holstein-Friesians, kept indoors in conventional cubicle housing from calving to July and offered complete mixed diets *ad libitum*. In each of the 4 years calving began early in September and all of the animals used calved between September and January in any year. More details about animals and recording have been given by Simm et al. (1993).

The herd comprises two genetic groups - a selection line S and a control line C. Since 1973 the selection line has been bred to bulls with the highest genetic merit for combined fat and protein yield available in the UK. The control animals have been bred to bulls of about national average genetic merit for fat plus protein yield, since 1976. The selection line is in the top 1% herds of the UK, ranked on average genetic merit for F + P, and genetic merit of the control line has increased only slightly since 1976.

Two complete diets were offered *ad libitum*. The diets were designed to achieve, over a full lactation, proportions (in total DM) of concentrates, brewer's grains and silage of 20:5:75 (LC) and 45:5:50 (HC), with annual average concentrate intakes of about 1.0 and 2.5 tonnes per cow, respectively. Animals were grouped according to stage of lactation and diet type, and for both diet types the proportion of the dry matter from silage in the diet was altered when the group had on average completed 100 and 200 d of lactation. Different compound balancer meals were included in HC and LC, with metabolizable energy and crude protein contents in the concentrate dry matter of about 13.0 $MJ.kg^{-1}$ and 180 $g.kg^{-1}$ for HC and 12.6 $MJ.kg^{-1}$ and 310 $g.kg^{-1}$ for LC.

The complete diets were dispensed into individual food bins, once daily. The weights of fresh diet offered and refused were recorded on 4 d consecutively each week. Daily samples from the different diets (early, mid and late; LC and HC) and refusals were analysed for dry matter. Daily samples of each diet were bulked to monthly samples and analysed to determine chemical composition. The LC and HC diets averaged an ME content of 11.55 $MJ.kg^{-1}$ and 11.90 $MJ.kg^{-1}$ and a crude protein content of 190 $g.kg^{-1}$ and 182 $g.kg^{-1}$ (DM basis).

Cows were weighed and condition scored once a week after milking. Condition scoring was based on Lowman et al. (1976). This system defines five scores, 1-5 (lean-fat), and describes each score in terms of the amount of tissue cover over the transverse processes of the lumbar vertebrae and around the tail head.

calculated as the average of the weekly records accumulated over 26 weeks of lactation, respectively. Fat (F%) and protein (P%) percentages were calculated as the average of the weekly percentages weighted by the weekly milk yields. Energy in the milk (LE) was based on Tyrrell & Reid (1965): $LE = (0.384 \times F\% + 0.223 \times P\% + 0.199 \times L\% - 0.108) \times MY$, where LE is milk energy (MJ) and F%, P% and L% are fat, protein and lactose percentages in the total milk yield (MY). Gross energetic efficiency (ENEF) was calculated as LE (MJ)/ME intake (MJ). Gross protein efficiency (PROTEF) was calculated as milk protein yield (kg)/CP intake (kg). Mean live weights (ALW) and condition scores (ACS) were calculated as the averages of the 26 weekly measurements. Liveweight changes (LWCH) and condition score change (CSCH) were the LW or CS measurements in week 26 minus those in week 3.

Estimates for energy requirements were for maintenance: $MN\ (MJ.d^{-1}) = 0.53 \times (ALW/1.08)0.67 + 0.0091 \times ALW$ and for live weight change, $LWCH = 27.36 \times (LW26 - LW3)$ based on AFRC (1991).

Analysis

The Genstat residual maximum likelihood (REML; Patterson & Thompson, 1971) option (Genstat 5 Committee, 1989) was used to estimate DIET, LINE and DIET x LINE effects. The model included fixed effects (lactation (1, 2-4 and >4), year (1988, 1989, 1990, 1991) and month of calving (Sept, Oct, Nov and Dec), covariates for Holstein percentage and age of calving and a random cow effect to account for covariance between subsequent lactations.

Energetic efficiencies (km, kl and kf) were estimated as partial regressions of ME intake (MEI) on MN, LE, LWCH, all expressed in MJ per day. In this regression model there was no constant. Non-significant interactions between the partial regression coefficients and DIET and LINE were 'backwards eliminated'.

Residual food intake was defined as the ratio = actual ME intake/estimated ME intake. The estimated ME intake was based on measured MN, LE and LWCH adjusted for different values for km, kl and kf. The values for km, kl and kf came from three different sources: (i) AFRC 1991 (residual intake derived is denoted as $RATIO_{AFRC}$); (ii) multiple regression of MEI on MN, LE and LWCH ($RATIO_{data}$); (iii) multiple regression of MEI on MN, LE and LWCH, plus interactions with condition score ($RATIO_{data+}$). DIET and LINE differences in MEI, estimated MEI, MN, LE, LWCH and the three different RATIOs were estimated with the same REML model as before.

Results

Estimated group means and the number of records in each group are given in Table 1. MILK and F + P yield showed positive line effects for the selection line, but DMI was not significantly higher for selected animals. Selection line animals lost more condition (CSCH) and gained less weight (LWCH) than controls.

DIET effects were not present for CSCH, ACS and ALW. The selection line showed higher gross energetic efficiency and higher gross protein efficiency on both diets. The high-concentrate diet had higher PROTEF than the low-concentrate diet, but there was

for any of the traits. Significance levels for LINE (S is selection and C is control) and DIET (HC and LC, high and low concentrate) are based on approximations of the standard error given by REML (***, <0.01; **, <0.05)

	S-HC	C-HC	S-LC	C-LC	DIET	LINE
N	102	86	117	78		
	mean	mean	mean	mean		
Milk (kg)	5660	4912	4693	4081	***	***
F%	4.12	4.13	4.46	4.42	***	
P%	3.07	3.16	3.00	3.07	**	
F + P (kg)	405	357	349	303	***	***
DMI (kg)	3447	3345	3018	2914	***	
ALW (kg)	600	594	593	587		
ACS (0-5)	2.47	2.58	2.39	2.55		**
LWCH (LW 26-LW 3)	33	55	13	30	***	**
CSCH (CS 26-CS 3)	-0.23	-0.07	-0.23	-0.14		**
PROTEF (kg/kg)	0.28	0.25	0.25	0.22	***	***
ENEF (MJ/MJ)	0.43	0.39	0.44	0.39		***

Table 2. Estimated values for k_m, k_l and k_f including significant interactions between k's and DIET and between k's and LINE (total model; $R^2 = 0.64$)

	S-HC	C-HC	S-LC	C-LC
k_m	.37	.34	.56	.50
k_l	.89	.89	.70	.70
k_f	2.0	2.0	2.0	2.0

Table 3. Corrected means for ME requirements ($MJ.d^{-1}$) based on MN, LE and LWCH and AFRC values for k's. MEI is the real ME intake and diet and line effects on residual food intake, expressed[a] as $RATIO_{AFRC}$, $RATIO_{DATA}$ and $RATIO_{DATA+}$ (DIET * LINE was not significant and excluded from the model)

	S-HC	C-HC	S-LC	C-LC
MN	58	58	57	57
LE	150	131	129	112
LWCH	9	15	4	8
Total	217	204	190	177
MEI	225	219	191	185
$RATIO_{AFRC}$	1.04	1.08	1.01	1.05
	LINE S	DIET HC		
$RATIO_{AFRC}$	-0.035 ***	0.033 ***		
$RATIO_{DATA}$	-0.034 ***	0.060 ***		
$RATIO_{DATA+}$	-0.034 ***	0.063 ***		

[a] Values for km, kl and kf are respectively, (i) 0.73, 0.64, 0.61 (AFRC; $R^2 = 0.57$), (ii) 0.50, 0.73, 1.04 (DATA; $R^2 = 0.59$), (iii) 0.42, 0.71, 1.3 (DATA+; $R^2 = 0.61$).

Table 2 shows estimated net energetic efficiencies for maintenance, lactation and liveweight changes, after backwards elimination. Estimates for km were higher for the low concentrate diet and for the selection line and estimates for kl were higher on the high-concentrate diet. Estimates for kf were greater than 1.0 and therefore not realistic.

About two-thirds of the ME requirements (averages varying between 112 MJ.d^{-1} for C-LC and 150 MJ.d^{-1} for S-HC) was needed for lactation energy (LE) (Table 3). The four groups consumed more ME than was predicted on the basis of these AFRC estimates. From Table 3 it also appears that residual food intake for the selection line, independent of the method to derive k values, was about 3.5% lower than residual food intake of the control line. Residual food intakes appeared to be higher on the high-concentrate diet.

Discussion

This study showed that in gross terms the selection line had higher protein and energy efficiencies than the control line. This advantage was present on both the high- and low-concentrate diets (HC and LC, respectively). Gross protein efficiency was higher on HC than on LC, as a consequence of a slightly higher P% and a much lower ratio of CP to ME in the diet.

Taylor et al. (1986) suggested that increased genetic merit for milk production would lead to increased scaled maintenance costs. As discussed earlier, increased maintenance costs are expected to reduce the advantage in gross efficiency of the selection line on the low-concentrate diet, and this was not observed. Estimates for net efficiencies suggested, if anything, that the selection line had even lower maintenance costs.

For all four groups, ME intakes were higher than the requirements based on the AFRC k values and the measured MN, LE and LWCH. Experimental losses under practical circumstances (e.g. diet spillages and exercising of the cows) compared with calorimetric experiments are likely to be amongst the contributing factors. Alternatively the ME contents of the diets could have been estimated with consequential effects on the animals' performances.

We expressed residual food intake as a ratio, unlike Luiting (1990) who defined residual food intake as the absolute difference = actual MEI - estimated MEI. In our study we were interested in possible differences in net efficiencies between distinct groups and a ratio (like the k values) seemed more realistic. Although others (e.g. Grieve et al., 1976; Custodio et al., 1983) have suggested that the observed increase of energetic gross efficiency in high-genetic-merit animals was only due to increased tissue mobilization during the period of measurement, residual intakes in this study were 3.5% lower for the selection line than for the control line, on both diets. Obviously, this was under the assumption of the same k's and homogeneous MN, LE and LWCH between the lines. Heterogeneous ALW (used to calculate MN) and LWCH between the lines is likely, given the differences in ACS, ALW, CSCH and LWCH (Table 1) between the lines. The effect, however, was small when calculating residual food intake, because including the interaction between MN and ACS, and between LWCH and CSCH, had no effect on the observed difference in residual intake between the two lines.

Lactation energy (LE) had been calculated as the heat of combustion value of milk.

k for LE. Within diets the effect might be small, because there was no significant difference in F% and P% observed. However, assuming homogeneous LE between diets is more hazardous; F% is much higher and P% is significantly lower on the low-concentrate diet. Likewise, significant differences between the diets in dry matter intake will result in different gut fills, and therefore it might not be appropriate to assume homogeneous live weights and changes in live weight between the diets. Other important inaccuracies which might affect the comparison between diets come from errors in the estimation of ME. Inaccurate estimation of ME in, for example, silage might bias differences between the two diets. Therefore, comparison of efficiency and residual food intake between high- and low-input diets is difficult.

But on both diets, the results showed clear differences in gross efficiency between the selection and control line, in favour of the high-genetic-merit animals. Observed lower residual food intakes for the selection line indicate that there are apparent differences in one or more of the net energetic efficiencies, also in favour of the high-genetic-merit animals.

Acknowledgements

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Partitioning of dietary nitrogen between body components and waste in young growing pigs [•]

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Summary

Two experiments were conducted to determine the effect of protein and energy intake on (1) protein deposition and nitrogen utilization, (2) partitioning of body protein between edible products and offal, and (3) weights of metabolically active organs. In the first experiment, 90 female pigs were fed at two energy intake levels and 15 protein intakes from 20 to 45 kg. Protein deposition increased linearly with increasing protein intake until a plateau in deposition was reached at 106 and 126 $g.d^{-1}$ at the low and high energy level respectively. Marginal efficiency of utilization of ileal digestible lysine was 0.74 for the two energy levels.
In a second experiment, 24 female pigs were fed a protein- adequate diet at six levels of energy intake ranging from 1.7 times maintenance to *ad libitum*. Protein deposition increased from 70 to 172 $g.d^{-1}$ with increasing feed intake. The proportion of body protein deposited as lean tissue decreased from 0.62 to 0.55 with increasing feed intake. Consequences of these results for a more sustainable animal production are discussed.

Keywords: pig, energy, protein, lysine, deposition, partitioning, excretion, organs

Introduction

In practical pig husbandry, dietary protein is deposited in body tissue with an efficiency of about 30%. Consequently 70% is lost to the environment (Coppoolse et al., 1990). Nutritional research can contribute to increase this efficiency and reduce excretion considerably by improving protein digestibility, protein quality (amino acid pattern) and utilization of absorbed amino acids. On the basis of two experiments this paper discusses various aspects of efficiency of utilization of dietary amino acids, i.e. the effect of protein and energy intake on protein utilization and excretion, on protein partitioning in the body and on individual organs.

The objectives of Exp. 1 were to determine (1) the relationship between intake and deposition of ileal digestible protein and lysine respectively, (2) the utilization of ileal digestible protein and lysine, and (3) the separate effects of protein and energy intake on protein and lysine utilization.
The aims of Exp. 2 were to determine the relationship between energy intake and protein deposition and the effect of energy intake on partitioning of protein in the body. The design and results of these experiments are reported briefly and some consequences for

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Effects of interaction between genotype and feeding system on milk production, feed intake, efficiency and body tissue mobilization in dairy cows

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Effects of interaction between genotype and feeding system on milk production, feed intake, efficiency and body tissue mobilization in dairy cows

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Abstract

The objective of this study was to investigate genotype by feeding system interactions in Holstein-Friesian dairy cows. For this purpose, selection (S) and control line (C) cows, housed and managed at the Langhill Dairy Cattle Research Centre, were offered ad lib. complete mixed diets, with proportions (in total DM) of concentrates, silage and brewers grains of either 20:5:75 (LC) or 45:5:50 (HC), over a full lactation. No significant feeding system × genetic line interactions were observed for a number of traits, describing milk production, feed intake, efficiency and body tissue mobilisation, when compared as treatment means (128 heifer lactations and 249 cow lactations). However, regression coefficients of milk yield ($P<0.01$) and condition score ($P<0.05$) on pedigree index for fat plus protein yield were significantly different between LC and HC. This indicates that G × E might become of importance in the future, with continued selection for fat plus protein yield.

Keywords: Dairy cattle; G × E interaction; Feed intake; Efficiency; Live weight

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1. Introduction

There is a wide range in production circumstances both between and within countries. However, one of the major breeding goals of most dairy farmers, whatever the production circumstances, is to increase profitability. The introduction of quotas on milk production in the EC in 1984 has led to interest in reduced cost systems in some countries. For this reason, the large influx of North American Holstein semen to most EC countries, and also because of the introduction of new breeding schemes involving testing bulls in nucleus herds, investigating genotype × environment (G × E) interactions is particularly important at the present time.

Danell (1982) reviewed several studies in which interactions between feeding regime and sire, production level and sire, and housing system and sire were found to be of no importance. More recently, Van der Werf and Ten Napel (1991) found a genetic correlation for milk traits of 0.78 between high and low yielding herds, and the sire by herd interaction accounted for only 3% of the phenotypic variance. Most previous studies have focussed primarily on milk production traits. In some studies G × E interaction for food intake or efficiency of milk production has been considered when animals were fed according to yield (Richardson et al. 1971; Lamb et al., 1977; Wang et al. 1992), however feeding according to yield makes biological

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interpretation of the results difficult. Studies where animals were not fed according to production have been performed by Korver (1982) and Oldenbroek (1988), but together these studies present a rather confusing view of the positive existence and magnitude of genotype × feeding interactions in dairy cows.

We have been concerned to establish whether the advantages of high genetic merit for milk solids production in a high input system of feeding (Persaud et al., 1990; Simm et al., 1994) in an earlier study from the Langhill Dairy Cattle Research Centre, are maintained under a regime of lower input feeding. Indications that high genetic merit animals might not be able to maintain their advantage under a low input system (hence, a G × E interaction) come from other studies (e.g. Grieve et al., 1976; Custodio et al., 1983), which have indicated that the increase in gross energetic efficiency of high genetic merit cows is not due to better utilization of feed, but rather to a higher degree of body tissue catabolism and to a simple dilution of maintenance. If there was a limit to the rate of tissue mobilization or the amount of mobilisable tissue, high genetic merit cows might lose their advantage on a low input diet, i.e. there could be a genotype by feeding system interaction for production, or for efficiency or for body composition. Because tissue reserves in dairy cows are substantial (e.g. Gibb et al., 1992; Butler-Hogg et al., 1985) it is possible that the use of these reserves in one lactation might buffer high merit animals against nutritional adversity and so diminish interactions in the short term, with these only becoming evident in the longer term (i.e. in subsequent lactations). For these reasons we have established a long-term study of genotype × feed system interactions. In this experiment which started at Langhill in 1988, cows have been offered ad lib. two complete mixed diets, varying in the proportions of concentrate and grass silage.

The objective of this part of the study is to use preliminary records from the Langhill G × E experiment to estimate the effects of genotype by feeding system interaction, within a single lactation, on performance traits and body composition of heifers and cows.

2. Material and methods

2.1. Animals

Records were obtained from cows housed and managed at the Scottish Agricultural College/University of Edinburgh Langhill Dairy Cattle Research Centre. In each year calving began early in September and animals joining the trial all calved between September and January in any year. All cows involved in the study were Holstein-Friesians, kept indoors in conventional cubicle housing from calving to July and offered complete mixed diets ad lib. Through the use of Calan Broadbent electronic gates the extended indoor period allowed measurement of feed offered to, and refused by, individual cows for four days a week, from calving to a minimum of 26 weeks and up to 38 weeks after calving (depending on the calving date of each cow). The data reported here are for performance over the first 26 weeks of lactation, recorded over four consecutive years from 1988–1991 inclusive. Cows were milked twice daily (0500 and 1500 hours) and 0.4 kg concentrates was fed in the parlour at each milking during the housed period.

2.2. Genetic groups

There were two genetic groups: a selection line (S) and a control line (C). Since 1973 S animals have been bred to bulls with the highest genetic merit for kg fat plus protein (F + P) available in the UK. Since 1976 the C animals have been bred to bulls of about national average genetic merit for F + P. For each line every year 4–5 bulls are selected solely on their predicted transmitting abilities (PTA). The bulls are then each used randomly over the cows and heifers in the relevant line. The only exceptions are that a bull is not mated to a close relative and bulls known to cause a high incidence of calving difficulties are not used on heifers. The S bulls were originally selected on their UK proofs, but during the last 15 years predicted transmitting abilities of foreign bulls have been converted to British proofs. In 1986 animals were re-allocated to S and C to balance these lines for average Holstein percentage. Allocation was based on genetic merit for F + P and Holstein percentage. Since the beginning of this experiment heifers were selected on pedigree index (predicted genetic merit, based on pedigree information) and allocated to either the high concentrate (HC) or low concentrate (LC) feeding system. Allocation to the diets was random, except that offspring from the same bull were allocated equally to the two diets (similarly in the first year multiparous cows were allocated equally to the two diets). Cows have been maintained on the same diet in subsequent lactations and the objective is to record at least three lactations from each cow on a single diet. The mean PTAs (on the 1990 base) for fat + protein yield were 4.3 kg (s.d. = 7.7) for the C and 18.8 kg (s.d. = 9.9) for the S animals involved in the study reported here.

2.3. Diets

A complete diet based on grass silage, brewers grains and concentrates, was offered ad lib. to all animals. The feeding systems were designed to achieve, over a full lactation, proportions (in total DM) of concentrates, brewers grains and silage of 20:5:75 (LC) and 45:5:50 (HC). The animals on HC had an annual average concentrate intake of about 2.5 tonnes per cow. The LC animals ate about 1.0 tonnes of concentrate per annum. Animals were grouped according to stage of lactation and diet type. For both feeding systems the proportion of the dry matter from silage in the diet was altered when the group had completed 100 and 200 days of lactation, on average, so that problems of underfeeding in early lactation were minimised but a substantial differential between feeding systems was maintained. Silage dry matter as a proportion of total DM in the diet was designed to average 0.40, 0.50, and 0.60 for HC and 0.65, 0.75 and 0.85 for LC in early, mid and late lactation respectively. Different compound balancer meals were included in HC and LC, with metabolisable energy and crude protein contents in the concentrate dry matter of about 12.9 MJ kg^{-1} and 209 g kg^{-1} respectively for HC and 12.4 MJ kg^{-1} and 310 g kg^{-1} for LC. This was done so that protein, mineral and micronutrient contents of both feed systems were not limiting performance (AFRC, 1991 and 1992) leaving forage:concentrate ratio as the key feed variable. The chemical composition of the diets used in the four years of study reported here is given in Table 1.

2.4. Milk yield and composition

Milk yields and milk composition analyses were recorded once every week, for a morning and afternoon milking separately.

Fat, protein and lactose percentages were calculated as the average from the morning and afternoon sample, weighted by milk production. Average weekly milk, fat, protein and lactose yields for each cow were calculated as the sum of the morning and afternoon yields, multiplied by 7. The energy (MJ) in the milk was estimated from the morning and afternoon samples, using the formula of Tyrrell and Reid (1965):

$$LE = (0.384 \times F\% + 0.223 \times P\% + 0.199 \times L\% - 0.108) \times MY$$

Table 1
Chemical composition of the early-, mid- and late lactation diets*

	HC			LC		
Lactation period (days):	Early 0–100	Mid 100–200	Late 200>	Early 0–100	Mid 100–200	Late 200>
DM (g/kg)	350	327	311	277	265	256
ME(MJ/KG DM)	11.96	11.82	11.56	11.60	11.45	11.15
CP (g/kg DM)	180	180	169	193	183	166
NH_3-N	78	88	90	102	89	97
ADF	218	240	265	254	276	308
NDF	370	412	445	405	450	493
AHEE	61	61	64	52	55	58
pH	4.3	4.4	4.4	4.3	4.2	4.2

*All values per kg DM values indicated. DM = g dry matter/kg diet; ME = metabolic energy (MJ) (see text for details); CP = crude protein (g); NH_3-N = ammonia N (g) per kg total N; ADF = acid detergent fibre; NDF = neutral detergent fibre; AHEE = acid hydrolysed ether extract.

Table 2
Structure of the data set (data are the number of records for each category)[1]

Group[2]:		Month of calving:		Year of calving:		Lactation number:	
C-LC	74	Sept	118	1988	83	1	128
S-LC	117	Oct	94	1989	78	2—3	157
C-HC	84	Nov	102	1990	110	>3	92
S-HC	102	Dec	63	1991	106		

Number of cows: 204.
Number of records[1]: 377.

[1] 1 record = data for one cow in one lactation.

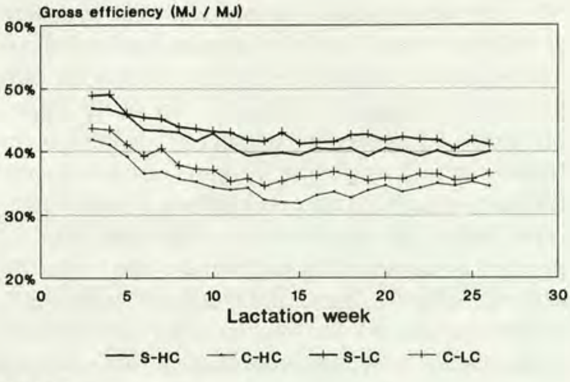
[2] C and S are the control and selection line on the high and low concentrate diets (HC and LC respectively).

Table 3
Estimates for the mean effects of genetic line and feeding system, corrected for fixed effects and the covariance of repeated lactations of the same cow (records are up to 26 weeks of lactation)

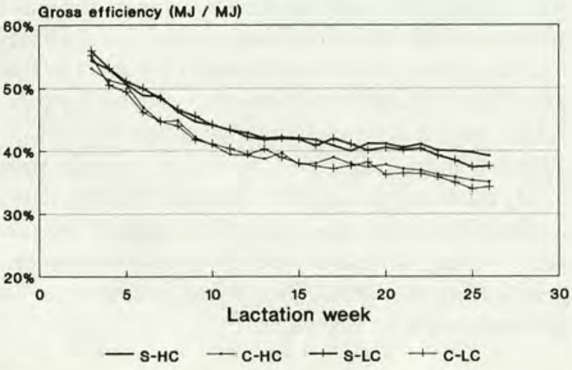
Cows only, ($N=249$)	S-HC[1] mean	C-HC mean	S-LC mean	C-LC mean	s.e.d.[2]	Diet	Line	Line × Diet
Milk (kg)	6123	5425	5031	4533	166	**	**	–
F%	4.10	4.11	4.50	4.37	0.13	*	–	–
P%	3.05	3.12	3.02	3.01	0.05	*	–	–
F+P (kg)	436	391	375	334	12	**	**	–
DMI (kg)	3648	3474	3232	3099	87	**	–	–
ENEF (%)	43.6	40.9	43.9	40.6	1.2	–	*	–
PROTEF (%)	28.1	26.7	24.7	23.2	0.7	**	*	–
ALW (kg)	633	614	622	612	11	–	–	–
ACS	2.43	2.56	2.35	2.52	0.08	–	*	–
GF (kg)	109	104	100	96	3	**	–	–
Lipid (kg)	132	136	126	135	7	–	–	–
LFEBW (kg)	393	374	396	381	6	–	*	–
Heifers only, ($N=128$)	S-HC mean	C-HC mean	S-LC mean	C-LC mean	s.e.d.	Diet	Line	Line × Diet
Milk (kg)	4769	3962	3924	3234	147	**	**	–
F%	4.09	4.06	4.42	4.33	0.13	*	–	–
P%	3.11	3.22	3.01	3.14	0.05	–	*	–
F+P (kg)	343	286	290	240	10	**	**	–
DMI (kg)	3096	3044	2614	2512	72	**	–	–
ENEF (%)	40.6	34.3	42.6	36.3	1.3	–	**	–
PROTEF (%)	26.2	22.9	23.8	21.3	0.8	*	**	–
ALW (kg)	537	552	535	530	10	*	–	–
ACS	2.52	2.65	2.48	2.60	0.06	–	*	–
GF (kg)	93	91	81	78	2	**	–	–
Lipid (kg)	116	127	116	123	5	–	–	–
LFEBW (kg)	329	334	338	330	6	–	–	–

[1] C and S are the control and selection line on the high and low concentrate diets (HC and LC respectively).

[2] Standard error of the differences (s.e.d.) is the average of the 6 approximate s.e.d.'s. Approximated significance levels for Line, Diet and Line × Diet effects are specified as: * < 0.05; ** < 0.01.

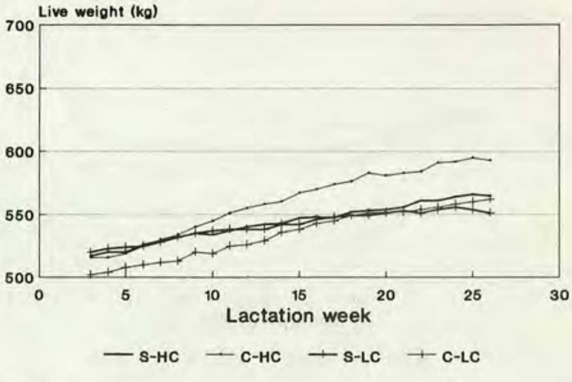


Heifers



Cows

Fig. 1. Mean gross energetic efficiency during lactation, for selection (S) and control (C) line heifers and cows, on high- and low concentrate diets (HC and LC, respectively).



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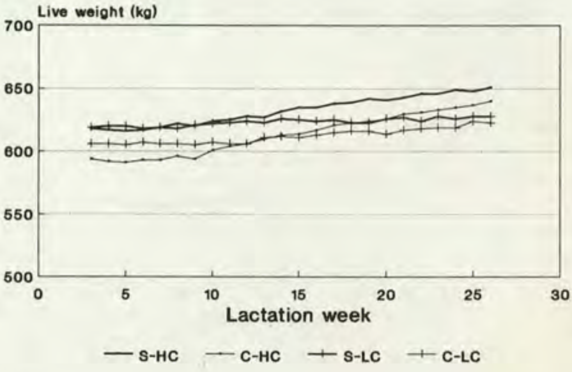


Cows

Fig. 2. Mean live weight during lactation, for selection (S) and control (C) line heifers and cows, on high- and low concentrate diets (HC and LC, respectively).

LE = milk net energy (MJ); F%, P%; L% = fat, protein and lactose percentage and MY = milk yield (kg)

2.5. Feed intake and diet composition

Heifers were trained before calving to use individual electronic feeding gates. The complete diet was dispensed into individual feed bins, once daily. The weights of fresh diet offered and refused were recorded on 4 days consecutively each week. Daily samples from the different diets (early, mid and late lactation; HC and LC) and daily samples from refusals were analysed for dry matter. Each daily intake was calculated as:

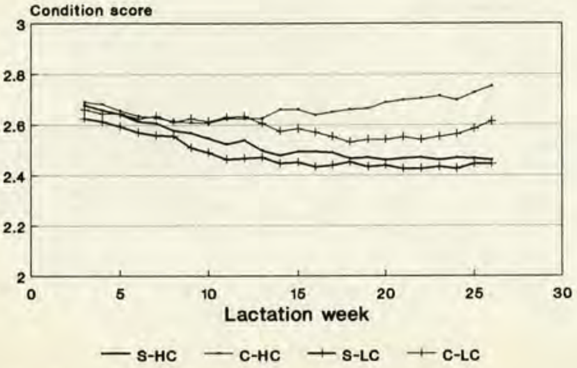
$$DMI = (FF \times DMFF) - (FR \times DMFR)$$

DMI = dry matter intake (kg); FF, FR = Feed offered and feed refused; DMFF, DMFR = Dry matter proportion of feed offered and refused.

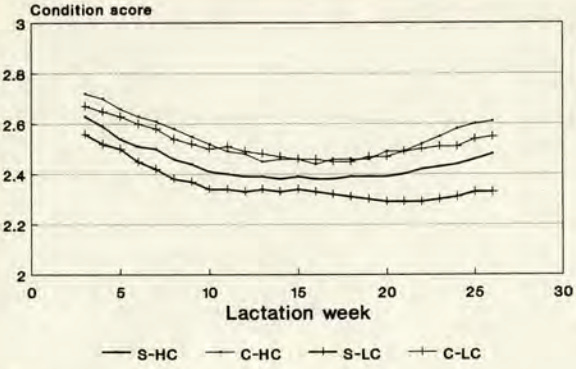
Daily samples of each diet were bulked to monthly samples and analysed to determine chemical composition. The estimated metabolisable energy content (ME MJ kg dry matter) was based on the summation of the estimated ME contents of the different dietary components (Thomas et al., 1988). The ME of silage was based on in vitro digestibility, and the ME contents of the balancer meal and brewer grains were estimated with neutral cellulase gammanase digestibility (NCGD) incubation techniques.

2.6. Live weight and condition score

Cows were weighed and condition scored within 24 hours post calving and thereafter once a week after



Heifers



Cows

Fig. 3. Mean condition score during lactation, for selection (S) and control (C) line heifers and cows, on high- and low concentrate diets (HC and LC, respectively).

milking. Condition scoring was based on a system used by Russel et al. (1969) in sheep and further adapted for cattle by Lowman et al. (1976). This system defines 6 scores 0–5 (with increasing score indicating increasing fatness), and describes each score in terms of the amount of tissue cover over the transverse processes of the lumbar vertebrae and around the tail head.

2.7. Data handling

About 13250 weekly records were available, on 391 lactations (210 cows). All lactations with fewer than 20 weekly records and all lactations with fewer than 7 weekly records in the first 15 weeks and no record after 23 weeks of lactation were discarded. Range checks were carried out before entering the data, and additionally a simple procedure was used to check for outliers as follows: for each separate lactation a cubic polynomial was fitted through the weekly records for milk yield, fat %, protein %, lactose %, dry matter intake, ME intake, CP intake, live weight and condition score. Outliers were discarded on the basis of the estimated variance, within each separate lactation, about the fitted curve. When the observed value was more than 3.5 standard deviations different from the fitted value the observed value was rejected. In total 161 weekly milk yields were rejected, and from the other recorded traits the number of records discarded varied between 8 and 48. Given the fact that at least twenty weekly records were available in each lactation to estimate the curve and the low number of discarded records, it is not likely that any strong bias was introduced by this method. Missing and discarded records were replaced by fitted values from a second polynomial, fitted without the outliers (fewer than 5% of the weekly records were finally estimated in this way). Records from the first 2 weeks of lactation were ignored throughout, because most missing values for yield and intake were in this period. Also previous studies at Langhill have shown that these are of limited value.

2.8. Dependent variates

The weekly records were combined to form 12 traits of interest during the first 26 weeks of lactation: Milk yield (Milk), fat plus protein yield (F+P) and dry matter intake (DMI), were calculated as the average of the weekly records multiplied by 26. Fat (F%) and protein (P%) percentage, were calculated as the average of the weekly percentage weighted by the weekly milk yields. Gross energetic efficiency (ENEF) was calculated as 100 × LE (MJ)/ME intake (MJ). Gross protein efficiency (PROTEF) was calculated as 100 × protein yield (kg)/CP intake (kg). Average live weights (ALW) and condition scores (ACS), were calculated as the average weekly measurements.

Measured ALW is the aggregate of gut fill (GF), lipid (L) and lipid free empty body weight (LFEBW). ACS is an index of L/(ALW-GF). To evaluate changes in body composition an attempt was made here to estimate the different components contributing to ALW and ACS. The value of GF was estimated as (Emmans, personal communication): $GF = DMI$ (kg/day) $\times (11 - 7 \times D)$ where D, the digestibility of feed,

Table 4

Estimates for the regression coefficients of a range of traits on pedigree index for kg fat + protein (on the high concentrate diet) and regression coefficients for the interaction between PI × DIET (the difference between the regression coefficient on HC and LC)

	Cows only 26 weeks				Heifers only, 26 weeks			
	PI		PI × Diet LC		PI		PI × Diet LC	
	b	se[1]	b	se	b	se	b	se
Milk (kg)	47**	8	−29**	11	34**	6	−8	8
F%	−0.007	0.006	0.016	0.009	0.002	0.005	−0.002	0.007
P%	−0.005*	0.002	0.003	0.003	0.005*	0.002	−0.003	0.003
F + P (kg)	2.53**	0.64	−1.18	0.86	2.35**	0.42	−0.67	0.58
DMI (kg)	11**	4	−8	6	1	3	0	4
ENEF (%)	0.16**	0.06	−0.03	0.09	0.28**	0.05	−0.03	0.070
PROTEF (%)	0.10*	0.04	−0.06	0.05	0.15**	0.03	−0.05	0.04
ALW (kg)	0.3	0.6	−0.1	0.8	−0.7	0.4	0.9	0.6
ACS	−0.014**	0.004	0.010*	0.005	−0.007**	0.002	0.001	0.003
GF (kg)	0.3**	0.1	−0.3	0.2	0.0	0.1	0.0	0.1
Lipid (kg)	−0.9*	0.4	0.6	0.5	−0.6**	0.2	0.3	0.3
LFEBW (kg)	0.8**	0.3	−0.5	0.4	−0.2	0.2	0.6*	0.3

[1] Standard errors are approximates given by REML function ($*P < 0.05$; $**P < 0.01$: $H_0 = 0$).

was estimated as diet ME density (MJ/kg)/15. Based on data from Wright and Russel (1984) lipid (kg) per kg EBW was estimated as: $L/EBW = -0.0431 + 0.120 \times ACS$.

2.9. Analysis

Residual maximum likelihood (REML) (Patterson and Thompson, 1971) was used to estimate fixed effects. The Genstat REML (Genstat 5 Committee, 1989) option was used, with a random cow effect to account for covariance between subsequent lactations of the same cow. This REML routine approximates standard errors (s.e.) and standard errors of the differences (s.e.d.) for the effects in the model included. Two univariate models were used for the heifer and cow data separately:

Model 1:

$$Y_{ijklm} = U + Y_i + M_j + LN_k + DIET_l + LINE_m + DIET_l \times LINE_m + b_1\,AC_{ijklm} + b_2 H\%_{ijklm} + C_{ijklm} + E_{ijklm}$$

Model 2:

$$Y_{ijkl} = U + Y_i + M_j + LN_k + DIET_l + b_1\,AC_{ijkl} + b_2\,H\%_{ijkl} + b_3\,PI_{ijkl} + b_4\,(DIET_i \times PI_{ijkl}) + C_{ijkl} + E_{ijkl}$$

where

Y_{ijklm} = Milk, F%, P%, FP, DMI, ENEF, PROTEF, ALW, ACS, GF, Lipid or LFEBW aggregated over 26 weeks
U = overall mean
Y_i = year of calving (1988, 1989, 1990, 1991)
M_j = month of calving (Sept, Oct, Nov, Dec)
LN_k = lactation number (2–3, > 3 in cow data set only)
$b_1\,AC_{ijklm}$ = linear regression on age at calving in days
$b_2\,H\%_{ijklm}$ = linear regression on Holstein percentage
$DIET_i$ = diet effect (concentrate nor forage)
$LINE_m$ = genetic line effect (Selection or control)
$DIET_i \times LINE_m$ = interaction between line and diet
$b_3\,PI_{ijklm}$ = regression on pedigree index
$b_4\,(DIET_i \times PI_{ijklm})$ regression on interaction between pedigree index and diet
C_{ijklm} = random cow effect (only in cow data set)
E_{ijklm} = residual effects

The pedigree index for F + P yield (PI) was calculated as 0.50 × sires' predicted transmitting ability (PTA) for F + P plus 0.25 × maternal grandsires' (MGS) PTA for F + P. PTAs of sires and MGS came from the August 1992 national animal model BLUP analysis (Wiggans et al., 1988; Animal Data Centre, 1993), but no Langhill records were included in this particular national run. This made the regression coefficients of phenotypic values on PI equivalent to genetic regressions, because there is no environmental covariance between PI and the phenotypic measurement. Model 1 (without the random cow effect) was used to estimate least square means for the weekly performance in the 4 groups.

3. Results

The number of cows and records within each of the fixed effect classes for both data sets is given in Table 2. Table 3 shows means corrected for fixed effects and for covariance between lactations of the same cow. Selected animals yielded more milk and fat + protein (kg) than control line animals ($P < 0.01$). There was no line effect on milk composition of older cows, but in heifers milk protein concentration was slightly, but significantly ($P < 0.05$) higher in control than selected animals.

The numerically greater dry matter intake (DMI) in selected animals was not significantly different from

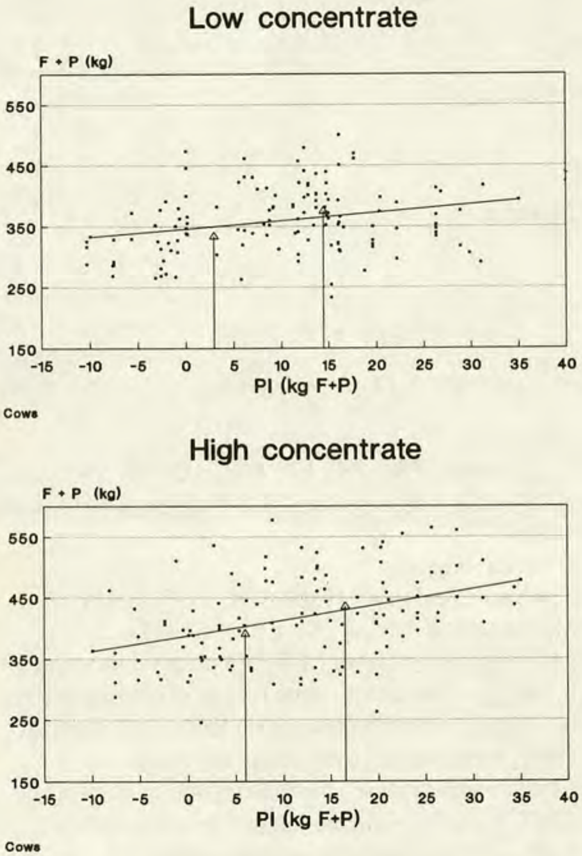


Fig. 4. Relationship between pedigree index (PI) for F + P and F + P yield during the first 26 weeks of the lactation, on both low and high concentrates diets (no heifers included). Arrows indicate the means for S and C.

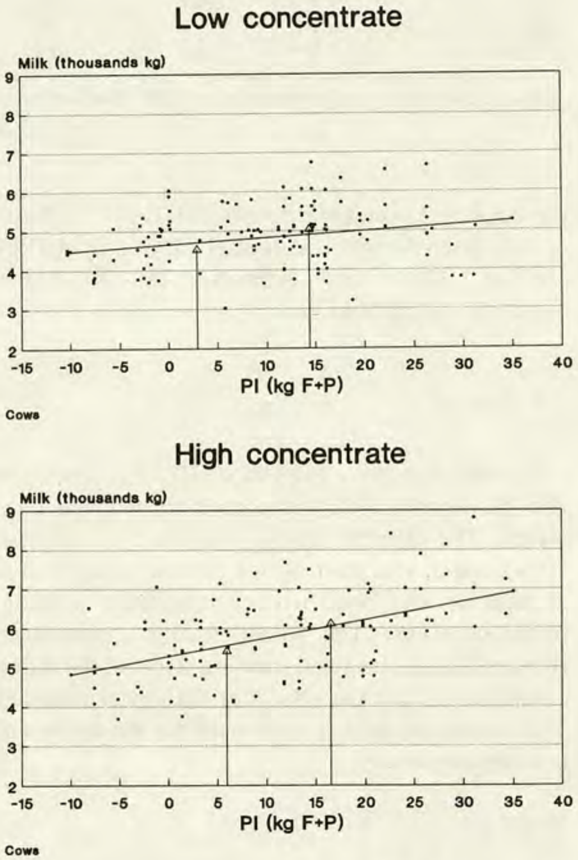


Fig. 5. Relationship between pedigree index (PI) for F + P and milk yield during the first 26 weeks of the lactation, on both low and high concentrate diets (no heifers included). Arrows indicate the means for S and C.

the controls; the difference in mean DMI between lines was small compared with the differences in milk production. As a result energetic and protein efficiency were both significantly ($P<0.05$) greater in selected animals than in controls. The pattern of change in gross efficiency was similar for heifers and cows in the same genetic groups (Fig. 1).

Mean condition score (ACS) was significantly lower ($P<0.05$) in selected animals. As there were no diet × line interactions this difference applied in each of the dietary treatments.

Differences between the diets were observed for DMI and calculated gut fill (GF), which were greater with HC than LC. In heifers only this was associated with a greater average live weight (ALW; $P<0.05$). The HC diet supported higher rates of milk, and fat + protein yield ($P<0.01$), a lower milk fat concentration ($P<0.05$) and, in cows only, a higher milk protein concentration ($P<0.05$) than diet LC. Protein efficiency was greater ($P<0.01$) with HC than LC. There was no significant diet effect on energetic efficiency in the cow data, but significance was approached in the heifer data for energetic efficiency. Control heifers on HC produced a similar yield of F + P to selected animals on LC, but with a lower fat concentration.

Differences in live weight and condition score during lactation are shown in Fig. 2 and 3 for heifers and cows, respectively. Heifers from the C line on HC become heavier during lactation than the other three groups (Fig. 2), probably through a combination of higher GF and, by calculation, more lipid stored. Most of the difference in condition score (Table 3), between control line animals and selection line animals, is created at the end of the lactation (Fig. 3). In early lactation, condition scores on the 2 diets were very similar within genetic line. However selection line cows on LC were clearly leanest by week 26 (Fig. 3).

Regressions on PI showed correlated responses for most traits (Table 4). Milk, F + P, ENEF, PROTEF all showed positive regressions on PI. The regression of milk production on PI was significantly different between LC and HC. Figs. 4 and 5 show these relationships graphically. For each PI point cows produced 18 kg and 47 kg more milk on LC and HC, respectively and 1.35 kg and 2.53 kg more F + P.

The interaction between PI and Diet LC was significant for milk yield (but not F + P) which suggests a genotype × feed system interaction. High PI cows appear to be leaner than low PI cows, but this was primarily observed on the high concentrate diet (Table 4).

4. Discussion

The aim of the long-term study at Langhill is to explore whether or not genotype × feeding system interactions exist and, if so, whether these are large enough to give rise to different selection decisions in different feeding systems which might be employed in the UK or elsewhere. From the treatment means for single lactation records which are reported here, there were no genotype × feeding system interactions detected (Table 3). However regression of performance measures on PI and the PI × Diet LC interaction indicated that interactions of potential importance may exist. The results are discussed against this background.

4.1. Milk yield

The decreasing effect of extra concentrate on fat % has been found by several other authors (for a review see Sutton, 1989). The magnitude of the effect of feed system on fat % was relatively large given that the HC feed contained, on average, only 45% concentrate, and the LC feed 20% concentrate in diets based on grass silage. A wide range of concentrate allowances (with grass silage available ad lib.) spanning this range of concentrate : forage failed to yield any response in milk fat % in Gordon's (1984) work. Also, concentrate manipulation (in kind or amount) when concentrates form less than 0.6 of feed DM has generally promoted only small changes in milk fat content (Sutton, 1989). It has been held that dietary effects on milk fat concentration are less extreme with diets containing a large proportion of grass silage (than, for example, with diets based on hay or maize silage) because the characteristics of the silage have such a major influence on patterns of rumen fermentation (Chalmers et al., 1978). Our data, collected over four years, show that diet effects on milk fat % can be substantial with complete mixed diets based on grass silage, and that the effects are in the direction expected from wider studies on forage : concentrate ratio and milk composition. In this study estimates for the diet effect on P% were just significant (Table 3) in the cows. Weekly records showed a clear decline in P% at peak lactation on LC for both S and C (results not shown), but there was no difference between LC and HC for P% during mid and late lactation.

Regression coefficients for complete lactation F + P yield on PI are expected to be 2 for both cows and heifers because PI were estimated transmitting abilities. Higher regression coefficients were observed on HC and lower regression coefficients were observed on LC for the 26 week period included in this study. This might suggest that individuals of very high merit for milk solids production may have the expression of their potential compromised by inadequate nutrition, but the magnitude of this "trend" was not sufficient to indicate a statistically significant interaction. In contrast to the regression coefficients for F + P, regressions of milk on PI were significantly different between the diets. A log transformation and models with different combinations of diet, line and PI did not change this significant interaction between diet and genetic merit for milk yield (results not shown), and therefore there is a suggestion of G × E interaction in this data set for milk. Lamb et al. (1977) found no genotype by diet interaction between daughters of USA Holstein Friesian bulls, but also concluded that regressions on index seem to have a stronger slope on high input diets. These differences between regression lines on high and low input diets suggest that continued selection for F + P in S is likely to make detection of any diet × line interaction easier. There is obviously something of a conflict here between the interpretation of the comparison between group means – which show no genotype × environment interactions – and the indications from the regression analysis (Fig. 5) that an interaction exists, at least for milk. By way of explanation the group mean values for F + P (kg) are shown on Fig. 5 from which it is readily seen that these are fairly close together in comparison with the full spread of the data and it is probably for this reason that the group mean contrasts failed to identify a significant interaction while the regression analysis did. A biological interpretation of this putative interaction should await a more definitive demonstration of its existence. The purpose of this report is to provide a first intimation that such an interaction may exist.

At the phenotypic level there has been interest for a long time in the response of cows at different yield levels to differential feeding strategies. In this study we are using forage : concentrate ratio in complete mixed diets to achieve different levels of nutrient and energy provision; in other studies variable concentrate allocations with forage rationed or available ad lib. have been used (Broster and Thomas, 1981). Neither Gordon (1984) nor Ostergaard (1979) were able to show any increase in the milk yield response to additional concentrates on milk yield per animal increased. The data presented here are consistent with this view in that the difference in F + P yield between HC and LC was around 60 kg for cows and 50 kg for heifers within each line when group means are used for the comparison. The interaction indicated in the regression analysis would suggest that a difference in response will become apparent as the PI difference (and hence difference in performance) becomes greater. Broster and Thomas's (1981) analysis of the situation in which yield responses to differential feeding are a function of yield level when feed is rationed, but independent of yield level when feed (usually forage) is available ad lib. might therefore be challenged. In light of Gordon's (1984) comment that "It is...important to clarify if the lack of a relationship (between response to concentrate allowance and cow yield level) would occur at a wider range of milk yields (than those used in his trial)" our work is perhaps giving the first indications of a differential response according to genotype.

4.2. Intake and efficiencies

Both heifers and cows were able to eat more of the drier and less bulky HC diet than they did of LC. That there was a small (though non-significant) difference in DMI between lines (with selected animals eating more) poses the interesting question of why the control animals on LC failed to eat more than they did; selected animals on that diet ate a little more than the controls on LC – but not as much as controls on HC. Whatever the factor that limited intake of the LC diet to less than that for HC, the intake difference between lines, though not statistically significant, might suggest that dietary factors alone could not account for the consumption of that feed.

Although the diets used had been designed to exclude dietary protein concentration (or metabolisable protein yield, AFRC, 1992) as a constraint on performance, gross protein efficiencies are reported here – not least because of the rapidly increasing interest in management factors which can reduce dietary N wastage in intensive production systems (Tamminga, 1992). Higher gross protein efficiencies were observed on HC, which was a consequence of higher milk P% and a lower protein/energy ratio in the diet. In neither case, however, was the protein efficiency of a magnitude which would suggest that dietary protein was limiting performance. In energetic terms S were more efficient than C on both diets. Although there was a large difference between LC and HC in condition score at the end of the lactation (Fig. 3), this does not seem to have affected energetic efficiencies in the same period (Fig. 1). Similarly, the cows on HC produced much more milk than those on LC and therefore diluted their maintenance costs over more output. Nevertheless, energetic efficiency was not different between the diets (over 26 weeks), and the major component affecting gross efficiency in this study seems to have been genetic line. Even after correcting gross energetic efficiencies for maintenance, lactation and live weight change there was still a 3.5% advantage for the selection line (Veerkamp et al., 1993). This suggests that there may be differences in energetic efficiency of performance between the two lines which are not simply a reflection of different combinations of maintenance and ''performance'' elements.

4.3. Live weights and body tissue

No significant diet effects were apparent for ACS or lipid, and from early to mid lactation, heifers and cows in the same genetic line had surprisingly similar condition scores (Fig. 3), with S being slightly leaner than C. This suggests that cows ''seek'' to reach a certain condition score in mid lactation, which is affected by genotype. It also supports the view presented by Emmans and Neilson (1984) that animals reduce their feed intake (or increase production) when more lipid is available for mobilization, rather than the view that animals mobilise lipid because they produce more milk than they can support from intake alone. Regression of the interaction between PI and diet on ACS and LIPID indicate that for every kg reduction in PI for F + P, 0.9 kg LIPID is deposited during the first 26 weeks of lactation. Lamb et al. (1977) also concluded that daughters of high genetic merit bulls used less of their feed intake for increase of body tissue, although in their experiment cows were fed according to yield. Korver et al. (1985) found a clear influence of diet on ''stage of lactation at minimum live weight'' and ''maximum live weight decrease''.

4.4. Conclusions

The objective of this study was to evaluate effects of genotype by feeding regime interaction within a single lactation, on performance and body tissue mobilization. The results clearly showed that selection line animals were leaner after 26 weeks of lactation, but the interaction between diet and PI for ACS suggest that this is not due to extra body tissue mobilisation of selected animals, but rather to a relatively higher feed consumption of the control line animals at the end of the lactation. The line × diet interaction was not significant which would suggest that G × E is not expected to have a large impact for dairy herds in the UK, within the range of diets and PI examined here. However regressions of performance on PI did show an interaction which, though small, may have more substantial implications for the very highest PI animals if feeding is not adequate.

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Résumé

Veerkamp, R.F., Simm, G., et Oldham, J.D., 1994. Effets de l'interaction entre le génotype et le régime alimentaire sur la production laitière, la consommation alimentaire et la mobilisation corporelle chez les vaches laitières. *Livest. Prod. Sci.*, 40: 229–241 (en anglais).

L'objectif de cette étude a été de rechercher les interactions génotype&régime alimentaire chez les vaches Holstein. Dans ce but, des vaches de la lignée sélectionnée (S) et de la lignée de contrôle (C) au centre de recherche de Longhill ont reçu des aliments complets mixtes, offerts ad lib. sur toute la lactation. Les proportions de la matière sèche totale expliquées pour les concentrés, l'ensilage et les drêches de brasserie ont été respectivement 20/5/75 pour le régime bas (LC) et 45/5/50 pour le régime haut (HC). Aucune interaction lignée × régime n'a été trouvée pourun certain nombre de caractères décrivant la production laitière, la consommation alimentiares, l'efficacité alimentaire et la mobilisation corporelle. (128 lactations de génisse et 249 lactations d'adultes). Cependant, les coefficients de régression de la production laitière et de la note d'état sur l'index laitier (production de matière grasse et de matière protéique) ont été significativement différents ($P<0,01$ et 0,05 respectivement entre régimes. Ceci indique que l'interaction génotype × milieur pourrait devenier importante dans le futur, avec la sélection continue sur la production de matière grasse et protéique.

Kurzfassung

Veerkamp, R.F., Simm, G. und Oldham, J.D., 1994. Interaktionen zwischen Genotyp und Fütterungssystem bei den Merkmalen Milchproduktion, Futteraufnahme, Futterverwertung und Körperenenergiemobilisierung von Milchkühen. *Livest. Prod. Sci.*, 229–241 (auf englisch).

Das Ziel der Arbeit bestand in der Untersuchung von Interaktionen zwischen Genotyp und Fütterungssystem bei schwarzbunten Milchkühen. Zu diesem Zweck wurde eine Selektions- und eine Kontrollinie im Longhill Dairy- Cattle Research Centre während einer Laktation mit zwei kompletten Milchrationen ad libitum gefüttert, die aus Konzentraten, Silage, und Braugerste zu folgenden Anteilen (in TM) bestanden: 20:5:75 (LC) bzw. 45:5:50:(HC). Es wurden keine signifikanten Interaktionen vom genannten Typ für die Merkmale Milchmenge, Futteraufnahme, Effizienz und Mobilisation von Energie aus Körpergewebe an Hand der untersuchten 128 Erstlingslaktationen und 249 Laktationen von Kühen gefunden. Jedoch war der Regressionskoeffizient der Milchleistung ($P<0,01$) und der Körperform ($P<0.05$) anhand eines Pedigreeindex (Fett- und Eiweißmenge) bei LC und HC signifikant verschieden. Esdeutet darauf hin, daß Interaktionen bei kontinuierlicher Selektion nach Milchfett- und Milcheiweißmenge in Zukunft Bedeutung gewinnen könnten.

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Potential value of linear type traits for the prediction of intake, efficiency and economic margins in dairy cattle

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Potential value of linear type traits for the prediction of intake, efficiency and economic margins in dairy cattle

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Abstract

Production, food intake, efficiency, health and reproduction are all of importance in dairy cattle breeding goals. Measuring these traits on a large scale is not easy and therefore there is great interest in correlated traits for potential use in selection indices. In this study the relationships between linear type traits, live weight and pedigree index for fat plus protein yield and (i) dry matter intake (DMI), (ii) gross energetic efficiency (EFF), (iii) margin over all food costs (MF) and (iv) margin over food, health and reproduction costs (MFHR) were investigated. Regression analysis showed that a large increase in the R^2 was achieved when average live weight during lactation, live weight at calving and (i) linear type scored as a heifer (number of records available was 164) or (ii) sire transmitting ability for type ($n=302$) were included in a regression model to predict either DMI, EFF, MF or MFHR. Different models showed that linear type traits were more valuable than live weight traits for the prediction of MFHR. Also, regression coefficients were obtained using Residual Maximum Likelihood procedures. Several linear type traits appeared to be of potential value for a selection index, eg angularity, rump angle and udder depth measured on the heifer. One s.d. change in angularity resulted in an increase of £79 in MFHR. The results were not conclusive enough to develop a selection index, but show that a combination of type, live weight and production are likely to be valuable components of future indices.

Key words: Dairy cattle; Type trait; Feed efficiency; Profit

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1. Introduction

Most milk producers would probably agree that improving the profitability of cows, consistent with their health and welfare, is the most important breeding objective for dairy cattle. Defining profitability on an individual animal basis is difficult, but clearly milk returns and food, health and reproduction costs are important components of it. Hence, in most studies which aim to address individual cow profitability, the breeding objective is often defined as a ratio or linear function of these major costs and returns. The most commonly used ratio is gross energetic efficiency. Whilst energetic efficiency may be of biological interest, it is often wrongly assumed to be synonymous with profitability. Linear functions of costs and returns, such as margin over food costs, are clearly more closely related to individual cow profitability.

Measurement of feed intake and recording of health events is expensive. This is one reason why breeding

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schemes in most countries are still based mainly on milk production (though there are notable exceptions, such as the health recording schemes operated in Scandinavian countries). Another reason for the lack of schemes involving direct selection on efficiency is the high genetic correlation between gross feed efficiency and milk yield (Korver, 1988). However, there is renewed interest in breeding objectives for dairy cattle as a result of (i) restrictions on output, imposed by quotas, (ii) the opportunity of more comprehensive recording in nucleus breeding schemes, (iii) more evidence of potential benefit from direct selection for intake or efficiency and (iv) evidence of unfavourable correlations between production and some health traits. For example, recent estimates of genetic correlations under ad lib. feeding (Persaud et al., 1991) showed that the correlated response from indirect selection for efficiency, by selection on fat + protein yield, is expected to be only 47–75% of that from direct selection for efficiency. Additionally, a range of low to high positive genetic correlations between milk yield and the incidence of some diseases have been reported by Christensen (1989), Solbu and Lie (1990), Simianer et al. (1991) and Eriksson (1991). Others (for example Whitmore et al., 1974; Wilk et al., 1984; Short et al., 1990) have reported a higher incidence of health events in cows selected for high milk production. Likewise, Van Arendonk et al. (1989), Hageman et al. (1991) and Bonczek et al. (1992) reported antagonistic relationships between reproductive performance and milk production. Therefore health and reproduction seem to become increasingly important with increasing production levels.

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 (McGuirk, 1990). 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. Therefore there is great interest in other traits which may help to predict the intake or efficiency of lactating cows. Van Arendonk et al. (1991) suggested measurements of food intake on growing bulls and heifers; Persaud et al. (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. Alternatively, linear type traits are measured on a relative large scale and there is evidence of genetic correlations between linear type traits and milk production (Meyer et al., 1987), reproduction (Dadati et al., 1986), longevity (Brotherstone and Hill, 1991) and somatic cell counts (Rogers et al. 1991). The latter suggesting an effect on mastitis resistance. Sieber et al. (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 type traits in a selection index for improving the profitability of dairy cows.

The aim of this study is to establish the possible benefit of combining linear type traits together with genetic merit for milk solids production in one index when the breeding goal is to maximise a function of milk production, food intake and the costs of health events and reproduction.

2. Material and methods

Milk production, live weights and dry matter intake records were obtained from the Langhill Dairy Cattle Research Centre. Full details of the recording procedures and missing data treatment is given by Simm et al. (1991), and more detailed information about the prices used is given in Simm et al. (1994). A summary of these and details specific to this study are given below.

Animals and data recording

All cows were pedigree Holstein-Friesians, and those involved in this study were kept indoors from September to May (1979 to 1982) or from September to July (1983 to 1989) and fed a complete diet ad lib. This period allowed measurement of individual intakes from calving to either 26 or 38 weeks after calving. In this study only records up to 38 weeks were used. Cows were milked twice a day and 1 kg concentrate was fed in the parlour during the housed period. The herd comprises two genetic groups, (i) a selection line and (ii) a control line. Since 1973 the selection line has been bred to bulls with the highest genetic merit for kg fat and protein available in the UK. The control line animals are bred to bulls of about national average genetic merit for fat plus protein yield.

Milk yields were recorded on a weekly basis. Milk composition analysis was undertaken every two weeks until 1986/87, and thereafter weekly analyses were carried out. Milk production and composition records were used to calculate weekly milk returns, using 1989/90 prices throughout. Milk energy was calculated with an equation from Tyrrell and Reid (1965). The prices were based on the payment system of the Scottish Milk Marketing Board, which then paid approximately equal value to fat and protein in milk.

Weights of food offered to and refused by individual cows was recorded for four days a week, during 38 weeks of lactation. Cows were fed a complete diet containing mainly grass silage, brewers grains and concentrates, although in some years sugar beet pulp pellets, molassine meal or straw were included. Fixed 1989/90 prices were used to calculate total food costs from the complete diet intakes (food offered minus refusals) and the fixed amount of parlour concentrates.

Health events were recorded throughout the period of investigation by veterinarians, farm or technical staff. A simple three digit coding system, allowing for 112 different codes, was used to code 512 individual health events. For each event, health costs (1989/90 prices) were calculated, based on: (i) a call-out charge where a vet was involved. The standard charge was increased where a long visit would usually be required and reduced for health events where several animals are usually seen on one occasion; (ii) The costs of drugs or materials used by the vet or farm staff; (iii) The lost revenue on milk withdrawn as a result of drug treatment, based on the production of the cow in the relevant week of lactation.

Several components contributed to the reproduction costs: (i) service and semen costs allowing a lower cost for successive inseminations, plus a storage charge; (ii) a pregnancy diagnosis charge and (iii) a cost for prolonged calving intervals of £3 per day (Esslemont, 1993), after 365 days. Costs were calculated for each event, based on 1989/90 prices. All lactations for which the next calving date was not known were discarded, since it was not possible to allow for the variable duration of calving intervals for these lactations.

Live weight was recorded in the 48 hours following calving and weekly thereafter at the same time of day after milking. To reduce variation due to gut fill, 3-week rolling average live weights were calculated for each week of lactation except that at calving.

Type classification

The Holstein Friesian Society of Great Britain and Ireland (HFS) operates a linear type classification scheme, details of which have been given by Meyer et al. (1987). Linear type scores were introduced in 1983, and therefore only a subset of the animals for which feed intake was recorded also had heifer type classification results (164 lactations). Genetic regressions were obtained by regression of the phenotypic measurements on each animal on the sires predicted transmitting ability for type (TAT). The advantages were that (i) more feed intake records could be used (302 lactations) to indicate genetic relationships between type traits and other traits of interest and (ii) partial regressions of margins on TAT gave economic values for the type traits. TAT were estimated with a sire and maternal grandsire model from HFS national data using Best Linear Unbiased Prediction (BLUP) (S. Brotherstone, personal communication). Only TAT of sires with 6 or more effective daughters in the BLUP analysis were included in the present study.

Dependent variables

The dependent variables considered in this study were: (i) Cumulative dry matter intake (DMI) to 38 weeks of lactation; (ii) Cumulative gross energetic efficiency (EFF) (1000 × cumulative milk energy yield (MJ)/cumulative metabolisable energy intake (MJ)); (iii) Margin over food costs (MF) (total milk returns − total food costs over 38 weeks of lactation); (iv) Margin over food, health and reproduction costs (MFHR) (total milk returns − total food, health and reproduction costs over 38 weeks of lactation).

Independent variables

Independent variables considered were: (i) Pedigree index (PI) for kg fat + protein yield, calculated as sire's transmitting ability +0.5 maternal grandsire's transmitting ability (i.e. final PIs were on the breeding value scale); (ii) Calving live weight (CLW); (iii) Average live weight (ALW)–the average of the weekly live weights over the 38 week period; (iv) Type traits as a heifer (LT) – total merit and the 16 linear type traits scored by the classifier; (v) Sires estimated transmitting ability for the 17 type traits (TAT). The fixed effects included in all analyses were: (i) year of calving (1983 to 1989); (ii) month of calving (September, October, November); (iii) feeding system (high and low concentrate); (iv) lactation number (1, 2, 3–5 and 5–9). Also (i) percentage Holstein and (ii) age at calving were fitted as linear covariates. Table 1 gives the summary statistics for the dependant and independent variables and some of their components. Table 2 shows the means and variances of the phenotypic heifer type scores and sires' TAT.

Method of analysis

Models with different combinations of the independent variables were fitted using the GENSTAT (Genstat 5 Committee, 1989) multiple regression option. The adjusted multiple correlation ($R^2 = 100 \times (1 - (\text{Residual mean square})/(\text{Total mean square}))$) was used to investigate the additional value of including extra variables in the model. Multiple regression assumes that the observations are independent and underestimates the standard errors in this case, because many cows had more then one lactation in the data set. The Genstat 5.2 Residual Maximum Likelihood (REML) option (Patterson and Thompson, 1971) is a powerful tool to analyse unbalanced data and account for random effects. Therefore this version of REML was used to estimate regression coefficients on PI and PI plus (i) ALW (ii) CLW, (iii) one of the 17 LT traits or (iv) one of the 17 TAT traits. All fixed effects were included and cow was included as a random effect. Including cow as a random effect accounts for the permanent environmental correlation and the genetic correlation between repeated records (subsequent lactations) of the same cow. Finally, MF and MFHR were regressed on PI and a subset of (i) TAT traits or (ii) LT traits.

3. Results

The mean of dependent and independent variables and the costs and returns contributing to MF and MFHR are given in Table 1. A large difference between the median and mean value for the health and reproduction costs was found: in the data set with 302 records the means were £33.30 and £140 for health and reproduction costs respectively, and the medians were £16.80 and £84.50 respectively. This shows that relatively few animals incurred a large proportion of the costs. Age at calving and lactation number are slightly lower in this trial than on most commercial farms.

Table 2 shows the definition of the linear type traits used in this study, together with their means and standard deviations for these traits. Table 3 shows multiple correlation coefficients for models combining PI, liveweight or type traits to predict DMI, EFF, MR or MFHR. Fixed effects alone explained a relatively high proportion of the variance in DMI (36.4 to 45.5). Only marginal increases in R^2 values were obtained by adding PI and ALW or CLW (or both) to the model. There was no single TAT important for the prediction of DMI, but adding a combination of TATs to the model increased the R^2 from 38.8 to 47.5%. When type traits of the heifers were included in a model with fixed effects and PI, the addition of live weight traits did not improve the prediction of intake. Of the heifer type traits, body depth showed a positive relationship with intake (although not significant in the data presented here) and udder depth a negative relationship (Table 5).

Of the total variation in MF, 24.7% and 27.2% were explained by pedigree index and fixed effects in the two data sets. Accounting for ALW increased the proportion of variation explained, but including CLW only gave an improvement when ALW was also included in the model. Including sires TAT increased the R^2 from 24.7 to 34.4% and including sires TAT and the animals own live weight in the model gave an R^2 of 57.1% (Table 3). Inclusion of the significant heifer type traits increased the R^2 to 50%. Fitting pedigree index, live weight and heifer type traits together explained 64.1% of the variation in MF. Likewise, large increases in the R^2 were obtained for EFF and MFHR, but less of the total variance was explained. Heifer type seems to be as valuable as ALW and CLW for the prediction of MF and heifer type seems to be of even more value than ALW and CLW for the prediction of MFHR (Table 3).

The benefit of a high pedigree index (breeding value) varies between £3.4 and £3.6 per kg fat plus protein in margin over all food costs per 38 week lactation (Table 4 and 5). A slightly lower benefit was apparent when health and reproduction costs were included in the margin. A high CLW and a low ALW were associated with the highest profitability and efficiency. TAT for rear legs (RLS, RLR, FA) seem to be

Table 1

Mean and standard deviation of dependent and independent variables pedigree index for kg fat + protein yield (PI; arbitrary base), average live weight (ALW), calving live weight (CLW), age at calving, lactation number, Holstein percentage, dry matter intake (DMI), gross efficiency (EFF), margin over food (MF) and margin over food, health and reproduction costs (MFHR) and the components contributing to the margins

	With TAT sires' type ($n=302$)		With type scored as a heifer ($n=164$)	
	mean	s.d.	mean	s.d.
PI	10	20	13	21
CLW (kg)	617	65	601	61
ALW (kg)	598	76	574	70
Age at calving (mths)	46.0	22	35.7	14
Lactation number	2.8	3.3	1.9	1.2
Holstein %	0.42	0.25	0.45	0.22
DMI (kg)	4457	520	4371	510
EFF (100 × MJ/MJ)	391	60	386	61
MF (£)	754	218	725	219
MFHR (£)	581	249	547	256
Milk returns (£)	1331	252	1294	242
Food costs (£)	577	75	568	68
Health costs (£)	33	44	29	41
Reprod. costs (£)	140	143	149	151

Table 2

Definition of type traits, means and phenotypic standard deviation (s.d.) for heifer linear type (LT) scores and sires transmitting ability for type (TAT)

	Score		Heifer score		Sire merit	
	min	max	mean	s.d.	mean	s.d.
Total (TM)	Negative	Positive	70.9	4.8	109	10
Stature (ST)	Small	Tall	5.22	1.09	4.56	12.20
Chest width (CW)	Narrow	Wide	6.20	1.20	−0.69	4.24
Body depth (BD)	Shallow	Deep	6.87	1.12	4.73	7.48
Angularity (ANG)	Coarse	Angular	5.17	1.28	5.64	8.22
Rump angle (RA)	High	Low pins	4.51	1.15	−0.21	6.29
Rump width (RW)	Narrow	Wide	6.13	1.21	1.32	4.05
Rear legs side (RLS)	Posty	Sickled	5.56	1.18	2.78	4.98
Rear legs rear (RLR)	Close	Straight	5.24	1.34	−2.49	5.57
Foot angle (FA)	Low	Steep	5.18	1.21	−2.08	4.07
Fore udder attachment (FUA)	Loose	Tight	5.38	1.23	−2.25	5.19
Rear udder width (RUW)	Narrow	Wide	6.09	1.24	0.77	4.19
Udder support (US)	Broken	Strong	6.60	1.16	0.95	5.50
Udder depth (UD)	Below	Above hock	5.17	1.35	−3.54	8.37
Teat placement rear (TPR)	Wide	Close	4.49	1.27	−1.38	5.81
Teat placement side (TPS)	Close	Apart	5.29	1.08	3.82	7.34
Teat length (TL)	Short	Long	5.17	1.15	3.12	7.18

[1] Standard deviations TAT and mean of TAT used are scaled values.

important (Table 4) for the prediction of EFF, but TPR and RLR were the only TAT, having a significant effect on EFF and MF. Of the heifers' type traits chest width, angularity, rump angle and udder depth showed associations with EFF, MF and MFHR (Table 5). Table 6 gives partial regressions of MF and MFHR on a subset

Table 3
Multiple correlation coefficients (%) for DMI, EFF, MF and MFHR, fitting fixed effects[1] and different combinations of pedigree index, ALW, CLW and (i) sires transmitting ability for type or (ii) type traits scored as a heifer

Traits in model	Sires transmitting ability for type				Type scored as a heifer			
	DMI	EFF	MF	MFHR	DMI	EFF	MF	MFHR
Fixed effects[1]	36.4	13.7	19.6	14.1	45.5	15.7	21.6	7.9
PI	38.8	15.4	24.7	18.4	48.5	16.5	27.2	11.8
PI+ALW	38.9	31.0	36.2	23.3	49.0	28.9	36.9	19.6
PI+CLW	39.5	15.6	24.6	18.1	48.9	15.9	26.7	11.5
PI+CLW+ALW	39.3	44.5	48.4	30.8	48.7	45.0	50.0	26.0
PI+Type[2]	39.5	20.1	28.4	19.4	51.7	30.5	43.4	25.1
PI+Type[3]	47.5	23.3	34.4	22.7	58.3	36.8	48.1	33.2
PI+Type[4]	47.6	21.9	34.6	22.3	57.7	37.7	50.0	31.7
PI+ALW+CLW+Type[3]	48.9	51.6	57.1	34.9	58.5	54.1	62.6	40.0
PI+ALW+CLW+Type[4]	49.0	49.4	57.0	34.9	58.6	55.5	64.1	40.1

[1] Year and month of calving, lactation number, feed system, percentage Holstein and age at calving were included in all the models.
[2] Model with single type trait that explained most of variance.
[3] Model with all type traits fitted.
[4] Model after backwards elimination of non significant type and live weight traits.

Table 4
Regression coefficients for regressions of DMI, EFF, MF and MFHR on pedigree index plus (i) one of the live weight traits or (ii) one of the sires transmitting abilities for type (See Tables 1 and 2 for abbreviations)

	DMI		EFF		MF		MFHR	
	b	se	b	se	b	se	b	se
PI	5.5**	2.0	0.6*	0.3	3.4**	0.9	3.2**	1.0
plus:								
ALW	2.0**	0.5	−0.4**	0.1	−1.2**	0.2	−0.9**	0.2
CLW	0.7	0.4	0.2*	0.1	0.7**	0.2	0.7**	0.2
TM	−0.6	3.4	−0.3	0.5	−1.1	1.6	−0.7	1.9
ST	−1.4	3.1	−0.2	0.4	−1.2	1.5	−1.7	1.8
CW	−6.6	7.9	0.5	1.1	2.8	3.6	3.1	4.1
BD	0.2	5.2	0.2	0.7	1.2	2.4	1.6	2.7
ANG	4.4	6.3	−0.7	0.9	−2.3	3.0	−2.9	3.5
RA	−6.5	4.5	−0.4	0.6	−3.6	2.1	−4.0	2.4
RW	−8.5	7.4	−0.5	1.0	−1.7	3.4	−4.3	3.8
RLS	−2.2	7.1	−1.3	1.0	−2.6	3.2	−1.8	3.7
RLR	1.2	6.2	1.8*	0.8	6.0*	2.8	5.3	3.4
FA	2.1	7.6	1.1	1.0	2.0	3.5	0.5	4.0
FUA	6.7	5.7	0.8	0.8	3.3	2.7	2.9	3.4
RUW	1.3	8.5	0.1	1.2	0.7	3.9	0.0	4.5
US	7.4	7.0	0.7	0.9	3.2	3.2	2.0	3.6
UD	−0.7	4.1	−0.0	0.6	−1.2	1.9	−2.2	2.3
TPR	−3.3	5.0	−1.7*	0.7	−5.2*	2.3	−2.9	2.6
TPS	3.8	5.6	−0.5	0.8	−2.6	2.6	−1.6	2.9
TL	1.1	4.3	0.9	0.6	2.2	2.0	0.1	2.3

*$P<0.05$; **$P<0.01$.

Table 5

Regression coefficients for regressions of DMI, EFF, MF and MFHR on pedigree index plus (i) one of the live weight traits or (ii) one of the heifer type traits (See Tables 1 and 2 for abbreviations)

	DMI		EFF		MF		MFHR	
	b	se	b	se	b	se	b	se
PI	5.8**	2.2	0.6*	0.3	3.6**	1.1	3.0*	1.3
plus:								
ALW	1.7**	0.6	−0.4**	0.1	−1.0**	0.3	−1.1**	0.4
CLW	0.9	0.5	0.3**	0.1	1.1**	0.3	0.7	0.4
TM	−1	6	0.3	1.0	1.0	3.3	2.8	4.1
ST	33	32	0.0	4.8	5.7	16.7	1.1	20.4
CW	18	28	−7.2	4.1	−26.0	13.8	−26.7	17.3
BD	54	32	−2.2	4.8	−3.0	16.2	−6.7	20.3
ANG	22	24	15.0**	3.2	56.4**	10.4	61.9**	13.4
RA	−12	28	−6.0	4.1	−28.4**	13.7	−40.6*	16.9
RW	−1	26	0.6	3.9	−0.2	13.3	0.5	16.5
RLS	−3	26	−0.6	3.9	−5.8	13.3	−17.5	16.7
RLR	24	22	−1.9	3.3	−0.6	11.4	9.9	14.2
FA	10	26	−3.4	3.9	−5.1	13.2	7.4	16.4
FUA	−36	25	−2.5	3.7	−9.0	12.7	3.5	15.7
RUW	−45	29	4.1	4.3	5.1	14.8	7.8	18.4
US	−3	28	0.7	4.1	4.7	14.0	−2.9	17.7
UD	−64**	25	−7.2	3.9	−28.5*	13.0	−31.6	16.5
TPR	−3	26	−1.3	3.8	−8.3	12.9	−1.4	16.1
TPS	55	30	−2.0	4.6	7.7	15.6	21.6	19.4
TL	28	27	−3.6	4.1	−0.2	13.9	−4.6	17.4

$*P < 0.05$; $**P < 0.01$.

Table 6

Partial regression coefficients for regressions of MF and MFHR on pedigree index and a combination of some of the (i) sire transmitting abilities for type or (ii) linear heifer type scores (see Table 1 and 2 for abbreviations)

	Sire TAT					Heifer Type			
	MF		MFHR			MF		MFHR	
	b	se	b	se		b	se	b	se
R^2	33.4		22.5			50.0		31.7	
PI	4.5**	1.2	4.1**	1.4	PI	1.9	1.0	1.4	1.3
ANG	−10.1**	4.2	−9.1	4.9	ANG	57.8**	9.8	65.4**	12.8
RW	−8.4*	4.0	−10.8*	4.7	RA	−30.6**	11.3	−39.3**	14.7
RLS	7.3	4.4	8.9	5.1	RUW	29.0**	12.1	30.9*	15.7
UD	−5.5*	2.6	−6.1*	3.1	UD	−35.3**	10.9	−45.4**	14.5
US	8.5**	3.4	7.3	4.0					
FUA	14.8**	3.8	13.3**	4.6					
TPR	−10.1**	2.6	−8.0**	3.0					

$*P < 0.05$; $**P < 0.01$.

of the type traits. Using 7 TAT traits and PI together in one index improved the variance explained from 24.7% to 33.4% (MF) compared with selection on PI only.

4. Discussion

Controls on the production of milk, together with evidence of unfavourable relationships between output and some health and reproduction traits have led to a re-evaluation of breeding goals in many countries. However, the difficulty of directly measuring many potential components of a 'broader' breeding goal has led to much interest in more easily measured correlated traits, such as linear type traits and live weight. The purpose of this study was to examine the potential value of some of the type traits as predictors of food intake, efficiency and profitability, as a preliminary step towards constructing a selection index.

Several authors have defined profit equations or functions to reflect the realised profitability of cows. Groen (1988) and Keller (1990) used deterministic models and Rogers et al. (1988) used a dynamic model to describe the profitability of individual cows. Other authors combined real measurements on cows (for example production and live weights) with mathematical models to estimate food costs, (for example Tigges et al., 1986; Balaine et al., 1981; Gill and Allaire, 1976). In this paper economic merit of dairy cows has been defined as milk returns minus food, health and reproduction cost per lactation (or 38 weeks thereof). In contrast to earlier work, MF and MFHR were based entirely on records on the cows and therefore accounted for biological variation in food intake and variation in gross efficiency of conversion of food to milk. The relevance of this profit equation depends on the relevance of the management conditions and animals at Langhill to the wider population. The Langhill control line comprises cows of around UK average genetic merit and the selection line is one of the highest in genetic merit for fat plus protein yield in the UK. Therefore the animals are representative of a wide range of Holstein Friesian cows in the UK. For the majority of cows in this study the feeding system was a relatively high input diet, with 2.5 tonnes of concentrate per lactation. The relevance of results from this high input system to lower input systems depends on the presence or absence of genotype by diet interaction, a subject which is currently under investigation at Langhill. However, results from Korver (1982) and Oldebroek (1988) do not suggest an important effect of G×E interaction. That MF and MFHR were based on a lactation period of 38 weeks favoured animals which lost weight during this period, but needed additional food to get back to the same body weight. Also, for future breeding strategies it would have been more appropriate to use price estimates for the future. However, these two effects had little impact on the relationship between margins and pedigree index in a related study (Simm et al., 1994) and are therefore not expected to have an impact in this study.

Phenotypic regressions are useful for identifying the traits which have a phenotypic effect (and hence possibly a genetic effect) on dry matter intake, profitability and gross efficiency. Gravert (1985) reported that chest circumference is an accurate predictor of feed intake. Consistent with these results, regressions on body depth approached significance in this study (Table 5). Average live weight and calving live weight had opposite effects on profitability and efficiency, suggesting that animals which are heavy at the start of lactation, but lighter in mid lactation are the most profitable cows. This may be partly an environmental effect due to the ad lib. diet, since animals which were heavy at the start of the lactation had more body tissue available for mobilization, whereas animals which were heavy during lactation, partitioned more food into body tissue. More angular heifers were £79 more profitable (MFHR) per s.d. unit in this study (Table 5) and the inclusion of angularity in a model with pedigree index increased the proportion of variance in MFHR explained from 11.8% to 25.1% (Table 3). Chest width, rump angle and udder depth were also associated with EFF, MF and MFHR. De Haan et al. (1993) reported that similar phenotypic type traits (dairy form, rump angle and udder depth) were important for the prediction of a profit function, although the regression of udder depth was in the opposite direction to that reported here. This may be due to the fact that they accounted for lifetime production in their profit function, and a high score for udder depth has an association with longevity (Brotherstone and Hill, 1991). Gilmore and McDaniel (1977) reported a significant correlation between dairy character and relative annual profitability. Tigges et al. (1986) reported that udder traits had an effect on a function of net economic merit.

The low accuracy of the pedigree index is reflected by the low percentage of variance it explained in MF and MFHR. More variation would have been explained if phenotypic values for production had been included instead of PI. Since the pedigree index is available earlier in life and refers back to the selection of the sire (and dam), it is often used for selection of replacements heifers. In that situation, four phenotypic measurements on the heifer (ANG, RA, RUW and UD) improved the prediction of (phenotypic) profitability considerably (Table 6).

Partial genetic regressions of profitability on genetic merit for individual traits in the breeding objective are equivalent to the economic value of these traits as defined by Hazel (1943). Breeding values used in this study were estimated primarily from data from outside the experiment. Consequently, environmental covariances between the breeding value and the dependant variable can be ignored, and the partial genetic regressions of phenotypic margins on estimated breeding values might be used as economic values (Table 6). However, TATs were used when 6 effective daughters were present in the BLUP analysis, so the accuracy was low for some of the sires' TAT. Also, half sib groups were small, on average there were only 3.2 half sibs in the data set. Therefore standard errors for the genetic regressions on TATs were still large. Nevertheless, a combination of TATs resulted in a considerable improvement in the variance explained.

The economic value of around £3.50 per kg PI for fat + protein (Table 4 and 5) is higher than the value of a kg F + P (about £2.70). This is a reflection of the large standard error (s.e. = £1.00), and the current pricing scheme which pays for milk yield predominantly (cows selected for fat plus protein yield gave higher milk yields with slightly lower fat and protein percentages). After deduction of health and reproduction costs from MF, regressions coefficients on several heifer type traits (eg. RA, RLS, RLR, FUA and TPs) showed remarkable changes. This supports the view that there is a relationship between type traits, health and reproduction. Explicit evidence comes from e.g. Rogers et al. (1991), who reported that cows with higher scores for udder depth had lower somatic cell counts (SCC) and that UD, FUA and teat placement were genetically correlated with SCC. Cue et al. (1990) found a negative phenotypic correlation between calf pin setting and calving ease but a positive correlation for maternal calving ease and rump pin setting. Dadati et al. (1986) found no phenotypic correlations between type traits and calving interval, but found genetic correlations between calving interval and chest floor, rear udder and capacity and antagonistic genetic correlations between calving interval and dairyness and dairy character. The relatively low cost of health and reproduction events compared with food costs and milk returns (Table 1) made associations with health and reproduction less important in this analysis. Also, only cows with a consecutive calving date available were included in this analysis. This therefore excluded animals culled and the consequence is that health and reproduction costs are likely to be underestimated in this study.

Results from this analysis showed that a breeding goal which is a function of production, feed intake, efficiency, health and reproduction, can be predicted best by a combination of pedigree index, live weight and linear type traits. Work is now in progress to produce more accurate estimates of genetic associations between these traits, and to construct a set of selection indices to improve profitability. These will allow for various combinations of measurements to be used depending on whether or not information is available on live weight, linear type traits and food intake.

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Résumé

Veerkamp, R.F., Simm, G. et Persaud, P., 1994. Intérêt des critères linéaires de morphologie pour la prédiction de la consommation, de l'efficacité alimentaire et des marges économiques chez les bovins laitiers. *Livest. Prod. Sci.*,, 38: 179–189.

La production, la consommation alimentaire, l'efficacité alimentaire, l'état sanitaire et la reproduction sont importants pour la sélection des bovins laitiers. La mesure de ces caractères à grande échelle n'est pas aisée et il est donc intéressant d'examiner l'intérêt des caractières corréleés à intégrer dans les index de sélection. Dans cette étude, on a examiné les relations entre critères linéaires de morphologie, poids vif, index pour production de maitière grasse et protéique et (i) consommation de matière sèche (DMI), (ii) efficacité energétique brute (EFF), (iii) marge alimentaire (MF) et (iv) marge finale en tenant compte des coûts alimentaires, sanitaires et de reproduction (MFHR)). Une analyse de régression a montré qu'une grande augmentation du R^2 pour la prédiction de PMI, EFF, MF ou MFHR a été obtenue quand on incluait dans le modèle de régression le poids vif moyen pendant la lactation, le poids vif au vêlage et (i) la note de pointage linéaire en première lactation ($n=164$) ou (ii) l'index morphologique du père ($n=302$). Les différents modèles ont montré que les caractères de morphologie sont plus intéressants que les caractères de poids vif pour la prédiction de MFHR. Les coefficients de régression ont été obtenus par maximum de vraisemblance restreinte. Les caractères de morphologie qui paraissent intéressants sont la profondeur de mamelle, l'angularité et l'inclaison du basin. Un écart-type de la note d'angularité correspond à 79 livres pour MFHR. Les résultats ne sont pas suffisamment concluants pour développer un index de sélection mais montrent qu'un combinaison du type, du poids vif et de la production est susceptible d'être retenue dans les futurs indices de sélection.

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ODELLING TO ESTABLISH THE ECONOMIC VALUE OF LONGEVITY IN THE DAIRY COW

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bstract

urplus of dairy products, public concern for animal welfare, the emergence of nucleus breeding schemes and changes in the arket for milk in western Europe have encouraged the development of a selection index for profit (PINII) that includes ngevity of the cow as a goal trait. The PINII needs a relative economic weight for longevity. Stochastic dynamic ogramming (SDP) establishes this as the increase in long term investment potential of dairy cows associated with a given nprovement in longevity. The SDP gives the economic weight under optimum replacement decisions. A simulation model of e dairy cow gives the economic performance of the cow in all possible states (lactation numbers and milk yields) for use in the DP. This paper describes the simulation model used in the construction of the PIN and identifies critical elements that require ore empirical information. There is in particular a need to establish the expected cost of health care over the lifetime of the ow.

troduction

both high and low input systems, cows of high genetic merit for milk solids give consistently higher financial returns than ntemporaries of only average genetic merit (Veerkamp et.al, 1994). Despite this, 'broader' selection goals are being developed r dairy cattle breeding for four main reasons:

(1) Surplus of dairy products in many western countries has led to production control and hence greater emphasis on reducing unit costs of milk production at the expense of higher production per se.
(2) Growing public concern for the health and welfare of farm animals.
(3) The emergence of nucleus breeding schemes which make the direct recording of 'new' selection traits more feasible.
(4) The expectation that the fat:protein price ratio will continue to decrease in the EC and that the extra processing costs of milk volume (e.g. transport and storage) may be directly levied on individual producers.

eerkamp et. al. (1994) have responded to this by developing a selection index PINII which includes the value of milk nstituents (carrier, fat and protein) and longevity as goal traits. Linear type traits are used as index traits because no ansmitting abilities for longevity are available in the UK, whereas reliable estimates for the genetic relationship between type nd longevity are available from Brotherstone and Hill, 1991. Economic weights were derived for all goal traits in PINII using a ochastic dynamic programming (SDP) model of the milk production process (Stott, 1994). The resulting index gave an pected £0.70 (5%) higher annual rate of genetic progress than a comparable production index (Veerkamp et. al., 1994).

n important feature of the SDP model in this context is that it brings together the concepts of an economic model and a ophysical model of the milk production process. The economic model is founded on the classical static production function Debertin, 1981). The financial output of a livestock production system responds to increasing inputs at a diminishing rate, this known as the 'law of diminishing returns.' An optimum level of input to the system therefore exists where the marginal cost of n additional unit of input is exactly matched by the value of the resulting additional unit of output. It is the purpose of the conomic model to establish this optimum level of input to the system. By contrast, the biophysical model of the same livestock roduction system is more likely to be dynamic and stochastic, reflecting the realities of the production process. It is unlikely owever to feature the economic concept of an optimal input level.

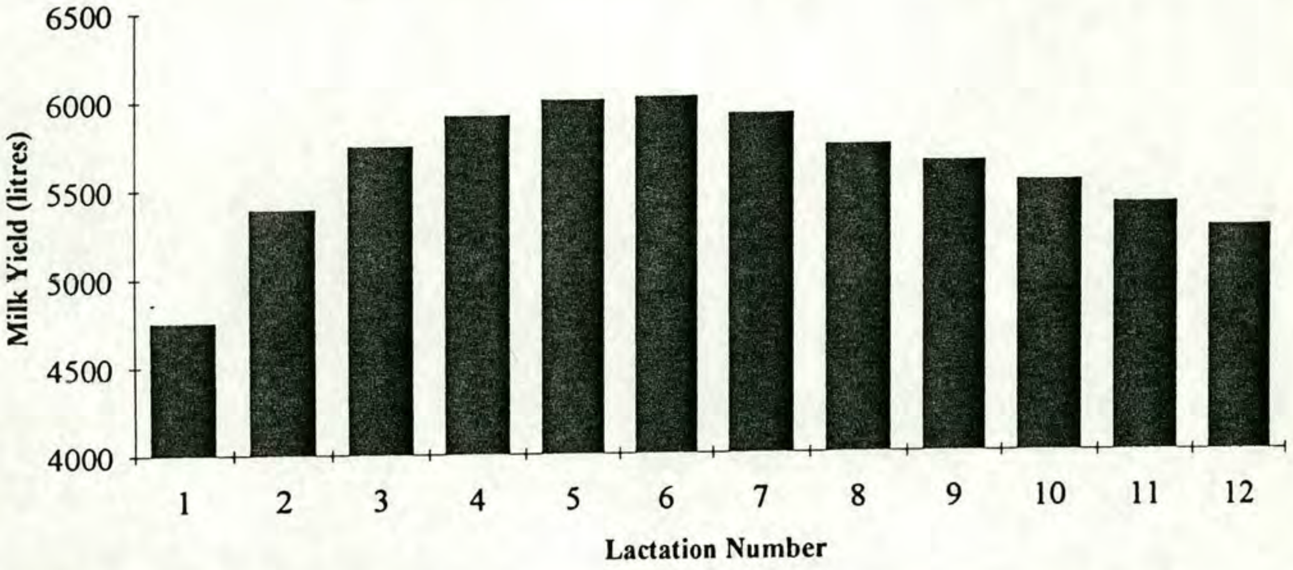
the law of diminishing returns applies, then the economic weights used in PINII are not fixed but depend on the relative tensity of the production process. The aim of this paper is to describe the SDP model used to derive economic weights for INII and use it to explore the extent of this phenomenon.

lethods

he long-term milk production process was represented approximately by a decision tree (Boehlje and Eidman, 1984). The rocess is assumed to begin with a current heifer. Milk production continues into the future in a series of 20 annual stages. uring each stage, the expected net revenue (stage return) is calculated. This will depend on the 'state' at each stage which is efined by yield production class and lactation number. There are 15 yield states representing, approximately, the Normal istribution of milk yield at each lactation state. Stage return will also include the cost of possible enforced (involuntary) eplacement of the cow at any stage and the consequences of the decision to replace a cow voluntarily. Replacement will also nfluence the state and hence stage return in subsequent stages. Dynamic programming (Bellman, 1957) makes it possible to btain the sequence of voluntary replacement decisions that maximise the discounted stage returns (net present value, NPV). he annual return from long-term investment in dairy cows can thus be expressed as an annuity equivalent of the NPV (Boehlje and Eidman, 1984). By examining the effect on this annuity, of a change in the probability of involuntary culling, it is possible to establish the economic value of longevity for use as an economic weight in a selection index. Economic weights of other goal traits can be established in the same way. Fuller details of this procedure are given by Stott (1994) and by Veerkamp et.al. (1994).

Average milk yield in each lactation state is given in Figure 1. The relative yields in each state were based on NMR records (G.Swanson, personal communication). Ideally, they should be obtained using data from the same cows in each lactation, not subject to selective replacement. This is difficult in practice. The possible effects of not doing this are explored by Stott (1994). The absolute milk yields used were chosen so as to produce a herd average yield of 5,500 litres, typical of UK dairy farms. The decline in milk yield with increasing lactation number in older cows provides the necessary incentive to voluntary replacement.

Figure 1: Average Milk Yield in each Lactation State



The model of Van Arendonk (1985) provided daily milk yields corresponding to the above lactation averages according to the parameters given in Table 1. It also provided daily estimates of protein concentration, fat concentration and weight change. From these inputs a daily minimum cost ration was formulated using the effective energy concept of Emmans (1994). The diet consisted of concentrate and either grass or silage according to the time of year (Table 1). Substitution rates were calculated between forage and concentrate according to intake capacity which was in turn a function of cow weight at calving, ME and dry matter of the ingredient. Diet ingredients could then be changed on a daily basis to meet the changing energy requirements for maintenance, growth, pregnancy and production. A margin over feed was then calculated using the milk and feed price assumptions given in Table 2. To calculate the stage return, a fixed calf value was added to and a fixed cost subtracted (Table 2) from total margin over feed. The voluntary replacement costs and expected involuntary replacement costs were also accounted for using a fixed replacement heifer price (Table 2) and the cull cow values and involuntary replacement probabilities given in Table 3. In the event of involuntary replacement, cull cow values were half those given in Table 3. This reflected the extra costs associated with involuntary replacement which include disease, death and reduced carcass value.

Table 1 Key Parameters used in the Dairy Cow Model

Milk Quality (Mature Average)		
Butterfat	4.10	%
Protein	3.35	%
Other solids	5.39	%
Reproductive Performance (Days)		
Month of calving	September	
Lactation length	305	
Calving Interval	365	
Days open	88	
Age at first calving	730	

Growth (kg)		
Mature cow weight	650	
Calf weight	48	
Maximum weight loss	50	
Nutrition		
ME grass	12	MJ/kg
ME silage	9.5	MJ/kg
ME concentrate	12.5	MJ/kg
Dry matter of concentrate	880	g/kg
Dry matter of forage	220	g/kg
Minimum of forage	25	%
Turn out to grass	15th	April
Turn in to silage	15th	September

Table 2 Parameters used in the DP model that were independent of state

Discount rate	5	% *
MILK PRICES		
Butterfat value	2.85	£/kg §
Protein value	4.27	"
Lactose value	0.00	"
Carrier value (Milk)	-3.00	p/kg
Seasonal Price Adjustment		See†
CALF VALUE	100	£/cow/year‡
REPLACEMENT HEIFER PRICE	700	£
FEED COSTS		
Concentrate	155	£/t
Silage	18.7	£/t
Grass	9.9	£/t
'OTHER COSTS'	350	£/cow/year Ø

* Approximate current real interest rate

§ S.Amies, personal communication

† Federation of United Kingdom Milk Marketing Boards (1992)

‡ SAC (1990)

Ø Thomas and Perry (1991). Costs excluding feed and replacement

Table 3 Probability of Involuntary Replacement and Cull Value[*] by Lactation Number

Lactation Number	Involuntary† Replacement	Cull Value‡ (£)
1	0.136	306
2	0.149	301
3	0.179	296
4	0.198	291
5	0.227	286
6	0.245	280
7	0.259	275
8	0.273	270
9	0.290	265
10	0.310	260
11	0.326	255
12	0.345	250

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[*] Cull values after involuntary replacement are assumed to be half the values given here.

† Taken from Van Arendonk (1985a)

‡ Based on Meat and Livestock Commission UK averages by grade for 1992

Results

The average feed requirements predicted by the model and the prices in Table 2 gave feed costs as shown in Figure 2. Feed costs are dominated by silage due to a higher price than standard (SAC, 1993) and due to the prediction of a higher forage to concentrate ratio by the model than normal standards. These two effects tended to cancel one another out, leading to margin over feed ranging from £720 (lactation 1) to £990 (lactation 5), both close to standard.

The economic weight of longevity using the model and assumptions described here (herd average level of involuntary culling 19%) was £5.52 pa per 0.01 fall in the level of involuntary culling (Table 3) in the first four lactations (Veerkamp et. al., 1994). Figure 3 shows how this economic weight changes at different herd average levels of involuntary culling. As herd average level of involuntary culling decreases, so the marginal benefit of additional improvement declines, i.e. there are diminishing returns to improvements in longevity in the dairy cow. The same effect is observed at higher herd average milk yields i.e. at higher production intensity.

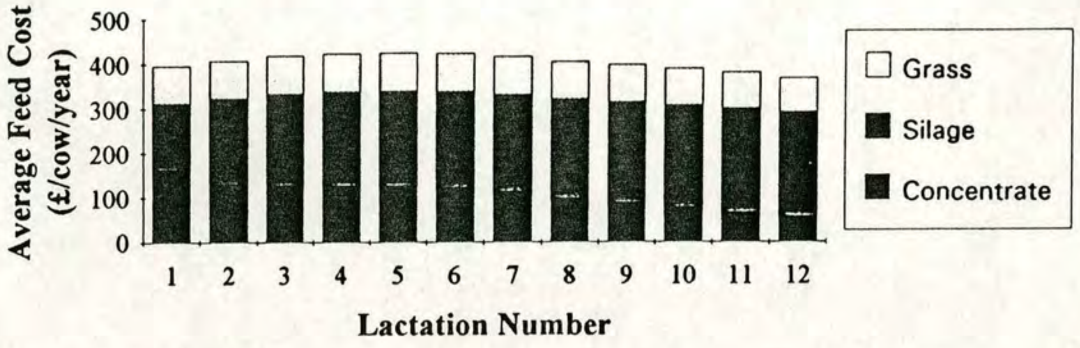


Figure 2 Average Feed Cost Predicted by the Model

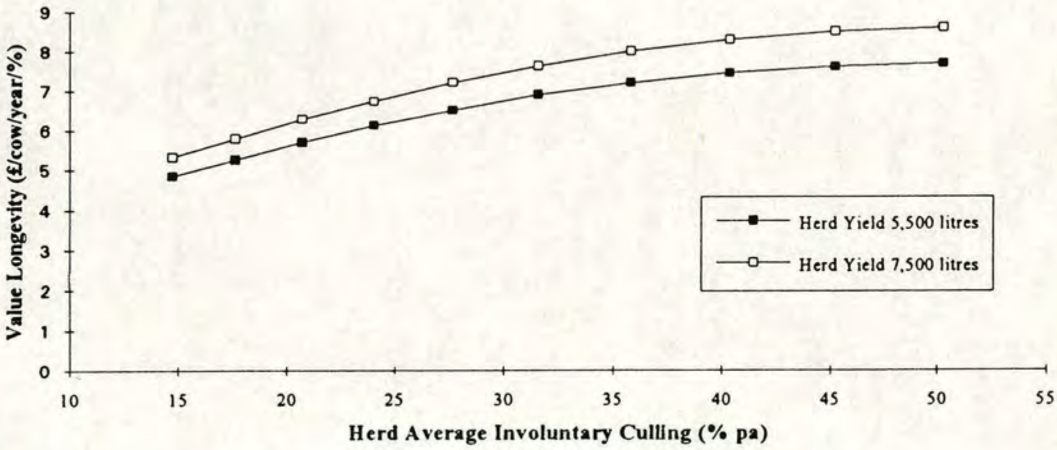
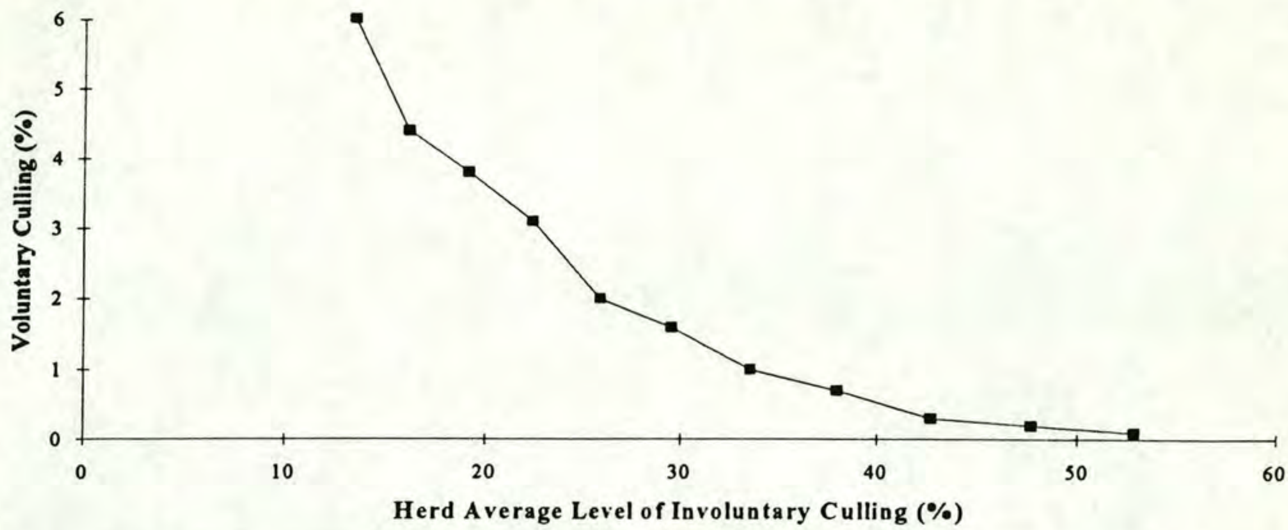


Figure 3: Economic Weight for Longevity

Discussion

The results from the SDP model exhibit the law of diminishing returns. A decrease in the levels of involuntary culling reduces the direct costs of replacement, results in the retention of a greater proportion of high profit cows and gives greater scope for voluntary replacement of low profit cows. As the absolute level of involuntary culling changes, so the relative contribution of each of these various benefits will alter. The level of voluntary culling rises exponentially as involuntary culling levels fall (Figure 4). This suggests that voluntary replacement of low profit cows becomes increasingly important at low levels of involuntary culling. The marginal net benefits of this might be less than for the savings in direct costs at higher levels of involuntary culling. This may explain the diminishing response effect observed.

Figure 4: Effect of Level of Involuntary Culling on Voluntary Culling



The change in the economic weight for longevity with level of involuntary culling is relatively small. It is not sufficient to seriously alter the efficiency of PINII as a selection index (Veerkamp et.al., 1994). In practice however, the change may be greater than shown here. The health costs associated with voluntary replacement are likely to exhibit diminishing responses too (McInerney, 1988). Here these health costs are crudely estimated and assumed fixed. Also, the marginal costs of making improvements are likely to increase as the benefits decrease. These issues together suggest that the economic weights of longevity and the relative net benefits of improvement will vary between individual herds and over time during a breeding programme. The same may well be true of other goal traits. Further study of this issue therefore seems justified and will be undertaken under an on-going research programme at SAC of which the work reported here forms a part.

Acknowledgements

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PROFIT INDICES FOR UK DAIRY CATTLE

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INTRODUCTION

The objective of many dairy farmers is to maximise profitability, consistent with the health and welfare of their animals. Although management and feeding play important roles in achieving high margins there is now good evidence that selection for higher milk solids production can also have a dramatic impact on profitability. The results from Brotherstone and Hill (1987) and Persaud *et al* (1990) clearly show that the nationally available 'selection tools' (formerly ICCs and CGIs, now PTAs) are useful predictors of yield. Results from Langhill give an excellent example of how selective breeding using these tools enhances not only yield, but overall economic performance of dairy cows as well. From the early 1970s cows at Langhill have been bred to bulls with the highest possible PTA for kg fat plus protein. Since the mid-1970s a control herd of around national average PTA for kg fat plus protein has also been maintained at Langhill, managed and fed identically to the selection herd. By the late 1980s, yields of the selection and control herds differed by about 20 per cent, or around 90 kg of fat plus protein. More recently, the performance of the cows has been evaluated under two different feeding systems. Both systems involve ad libitum feeding of a complete diet, based on silage, brewers grains and a compound balancer meal. Cows in the low forage group receive a diet averaging about 2.5 tonnes of concentrates per cow per year. The rest of the animals are maintained on a higher forage system with around 1 tonne of concentrates per cow per annum. Results from the first 4 years of these feeding systems are shown in the Table 1 below. These results show that in both high and lower input systems cows of high genetic merit out-perform contemporaries of only average genetic merit.

TABLE 1: Performance and efficiency of selection and control line animals to 38 weeks of lactation, over 4 years of the Langhill feed intake trial from 1988/89 to 1991/92.

	Low Forage: Selection	Control	High Forage: Selection	Control
Number of lactations	102	84	117	74
Milk yield (kg)	7569	6537	6372	5360
Fat %	4.19	4.20	4.54	4.37
Protein %	3.09	3.19	3.07	3.09
F + P (kg)	550	481	482	398
Dry Matter (kg)	4803	4603	4149	3948
Efficiency (MJ/MJ)	0.418	0.377	0.440	0.374
Live weight (kg)	610	610	601	590
Condition score (0-5)	2.55	2.70	2.45	2.59
Margin over feed costs (£)	1008	825	914	712

These results give valuable evidence on the economic benefits of selection on fat and protein yield alone, but there is now growing interest in 'broader' selection goals, stimulated by:

(i) The surplus of dairy products in many western countries. Quotas or price constraints have made higher production per se less attractive, and reducing costs of production more attractive.
(ii) Growing public concern for the health and welfare of farm animals, as well as the direct economic consequences of disease. (For these reasons the breeding programmes in Scandinavia now include evaluations for disease resistance).
(iii) New breeding schemes, initiated in the UK and elsewhere, which involve centralised nucleus herds of dairy cattle, rather than progeny groups dispersed over many commercial herds. These centralised schemes permit direct recording of 'new' traits for selection, e.g. food intake, health events.
(iv) The expectation from milk marketers that (i) the future fat:protein price ratio will continue to decrease in the EC and (ii) a charge will be included for volume of milk and number of milk collections. Hence, transport and storage costs become important.

The introduction of PIN in 1991 was the first initiative to take some of these alterations on board. PIN gave differential weightings to milk, fat and protein (-0.039, 0.94 and 2.75, respectively) and allowed farmers to asses the potential financial benefit of selecting on yield. It accounted for (i) an expected fat:protein price ratio of 1:1.2, (ii) quota leasing costs set against fat yield, (iii) differential feed costs required to produce fat and protein yield, (iv) feed costs to produce a kg milk, with the fat and protein extracted, but with lactose included and (iv) transport and processing costs set against milk yield. However, PIN does not use measurements on any traits other than production.

Further research at the University of Edinburgh (Brotherstone and Hill, 1991) and the Scottish Agricultural College (Veerkamp, Simm and Persaud, 1994) has shown that linear type traits and live weight traits are related to some traits (i) which are not easily measured in a progeny testing scheme, like feed intake and health costs or (ii) which are measured too late to be included in selection decisions, like cow herd life. Here, in this context, type traits become important, not because of the appearance of the cow, but because of scientific evidence of genetic correlations between type and economically important traits. For these reasons, a three year research project was launched in 1993 at SAC/University of Edinburgh, funded by MAFF, HFS and MMB, to investigate the possibility of combining production traits with several other traits, like type, health and reproduction, in so called profit indices. The results of this work will be a new set of compatible selection indices which can be used widely in the UK dairy industry. This paper reports on the first outcome of this project: a revised PIN index which will balance the economic importance of herd life and the economic importance of production into a single value available for selection of dairy bulls and cows.

METHOD

Since they were first proposed in the 1940s selection indices have been used widely to help define breeding goals and selection criteria in farm animals. In brief, they help to put the right emphasis on each of the traits of economic importance in the animals concerned. In principle, the construction of a selection index is straightforward, requiring:

(i) a list of traits of economic importance ('goal' traits);
(ii) relative economic values of these goal traits;
(iii) a set of measurements (index traits) which can be obtained on candidates for selection and/or their relatives to predict their merit for goal traits. These may be the same as, or different from, goal traits.
(iv) genetic and phenotypic parameters for (some of the) goal traits and for index measurements. These are heritabilities and correlations which indicate the extent to which different traits are under genetic control and the strength of the associations between the traits.

Milk (or more precisely 'carrier' - milk after extraction of fat and protein), fat and protein are all obvious 'goal' traits for an index of profitability. Hence these have been chosen as the first three goal traits for a "Mark II PIN". The fourth trait chosen as a goal trait for PINII was longevity. In this case longevity is defined as the chance that a cow is not culled, for any other reasons than yield, in the first four lactations. The genetic merit of bulls for each of the three milk traits is estimated directly through the PTAs for kg milk, fat and protein (by the Animal Data Centre). There is currently no direct estimation of genetic merit for longevity, although it is likely that direct evaluations will be available in the UK in the future. Hence, there is interest in indirect measures of longevity, such as linear type scores.

From studies in the UK (Brotherstone and Hill, 1991) and elsewhere, there is good evidence that some type traits provide a useful prediction of longevity. These results show genetic relationships between longevity and sires' transmitting ability for the following type traits: angularity (ANG), foot angle (FA), udder depth (UD) and teat length (TL) (with greater angularity, steeper foot angle, udders above the hocks and shorter teats being advantageous). The results from Brotherstone and Hill suggest that there is a linear genetic relationship between these traits and longevity, and there does not appear to be an intermediate genetic optimum for these traits. On the basis of this research evidence, these four type traits have been chosen as index traits for use in PINII to predict longevity (some other traits did not add additional information, because of the high genetic correlations between these traits and traits already in the index, e.g. between fore udder attachment and udder depth). As the research project progresses, the role of these and other type traits in predicting food intake, health events, reproductive success and longevity will be examined in greater detail and this may lead to new traits being included. However, the choice of these four type traits for the version of PINII proposed here is considered to be both robust and justified, in the light of sound research evidence. Hence the index measurements used to calculate PINII values will be PTAs for kg milk, fat and protein, and for angularity, foot angle, udder depth and teat length in standard deviation units. These evaluations are published routinely by the Animal Data Centre (ADC) (yield traits) and by the HFS (type traits). As with the current PIN, converted foreign proofs will be used as well as home proofs - the only change here is that conversions for foreign type proofs will be needed to get the full benefit of PINII.

Economic values

There are several different viewpoints which can be taken in calculating economic values (eg national returns, individual producers returns), but in this case they have been derived from the individual producers viewpoint. The perspective of individual producers will be to improve cow profitability. Therefore economic values for the goal traits should reflect the marginal returns minus the marginal costs of producing an extra unit of each goal trait. To avoid 'double counting', these economic values are derived separately for one goal trait at a time, whilst assuming that performance in the other traits is constant. The simplest way to calculate economic values from the producers viewpoint is to use current monetary values for each of the marginal costs and returns. However, cattle breeding is a long term business and it makes more sense to predict what the future costs and returns will be, at least where there is good reason to believe these will change. Hence in the current index a price ratio for fat:protein of 1:1.5 has been assumed, with absolute prices of £2.85 and £4.27 per kg, respectively. The marginal costs of producing each extra kg fat or protein needs to be set against these marginal returns. Also a cost of £1.46 per kg fat was included for leasing quota (6 p/kg for milk of 4.10% BF) because the fat 'trigger' within the quota regulations is now being triggered routinely. As payment is directly proportional to the weight of fat and protein, there is no marginal return from producing an extra kg carrier. However marginal costs for food to produce the lactose in 'carrier', and costs of transport and processing (£0.03 per kg) have been assigned to each extra kg milk, as in the current PIN.

Calculating the economic value of a longer herd life is more complicated. The benefits come from (i) lower replacement costs, (ii) increased income as a result of a higher proportion of the cows producing at mature level, (iii) reduced amount of feed necessary for non producing heifers and (iv) a greater opportunity to cull low producing cows (Rendel and Robertson, 1950). The approach used here is to simulate a whole herd (Stott, 1994) on the computer. The attractions of this approach, which is called dynamic programming, are that it allows a more realistic calculation of the true economic values, given the complexity of real dairy farms. For example, dynamic programming (DP) allows us to build into the economic evaluations the fact that farmers will feed as well as breed for higher profitability, and hence change feeding in response to a change in milk payment schemes, as well as altering bull selection decisions.

Whilst DP is most useful for evaluating the benefit of increasing herd life, this approach has been used consistently in this case to calculate economic values for all the goal traits. For this purpose the model used earlier by Stott, was modified to include a cow rationing model developed by G. C. Emmans at SAC. Hence, the marginal costs and returns mentioned elsewhere were not simply subtracted from one another, but were 'fed into' the DP model. (For anyone unnerved by this approach, the values finally derived for milk, fat and protein were close to those derived by 'pen and paper'). Table 2 shows the resulting economic values for the milk, fat, and protein yield and for longevity.

Genetic Parameters

Genetic and phenotypic parameters (Table 2) were taken from Brotherstone and Hill (1991 and 1993). Well known selection index equations (Hazel, 1943) were used to calculate optimal index weighting factors and evaluate the consequences of selection. Some re-scaling has to be applied to the weighting factors as these have to be applied to PTAs for milk, fat and protein and to genetic evaluations for the type traits (expressed in standard deviation units).

TABLE 2: Economic values derived with the Stott and Emmans models and heritabilities (diagonal), phenotypic (above the diagonal) and genetic correlations (below the diagonal) from Brotherstone and Hill (1991 and 1993).

	Longevity[1] (%)	Milk [2] (kg)	Fat (kg)	Protein (kg)	ANG	FA	UD	TL
Economic value (£)	5.52	-0.03	0.60	4.04				
Standard deviation	49	895	35	27	1.34	1.17	1.64	1.24
Longevity	.06	-	-	-	-	-	-	-
Milk	.00	.47	.83	.94	.27	- .03	- .28	.05
Fat	.00	.77	.52	.87	.25	- .02	- .25	.02
Protein	.00	.93	.85	.45	.24	- .02	- .27	.05
Angularity (ANG)	.11	.44	.42	.43	.26	- .04	.06	- .01
Foot angle (FA)	.09	.02	.05	.07	- .13	.27	.10	- .01
Udder depth (UD)	.21	- .48	- .40	- .44	.01	.03	.39	- .09
Teat length (TL)	- .19	.18	.12	.17	.08	- .09	- .21	.44

1 Percentage cows not involuntarily culled in the first 4 lactations, corrected for genetic differences in yield (hence the zero correlations with yield traits)

2 The value for milk is after removing all of the protein and fat.

RESULTS

The weighting factors calculated for PINII are given in Table 3, for two different breeding objectives: increasing margins from yield only (as for the current PIN, but with the new economic weightings) or increasing profit - a combination of yield and longevity. A third objective, longevity, is given for explanatory reasons. The four linear type traits are in the index, as they help to predict longevity. These index weightings give optimal economic responses and are calculated using the economic values and parameters in Table 2.

TABLE 3: Optimum index weightings for PINII, when the interest is in yield or longevity only or in profit (yield plus longevity).

Goal: Index:	profit PINII	yield YIN	longevity LIN	direction
PTA for:				
Milk (kg)	- 0.015	- 0.030	0.015	
Fat (kg)	0.60	0.60	0.00	
Protein (kg)	3.84	4.04	- 0.20	
Angularity (sd)	3.9	0.0	3.9	angular
Foot angle (sd)	1.8	0.0	1.8	steeper
Udder depth (sd)	4.8	0.0	4.8	above hock
Teat length (sd)	- 4.1	0.0	- 4.1	shorter

If selection is for yield only, then the expected maximum selection response of £15.3 per cow per year can be achieved (Table 4) in a simple breeding scheme. This response is a combination of 119 kg milk, 5.0 kg fat and 3.9 kg protein per year. When selection is for profit then a slightly lower rate of genetic gain is achieved for the production traits, but longevity of the cow is genetically improved (0.23 cows less culled involuntarily in the first four lactations in a 100 cow herd). This is predicted to increases the annual selection response by £0.70 per year (5%) compared to selection on a combination of milk, fat and protein only.

TABLE 4: Selection effect[1] (per cow per year), for an assumed breeding scheme, when the revised three indices are used.

Goal: Index:	profit PINII	yield YIN	longevity LIN
Response per annum in:			
H (£)	16.0	15.3	4.5
longevity(%)	0.23	0.00	0.81
milk (kg)	114	119	0
fat (kg)	4.8	5.0	0.0
protein (kg)	3.8	3.9	0.0

[1] calculated as $i \times \sigma_I \times b_I$, with $i = 0.22$, based on a four pathway breeding scheme.

Although only four linear type traits are included in the index, the mean values for some of the other type traits are expected to change, as a consequence of genetic correlations between the traits. The magnitude of these correlated responses is given in Table 5. The benefit from selection on PINII is shown, for example, when the selection responses for UD are compared. Selection for milk yield will result in deeper udders and selection for longevity will result in shallower udders, but selection on PINII will give a balanced rate of genetic gain, based on the economic values of longevity and yield. The same conclusions could be drawn for FUA, even though it is not included in the index. Another observation is that TL is not expected to change following selection on PINII, even though it has a negative weighting in the index. PINII simply counterbalances the expected increase in TL following selection on yield alone.

TABLE 5: Annual selection effect for linear type traits, assuming a simple breeding scheme and selection on PINII, YIN or LIN. The units are the scores from 1-9, with an approximately intermediate mean value.

Index:	PINII	YIN	LIN	min	max
STA	0.07	0.05	0.07	125 cm	149 cm
CW	- 0.03	- 0.02	- 0.05	Narrow	Wide
BD	0.04	0.04	- 0.01	Shallow	Deep
ANG	0.08	0.06	0.05	Coarse	Angular
RA	- 0.02	- 0.02	- 0.02	High	Low pins
RW	0.00	0.00	0.00	Narrow	Wide
RLS	0.00	0.01	- 0.01	Straight	Sickled
FA	0.02	0.01	0.04	Low	Steep
FUA	- 0.02	- 0.05	0.09	Loose	Strong
US	0.02	0.02	0.00	Broken	Strong
UD	- 0.05	- 0.10	0.15	Below	Above Hock
TPR	0.01	0.00	0.05	Wide	Close
TPS	0.06	0.06	0.01	Close	Apart
TL	0.00	0.03	- 0.11	Short	Long

Theoretically, the calculated weighting factors give optimum responses in the base situation only and therefore a sensitivity analysis on the economic values was carried out. Table 6 shows that the index proposed is robust to large changes in the economic value of longevity, milk, fat and protein yield. This indicates that producers can have confidence in using the index, even if they expect different market values or costs (eg. national or regional differences in payment schemes) to those assumed in calculating economic values for PINII.

TABLE 6: Efficiency (%) of using PINII compared to the optimum index, in situations where the true economic values for one of the goal traits (milk, fat and protein yield and longevity) differ by a factor of two (-50 and +50 percent) from the base values (Table 2), while keeping the other economic values at the base values.

	- 50%	+ 50%
Longevity	99*	99
Milk	100	100
Fat	100	100
Protein	96	99

*eg. the rate of genetic gain with PINII is 99% of the maximum genetic gain, when using the optimum index in the situation where the economic value of longevity is £2.76 instead of £5.52 and all other economic values are at their base value

The economic values of milk and protein are often the subject of debate and therefore it seems important to investigate the selection consequences of different indices. Part of this question has already been answered in the sensitivity analysis, but in Table 7 there are a few more practical examples. Obviously these values are approximations and the absolute values will differ, but they might give an indication of the consequences of selection on the different indices. For example, animals in the top 5% on an index combining fat plus protein yield will have a genetic merit of 1065 kg more milk per cow per lactation. However, protein percentage will drop and fat percentage will increase as a consequence of selection on F+P. The milk returns will not be highest with the proposed index, but the compositional quality is better, and given the feed costs and quota leasing costs the expected margins are expected to be highest with PINII.

TABLE 7: Approximate genetic advantage of the top 5% animals, using several different indices.

	Population average	Index: milk	F+P	PINI	YIN	PINII
longevity (%)						+ 2.1
milk (kg)	5500	6726	6565	6491	6577	6534
fat (kg)	226	264	275	273	271	269
protein (kg)	184	218	219	219	220	219
fat %	4.10	3.93	4.18	4.21	4.12	4.12
protein %	3.35	3.24	3.33	3.37	3.34	3.35
fat:protein	1.22	1.21	1.26	1.25	1.23	1.23
Milk returns[1] (£)	1264	1483	1519	1517	1515	1505
Margin[2] (£)	0	+ 123	+ 136	+ 138	+ 139	+ 146

[1] Based on -£0.03/kg milk, £2.85/kg fat and £4.27/kg protein.

[2] Margins are based on the economic values in Table 2.

TABLE 8: An example of the index values and the ranking on the different indices for the top 20 bulls (PINI, November 1993). For some bulls no type conversions were available, and therefore average type values were assumed (numbers in brackets).

	Scores:				Ranking:			
	PINI	PINII	YIN	LIN	PINI	PINII	YIN	LIN
Mountain	80	151	129	22	18 =	1	6	1 =
Hodges	88	147	128	19	6	2 =	7	4
Hardtac	92	147	133	14	2 =	2 =	4 =	6
Curious	87	145	135	10	7 =	4 =	3	11
Lux	98	(145)	145	(0)	1	(4 =)	1	(17 =)
Constantijn	92	141	133	8	2 =	6 =	4 =	15
Belt	84	(141)	141	(0)	10 =	(6 =)	2	(17 =)
Lexus	81	140	119	21	15 =	8	15	3
Mich	89	139	126	13	5	9	8	7 =
Inspiration	84	138	123	15	11 =	10 =	12	5
Nordkap	85	138	125	13	9	10 =	9 =	7 =
Benchmark	80	137	115	22	18 =	12 =	17 =	1 =
Carousel Amos	83	137	124	13	12	12 =	11	7 =
Burghorner	82	133	120	13	13 =	14	14	7 =
Fari's Wayne	87	131	122	9	7 =	15	13	12 =
Bluff	82	(125)	125	(0)	13 =	(16)	9 =	(17 =)
VicKai	81	124	115	9	15 =	17	17 =	12 =
Rabamba	92	120	111	9	2 =	18	18	12 =
Amos	80	109	108	1	18 =	19	19 =	16
Starmann	81	(108)	108	(0)	15 =	(20)	19 =	(17 =)

An example of the application of the new indices is given in Table 8. Table 8 gives the ranking of the top 20 bulls on PINI, YIN, LIN and PINII, using the November list (ADC, personal communication). As there are no French, German or Canadian type conversions available, these bulls received a base value for the LIN (zero). Although this might seem strange, it is normal practice in animal breeding to assume average values for animals for which no information is available to suggest otherwise. A re-ranking occurs, when the different indices are compared and most of the re-ranking is a consequence of the change from PINI to YIN (i.e. because of revised economic values), the next step to PINII hardly changes the ranking. The PINII values are expressed in pounds (£) and indicate expected differences in profit between daughters of different bulls over the next 20 years, but expressed as an annuity (discounted margin in pounds per cow per year). This longer time scale on which the economic values were expressed, compared with the current PIN, was needed to evaluate the full benefits of longevity. Obviously, it is important to realise that PTAs (and PINII) are relative to the base animals (eg. in 1990 for the yield traits) and an absolute value of PINII (eg PINII is £+100) indicates the extra profit compared with the base animals. PINII can also be used to *approximate* the average difference in profit using either bull A or bull B. For example, if PINII values are +150 and +125, for bull A and B respectively, than on average daughters of bull A are expected to be approximately £25 more profitable per year than daughters of bull B.

DISCUSSION AND CONCLUSIONS

The objective of this paper was to demonstrate how linear type traits and milk production traits can be combined in an economic index. A possible PINII was proposed combining PTAs for milk traits (published by the ADC) and for four linear type traits (published by the HFS). Selection on PINII gave an expected £0.70 higher annual rate of genetic progress (5%) compared with selection on an index combining PTAs for milk, fat and protein only. The extra benefit came as a consequence of the longer herd life of cows. Selection on PINII is expected to halt the decrease in udder depth score and fore udder attachment which would occur as a consequence of selection for yield alone. In genetic standard deviation units the final weighting for yield to type is 3:1. Although a fat and protein price ratio of 1:1.5 was assumed, and some other assumptions were made, the proposed index was relatively robust. When one of the economic values (for milk, fat, protein or longevity) differs by 50% from the values used, at least 96% of the optimum progress will be achieved still by using PINII. After consultation with the industry the intention is that the Animal Data Centre will include calculation of these new index values - possibly in the July 1994 evaluations. A decision is needed as to how many index values are calculated. In addition, as a consequence of this consultation, there may be some refinements to the index before then but the approach used, and the expected results should be similar to those reported here. A large part of the further effort in this project will be devoted to using the comprehensive set of data on production, food intake, type traits and health events from the SAC/University of Edinburgh Langhill Dairy Cattle Research Centre, as well as 'national' data sets on milk production and type classification for the estimation of genetic parameters and refining the calculation of economic weights. A lack of knowledge of many of the relationships amongst these traits prevented inclusion of more traits of economic importance in the index proposed here. The results of this further work, will be a set of compatible selection indices which can be used widely in the UK dairy industry. At one extreme there will be indices for farmers recording only production, and at the other extreme there will be very comprehensive indices for use in nucleus breeding schemes, or for breeders prepared to take more comprehensive measurements, for example of live weight, linear type traits and health events.

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COMBINING TRANSMITTING ABILITIES FOR YIELD AND LINEAR TYPE IN AN INDEX FOR SELECTION ON PRODUCTION AND LONGEVITY.

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SUMMARY

A profit index combining transmitting abilities for yield and angularity, udder depth, foot angle and teat length is developed for selection towards a goal comprising milk (£-0.03 /kg), fat (£0.60 /kg), protein (£4.04 /kg) and longevity (£5.52 /% of cows surviving till lactation 4). Sensitivity analysis showed that the index developed was robust towards changes in the assumptions made.

INTRODUCTION

The objective of many dairy farmers is to maximise profitability, consistent with the health and welfare of their animals. Clearly longevity of the cow is an important component of profitability (e.g. Rendel and Robertson, 1950). Because no predicted transmitting abilities (PTAs) for longevity (or similar traits) are available in the UK, the objective of this study was to combine PTAs for linear type traits and PTAs for milk, fat and protein in an index. PTAs for the type traits were used to predict longevity of the cow as a first step towards a 'total merit' index.

MATERIAL AND METHODS

Economic values: There are several different viewpoints which can be taken in calculating economic values (e.g. national returns, individual producers returns), but in this case they have been derived from the individual producers viewpoint. The perspective of individual producers will be to improve profitability (Moav, 1973). A dynamic programming model (Stott 1994) was used to calculate economic values for the goal traits - milk, fat and protein yield and percentage involuntary culling up to lactation four. The economic value for each goal trait was calculated as the change in the net present value of a replacement heifer (£ per unit, expressed as annuity) as a consequence of a unit increase in the goal trait concerned, whilst keeping the output of the other goal traits constant.

For each day energy requirements were calculated from energy needed for maintenance (based on live weight), energy required or gained from live weight change, energy required for pregnancy and when not in the dry period, energy required for fat, protein and lactose production. All equations used came from a commercial cow rationing program (G. C. Emmans, personal communications). Based on the calculated energy requirements a least costs cow ration was formulated combining grass or silage and concentrates. Dry matter intake capacity was based on (i) live weight of the cow and (ii) dry matter percentage and digestibility of the food.

Finally, dynamic programming was used to optimise the 'keep or replace' decisions (Van Arendonk, 1985a). Decisions were taken annually over a sequence of 20 annual stages and a maximum of 12 lactations was assumed with 15 yield states (chance nodes) within each lactation (Stott 1994). The influence of the repeatability of milk yield on the replacement decision was accounted for using the method of Bayesian updating (Lindley, 1965). In the absence of reliable UK information, the probabilities of involuntary replacement used were those of Van Arendonk (1985b). All other physical and financial assumptions were based on UK estimates.

A price ratio for fat:protein of 1:1.5 was assumed and costs of transport and processing have been assigned to each extra kg milk. In the absence of evidence suggesting otherwise, it was assumed that the expected small changes in individual traits would leave the number of animals in a typical herd unchanged. It was also assumed that quota can be freely leased when herds are 'above quota', reflecting current industry practice. The dynamic programming model was therefore based on a fixed number of animals in the herd, with quota considered as an pportunity cost associated with fat production. A sensitivity analysis of the economic values was used to justify hese assumptions. The economic values derived were £5.52 per % cows not involuntarily culled in the first four actations and £-0.03, £0.60 and £4.04 per kg for milk, fat and protein yield respectively.

Genetic parameters: Genetic correlations between linear type traits and longevity (or survival), adjusted for enetic merit for yield (Brotherstone and Hill 1991) were used (Table 1). Only four of the 16 linear type traits vere chosen for the index (based on the strength of the genetic correlations with survival).

ABLE 1: Heritabilities (diagonal), phenotypic (above the diagonal) and genetic correlations (below the diagonal) from Brotherstone and Hill (1991) and S. Brotherstone personal communication.

	Longevity	Milk	Fat	Protein	ANG	FA	UD	TL
Standard deviation	49	895	35	27	1.34	1.17	1.64	1.24
Longevity[1] (%)	.06	-	-	-	-	-	-	-
Milk (kg)	.00	.47	.83	.94	.27	-.03	-.28	.05
Fat (kg)	.00	.77	.52	.87	.25	-.02	-.25	.02
Protein (kg)	.00	.93	.85	.45	.24	-.02	-.27	.05
Angularity (ANG; 1-9)	.11	.44	.42	.43	.26	-.04	.06	-.01
Foot angle (FA; 1-9)	.09	.02	.05	.07	-.13	.27	.10	-.01
Udder depth (UD; 1-9)	.21	-.48	-.40	-.44	.01	.03	.39	-.09
Teat length (TL;1-9)	-.19	.18	.12	.17	.08	-.09	-.21	.44

Cows not involuntarily culled in the first 4 lactations, corrected for genetic differences in yield.

Derivation of index weights: In the usual way, genetic (G) and phenotypic (P) variance and covariance atrices were created. For the P-matrix it was assumed that 10 000 effective progeny records were available for timating the PTAs for yield and type. Selection index equations (Hazel, 1943) were used to calculate optimal dex weighting factors and evaluate the consequences of selection, using three different indices assuming that: (i) terest is in yield components only (YIN), (ii) interest is in longevity only (LIN) or (iii) interest is in yield and ngevity, hence profit (PIN). Some re-scaling has to be applied to the weighting factors as these have to be plied to PTAs for milk, fat and protein (in kg) and for the type traits expressed in standard deviation units. nnual selection responses were approximated assuming a four pathway breeding scheme (bulls to breed bulls, lls to breed cows, young bulls to breed cows, cows to breed bulls, cows to breed cows) with an overall selection sponse of 0.22 standard deviations of the appropriate index.

RESULTS

The weights calculated for the three indices are given in Table 2. Weights for the yield index (YIN) are uivalent to the economic values of the yield traits and no importance is given to the type traits, as expected cause PTAs are assumed to have large (>.99) accuracy's. The index weights for profit are the sum of the ights of the indices for yield and longevity.

TABLE 2: Optimum index weights, when selection goal is yield or longevity only or profit.

Goal:	profit	yield	longevity	
Index:	PIN	YIN	LIN	direction
PTA for:				
Milk (kg)	-0.015	-0.030	0.015	
Fat (kg)	0.60	0.60	0.00	
Protein (kg)	3.84	4.04	-0.20	
Angularity (sd)	3.9	0.0	3.9	angular
Foot angle (sd)	1.8	0.0	1.8	steeper
Udder depth (sd)	4.8	0.0	4.8	above hock
Teat length (sd)	-4.1	0.0	-4.1	shorter

If selection is for yield only, then the expected maximum selection response of £15.3 per cow per year can be achieved (Table 3). This response is a combination of 119 kg milk, 5.0 kg fat and 3.9 kg protein per year. When selection is for profit then a slightly lower rate of genetic gain is expected for the production traits, but longevity of the cow is expected to be improved (0.23 less cows culled involuntarily in the first four lactations in a 100 cow herd per year). This is predicted to increase the annual selection response by £0.70 per year (5%) compared to selection on a combination of milk, fat and protein only.

TABLE 3: Expected selection response (per cow per year) for the goal traits.

Goal:	profit	yield	longevity
Index:	PIN	YIN	LIN
Response per annum in:			
Profit (H) (£)	16.0	15.3	4.5
Longevity (%)	0.23	0.00	0.81
Milk (kg)	114	119	0
Fat (kg)	4.8	5.0	0.0
Protein (kg)	3.8	3.9	0.0

The benefit from selection on PIN is shown, for example, when the selection responses for UD are compared (Table 4). Selection for milk yield will result in deeper udders and selection for longevity will result in shallower udders, but selection on PIN will give a balanced rate of genetic gain, based on the economic values of longevity and yield. The same conclusions could be drawn for fore udder attachment, even though it is not included in the index. Another observation is that TL is not expected to change following selection on PIN, even though it has a negative weighting in the index. PIN simply counterbalances the expected increase in TL following selection on yield alone.

TABLE 4: Expected selection response (units per cow per year), for some type traits.

Goal:	profit	yield	longevity	Score:	
Index:	PIN	YIN	LIN	1	9
angularity	0.08	0.06	0.05	Coarse	Angular
foot angle	0.02	0.01	0.04	Low	Steep
udder depth	-0.05	-0.10	0.15	Below	Above Hock
teat length	0.00	0.03	-0.11	Short	Long
fore attachment	-0.02	-0.05	0.09	Loose	Strong

Theoretically, PIN gives optimum response in the base situation only and therefore a sensitivity analysis was ried out. Table 5 shows that the index proposed is robust to large changes in the economic value of milk and Most of the loss in efficiency of the profit index appears when the economic value of protein is overestimated.

BLE 5: Efficiency of using PIN (i.e. using weighting factors from the base situation), compared to the optimum PIN in situations where the true economic values for one of the goal traits (milk, fat and protein yield and longevity) differs by -100, -50, +50 and +100 per cent from the base values, while keeping the other economic values at the base values.

	Percentage change:			
	-100%	-50%	+50%	+100%
Longevity	0.960+	.990	.992	.970
Milk	0.994	.998	.997	.985
Fat	0.992	.998	.999	.996
Protein	0.140	.956	.994	.987

+ e.g. the rate of genetic gain with PIN is 96% of the maximum genetic gain, when using the optimum index in the situation where the economic value of longevity is zero (-100% of the base value) and all other economic values are at their base value.

DISCUSSION

The objective of this paper was to demonstrate how PTAs for linear type and milk production traits can be bined in an economic profit index, PIN. Selection on PIN is expected to give a £0.70 higher annual rate of etic progress (5%) compared with selection on an index combining PTAs for milk, fat and protein only. The a benefit come from the longer herd life of cows. Its use is expected to halt the decrease in udder depth and udder attachment scores that would occur as a consequence of selection for yield alone. In genetic standard ation units the final weighting for yield to type is 3:1. The index appears robust to 50% changes in economic es for protein yield and longevity, but very sensitive to a 100% change in the value of protein. Larger changes e economic value for milk or fat yield give efficiencies above 0.985, therefore allocation of quota costs to fat only does not seem critical (given the UK average quota situation about 20-25% of the quota leasing costs d be attributed to milk yield). Also, PIN appears to be robust when applied to bulls which fewer effective hters available (results not shown, but efficiency is > 0.985 when only 25 effective daughters with type or for records are available). Implementation of the derived index depends on the outcome of a consultation process the UK dairy industry.

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DIFFERENCES IN MULTIPLE TRAIT PREDICTION OF TRANSMITTING ABILITIES FOR HERDLIFE DUE TO DATA SOURCE

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SUMMARY

Data were production and herdlife information from herds participating in the Holstein Association of America classification program. Cows were divided into two data sets based on registry status. Production and herdlife information from all cows freshening for the first time in the same herd-year in classified herds indicated that the registered cows that were classified were not a random sample of their herds.

Genetic and phenotypic (co)variances among linear type traits, final score, first lactation milk and fat yields and productive life to 84 month were estimated with a multiple trait sire model for both registered and grade populations. Maximum accuracy of prediction of herdlife from the linear type traits was much higher in the registered analysis (59%) than in the grade analysis (25%). Addition of milk production to prediction raised the maximum accuracy in the grade analysis to 71%, while the maximum accuracy in the registered analysis was raised to 68%. Similar results were observed in using correlations from a previous study.

These results suggest that accuracy of evaluation of herdlife from the linear type traits is dependent on registry status, previous selection of the data for yield or a combination of these effects.

INTRODUCTION

Multiple trait BLUP analyses are useful for improving the accuracy and timeliness of evaluations for traits such as herdlife. However, the gains in accuracy with multiple trait evaluations are dependent on the accuracy of the estimates of genetic and environmental correlations used in the analysis (Schaeffer 1984).

Research by Boldman et al. (1992) used multiple trait PTA's for linear type traits to predict sire transmitting abilities for herdlife in a population of grade Holsteins. Research by Short and Lawlor (1992) indicates that estimates of genetic correlations between some type traits and herdlife are different for registered and grade populations.

The objective of this research was to evaluate differences in prediction equations for herdlife developed from multiple trait estimates of variances and covariances among productive life, the type traits, and milk and fat yield in populations of grade and registered Holsteins.

MATERIALS AND METHODS

Production and type data files were merged to obtain cows with both classification scores and 84 month opportunity length. Productive life was measured as total months in milk to 84 months. Edits required daughters to have matching sire identification from the two data sources and for herd-years to have at least 15 cows freshening for the first time. Additional edits removed sires born prior to 1960 and those sires with less than 7 daughters in 5 herds. Data were 153,341 registered daughters of 1117 sires and 45,610 grade daughters of 1082 sires.

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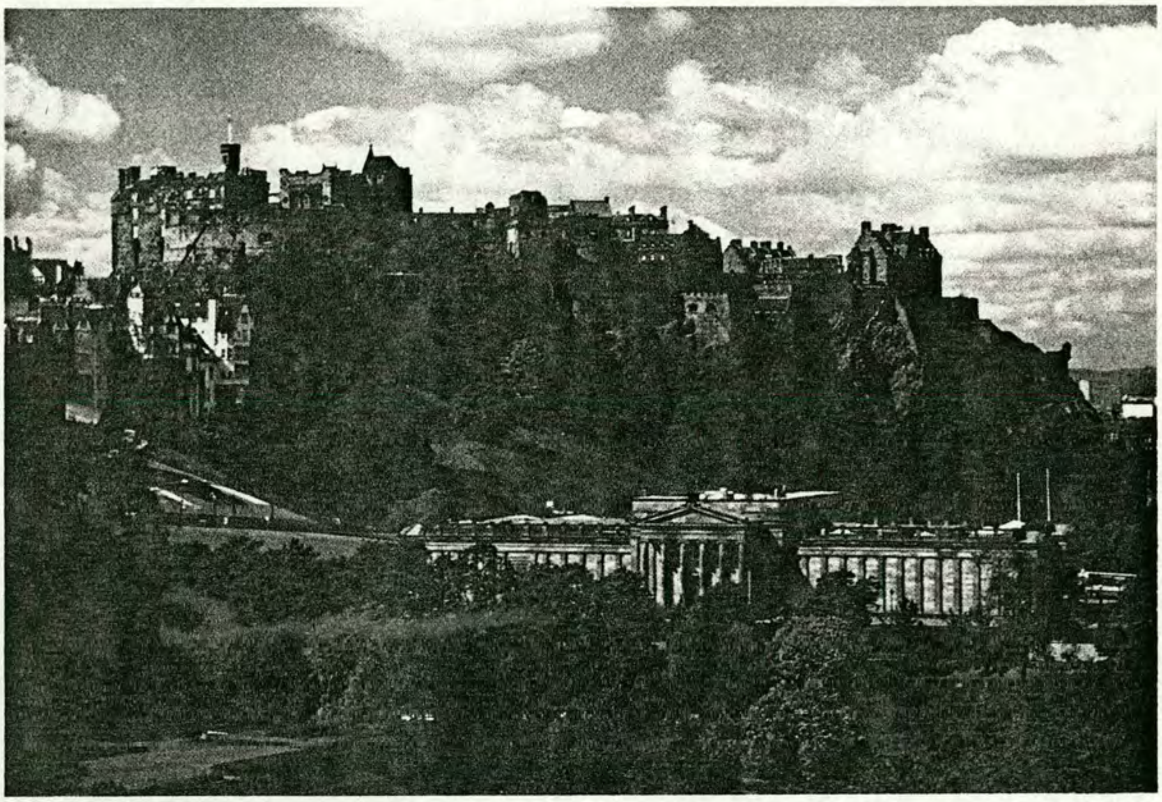

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SOURCES OF GENETIC VARIATION IN EFFICIENCY OF DAIRY COWS.

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Introduction

The breeding goal of many dairy farmers is to maximise profitability. Because feed costs account for about 0.80 of the total variable costs associated with milk production (MMB, 1990) possible genetic differences between cows in feed intake, or in the efficiency of converting feed to valuable products, are of considerable importance to those involved in the theory and practice of dairy cattle breeding. Genetic sources of variation that may be present for feed efficiency are also of importance for animal production for other reasons. Models of the use of energy by cows are used as guides to feeding decisions and for rationing and are used for predicting the economic and environmental consequences of genetic change using so-called bio-economic models. The equations currently used in cow rationing models in many countries, e.g. in the UK those of AFRC (1991), were estimated from data collected on cows of inferior genetic merit to most Holstein Friesian cows currently in the UK. An obvious question is whether these equations, which describe the presumed relationships between, for example, liveweight and feed intake, or the amounts of energy needed per unit of metabolic body weight and per unit of energy produced in milk, can properly be applied to the current cow population. If sources of genetic variation can be identified and quantified, then such equations may be able to be improved and the consequences of further selection predicted more accurately.

Under current conditions in the UK, and in many other countries too, it is the cost of supplying the cow with energy that contributes most to feed costs. However, the cost of supplying protein is far from negligible and protein supply also has effects on pollution from excreted N, which is of increasing concern. The calculation of feed requirements, however, usually starts with energy, which is one of the reasons why the problem of estimating the overall energetic efficiency has been of most interest. In this paper we will concentrate on energetic efficiency as it is of current, and likely future, economic importance. However, we accept that in the longer term, this can only be a small part of a much broader picture when all the inputs to dairy farming (e.g. land use, fertiliser, labour and capital) are considered.

The objective of the paper is to review possible ways of identifying sources of genetic variation in energetic efficiency. Possible physiological pathways which could give rise to such variation are discussed in more detail by Serjsen and Neimann-Sorenson (1994) in this session. Reviews relevant to this paper include those by Freeman (1975), Kennedy (1984), Blake and Custodio

(1984), Bauman *et al.* (1985), Gravert (1985) and Korver (1988). They provide an historic perspective; the emphasis in this paper is on developments since 1985.

Energetic efficiency

In most places, and at most times, feed energy cost is the major contributor to feed costs, which is one of the major reasons why energetic efficiency has been of such interest to researchers. However, undue emphasis on energetic efficiency would be unwise.

Several alterations to current production circumstances could further diminish the importance of energetic efficiency in the future. For example, the major impact on future production systems of the 1991 reform of the E.U. Common Agricultural Policy will be in terms of feed costs. Cereal prices are expected to drop and grass silage is expected to become a relatively expensive feed (Lowman, 1994). This will reduce the importance of energetic costs as the major variable cost related to milk production and so energetic efficiency might become economically less important than it is currently.

Also, in some countries animal production systems contribute substantially to environmental problems (Heij and Schneider, 1991). For example in dairy cattle there appears to be an increasing demand for milk protein, but N losses are inherent to animal protein production (Hof and Tamminga, 1994). In other countries, public acceptability of animal production systems related to welfare, seems to be a great concern for the sustainability of agriculture (Broom, 1994). Hence in general there appears to be the risk that focusing on one aspect of efficiency (energetic efficiency in this study) might sacrifices the future efficiency (or sustainability) of animal production systems (Halberg *et al.*, 1994). Therefore it is important to realise that the definition of efficiency used in this study (energetic efficiency) is part of a complex function describing overall efficiency which ought to include several other factors such as animal welfare (Broom, 1994) or N efficiency (Hof and Tamminga, 1994). Nevertheless, because the additive genetic variation of an overall complex function is the aggregate of the genetic variation of the separate components, identification of possible source of genetic variation in energetic efficiency still makes a useful contribution.

Selection for efficiency

Another issue is whether it is sensible to select for efficiency directly. Efficiencies are defined as ratios of outputs to inputs, measured in the same units. There are statistical problems associated with the use of ratios, including difficulty in predicting or controlling the selection responses for the components of the ratio (Sutherland, 1965; Simm *et al.*, 1987). These are likely to be compounded if the breeding goal for dairy cattle also includes components of the ratio (e.g. yield) or traits associated with them. Moreover, there are strong arguments in favour of deriving breeding goals from the economic viewpoint of individual producers; not least of these is the fact that producers are not likely to use selection indexes if they are derived from a different viewpoint. In practice, for individual producers, the absolute margin between returns and costs is likely to be

of more concern than their relative magnitude (Moav, 1973). Hence, defining breeding goals in term of some linear combination of milk yield and feed intake, weighted by their economic values, is likely to be of more practical value than an index incorporating direct measures of efficiency, though they usually will be highly correlated.

Feeding systems for cows

The three 'pure' feeding systems for animals were identified by Emmans (1981) as: controlled feeding, where one homogeneous feed is given at a rate such that all of it is eaten; *ad libitum* feeding, where the animal is given free and continuous access to one homogeneous feed; choice feeding, where the animal is given free and continuous access to two or more homogeneous feeds. The actual systems used for cows are usually mixtures of these pure systems which may lead to theoretical problems in dealing with the data that they produce. A well known example is the high genetic correlation between milk yield and feed efficiency which is partly induced as a consequence of feeding animals according to yield (Freeman, 1975; Morris and Wilton, 1976).

Most studies investigating sources of variation in feed efficiency can be classified as being: (i) based on analyses of very large data sets from field records, but with individual cow feed intakes predicted from herd averages (sometimes adjusted for yield and liveweight, or both), (ii) studies based on analyses of a much smaller number of individual feed intake records from experimental herds, or (iii) studies on very few animals of uncertain genetic background in calorimeters which allow the components of the energy balance to be measured. In studies to separate genetic effects from environmental effects the most common methods are: (i) comparison of the means of a trait for different genotypes (breeds or selected versus control animals) in the same environment (e.g. Falconer, 1991) , (ii) within breed estimation of the genetic variance components, using relationships between animals to separate the genetic variance from environmental variance (e.g. Falconer, 1991; Meyer, 1991) or, (iii) a combination of these two methods (Thompson and Atkins, 1991). The genetic variance is most often expressed relative to the total (phenotypic) variance, which is the heritability for a trait; depending on the relationships between the animals a large data set is often required to obtain accurate estimates of the parameters.

Gross energetic efficiency

Gross efficiency is widely used as a measure of the efficiency with which the cow uses feed. Gross energetic efficiency is defined as the energy in the milk produced divided by the total energy intake (Brody, 1945), where the energy intake may be measured as the heat of combustion of the food, or as the digestible, or metabolisable, energy yielded by the food to the cow.

There is abundant evidence of genetic variability in feed efficiency (for reviews see Blake and Custodio, 1984; Korver, 1988; Persaud, 1991), and thus in gross energetic efficiency, measured as between breed (Gibson, 1986; Oldenbroek, 1988) or selection line/group differences (Persaud *et al.*, 1990; Veerkamp *et al.*, 1994b) or expressed as heritabilities (Persaud *et al.*, 1991; Van

Arendonk *et al.*, 1991; Jensen *et al.*, 1991; Svendsen *et al.*, 1993). Published heritabilities for gross efficiency are moderately large and often very similar to the heritability of milk yield (Persaud, 1991).

The problem with gross efficiency is that it does not distinguish between the energy used for the separate functions of maintenance, lactation and body tissue gain, or loss, which can be seen as having different partial efficiencies. Where metabolisable energy, ME, is used as the input scale these three efficiencies are conventionally called k_m, k_l and k_f respectively.

The simple model which relates milk energy yield to feed energy intake with zero state change is illustrated in Figure 1. As there is a fixed requirement for zero output, in this model the quantity of energy needed for the maintenance of the cow, the gross efficiency of the cow will increase as both intake and output increase. A strong assumption is that the model applies not just to an individual cow but across cows or, at least, that the two axes can be scaled in ways such that it can be applied across cows. The usual scaling is to divide both axes by 'metabolic body weight' i.e. that function of weight to which maintenance is proportional, to give Figure 2. This model is more general, in that it is assumed to be constant across cows with different absolute maintenance requirements, and it rests on two assumptions. The first is that maintenance is proportional to 'metabolic body weight' across cows, and that it is not correlated with yield, or the potential to yield, across cows. The second is that the marginal efficiency of converting food (energy) to milk (energy) is constant across cows and constant across levels of yield for a given cow. The model is simplified to assume zero state change and hence no body tissue mobilisation should take place.

The last assumption can easily be shown to be unrealistic in a data set previously described by Veerkamp *et al.* (1994b). In Figure 3, ME intake and energy output for maintenance, lactation and liveweight change are shown for four groups of animals, housed and managed at the Scottish Agricultural College/University of Edinburgh Langhill Dairy Cattle Research Centre[1]. These graphs show how selected cows on the low concentrate (LC) diet produced similar amounts of milk energy as the control cows on the high concentrate diet (HC). However, between these two groups, ME intake is higher for the controls and energy put into liveweight is lower for the selection line animals. Based on liveweight measurements during lactation and AFRC (1991), the requirements for maintenance are indistinguishable between the four groups. These graphs make it clear how tissue balance is an important source of variation in gross energy utilisation during at least some periods of lactation.

Furthermore, because tissue reserves in dairy cows may be substantial (e.g. Butler-Hogg *et al.*, 1985; Gibb *et al.*, 1992), it is possible that the use of reserves in a part of one lactation, or over

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[1] The Langhill herd comprises two genetic groups - a selection line S and a control line C. The selection line is in the top 1% herds of the UK, ranked on average genetic merit for fat plus protein yield, and genetic merit of the control line is close to the UK average. Two complete diets were offered *ad libitum* to both genetic groups. The diets were designed to achieve, over a full lactation, proportions (in total DM) of concentrates, brewers grains and silage of 20:5:75 (LC) and 45:5:50 (HC), with annual average concentrate intakes of about 1.0 and 2.5 tonnes per cow. For more detailed description see Veerkamp *et al.* (1994b).

one whole lactation, might buffer some animals against the effects of temporary nutritional adversity. Consequently, variation in gross efficiency which becomes apparent during part of the life span, might diminish in the longer term e.g. when considered over a whole series of lactations and their associated dry periods. Also, simply increasing yield, by either selection or feeding more concentrates, would increase gross energetic efficiency, because maintenance cost are then diluted across more units of output. For these reasons, gross efficiency is not very useful for identifying specific sources of genetic variation in feed efficiency. The ample evidence of genetic variation in gross efficiency indicates some genetic component in the whole complex function of intake, maintenance, body tissue mobilisation and yield. However, this is not surprising because there is also substantial evidence for genetic variation in yield and intake separately.

Genetic correlation between efficiency and yield.

Phenotypic and genetic correlations between yield and efficiency are often high, suggesting that selection for milk yield automatically increases efficiency. Besides a possible pleiotropic effect of genes affecting both yield and efficiency, the explanations most often given for the increase in gross efficiency as a consequence of selection for yield (or the high genetic correlation between yield and efficiency) are: (i) dilution of the maintenance costs means that high producing animals look more efficient or, (ii) high efficiency is a result of increased tissue mobilisation at higher yields or, (iii) feeding according to yield has inflated the differences in efficiency between high and low (potential) yielders (Blake and Custodio, 1984).

Another, more formal, argument could be that the high genetic correlation between yield and gross efficiency is purely a consequence of the higher coefficient of variation (CV) and/or the higher heritability (h^2) of yield compared with these values for intake. This is because, when small second order terms are ignored, the genetic correlation between a ratio trait (defined as y / x, e.g. energy intake / energy in yield) and one of the components (x) can be calculated as (Sutherland, 1965):

$$r_{gx,y/x} \approx \frac{HCr_{gx,y} - 1}{\sqrt{1 + H^2C^2 - 2r_{gx,y}HC}}$$

$$H^2 = h_y^2 / h_x^2$$

$$C = CV_y / CV_x$$

This equation shows that the genetic correlation between yield and the food conversion ratio ($r_{g\ x,y/x}$) is dependant only on the ratios of the coefficients of variation and heritabilities for yield (x) and intake (y) (not the absolute values), and the genetic correlation between yield and intake ($r_{g\ x,y}$). Figure 4 shows that even with similar variation in yield and intake (ratio HyCy /HxCx =1), and a correlation between yield and intake of 0.6, the genetic correlation between yield and food conversion ratio will be close to -0.5. In practise stronger correlations are expected because the reported values for the CV for yield are generally between 1.0 and 3.0 times larger than the CV for intake (e.g. Moore *et al.*, 1990; Persaud *et al.*, 1991; Van Arendonk *et al.*, 1991; Jensen *et al.*, 1991; Svendsen *et al.*, 1993).

A similar equation can be used to calculate the heritability for gross efficiency (Sutherland, 1965). The only extra factors needed are the heritability for yield and the phenotypic correlation between yield and intake. In Table 1 reported parameter estimates for yield, intake and gross efficiency and the predicted values based on Sutherland (1965) are compared. The calculated values for r_g and h^2 are close to the values reported. Hence genetic variation in gross efficiency can be fully explained by the (estimated) variance components for yield and intake. In terms of identifying biological sources for the covariance between efficiency and yield, or the increase in efficiency as a consequence of selection on yield, the question can be re-cast as the interesting biological question: 'why is there relatively more genetic variation in yield than there is in intake ?'.

Residual feed intake

To try to overcome, at least in part, some of the problems arising from the use of gross efficiency, an alternative measure of overall efficiency can be used. This is the 'residual feed intake' (RFI), or energy balance, (Koch *et al.*, 1963; Luiting, 1991). Unlike gross efficiency, RFI attempts to apportion total feed intake to those functions for which it is used. Overall the value of RFI for a particular cow reflects the difference, or differences, in its utilisation of energy compared with a population mean. If the model describing ME utilisation was known perfectly, and there was no variation between cows, and the components into which ME was partitioned could be measured without any bias, then variation in RFI would be expected to be of a random nature.

Practically, residual feed intake may be defined as RFI = (actual ME intake) - (the estimated ME requirement, MERQ). Two different methods may be used to estimate MERQ: (i), ME intake can be regressed on the presumed component traits such as milk energy yield, body weight change and units of maintenance, such as 'metabolic body weight days'; the fitted values are taken to be the MERQ values for each animal, or, (ii) AFRC (1991) values (or other similar values) for the partial efficiencies k_m, k_l and k_f, are assumed to apply to all cows and are multiplied by the values of the component traits to calculate the MERQ values for each cow. Across species, about 30 - 50 % of the variation in intake is explained by the component traits (Luiting *et al.*, 1994). In dairy cattle values of around 60% were obtained on one data set (Veerkamp *et al.*, 1993).

Figure 5 shows the residual feed intake during lactation for the Langhill selection and control line cows fed two diets as was described above. The selection line and the low concentrate diet clearly have lower mean values for RFI. This shows that non-random deviations from the AFRC equations occur for the apparent overall efficiency of energy use with the line difference suggesting that there may be a genetic component to RFI. For all four groups, ME intakes were higher than the requirements based on the AFRC k values and the calculated requirements for maintenance, lactation and liveweight change (based on measured milk component yield, liveweight and liveweight change). At the end of the 24 week period, control line cows on the high concentrate diet had eaten nearly 2500 MJ more than could be accounted for by their performance. Experimental losses under practical feeding circumstances (e.g. feed spillage) compared to those in calorimetric experiments are likely to be major contributing factors.

Table 2 summarises the results of some of the studies reporting genetic parameters for residual feed intake in dairy cows. Van Arendonk *et al.* (1991), Kennedy *et al.* (1993) and Veerkamp *et al.* (1994), reported heritability estimates of 0.14, 0.19 and 0.32 for RFI, respectively. Ngwerume and Mao (1992) and Svendsen *et al.* (1993) found no evidence for any additive genetic variation in RFI.

There are several possible explanations for genetic variation in residual feed intake, because RFI expresses possible differences from the population mean in (i) some combination of the partial efficiencies k_m, k_l and k_f, or, (ii) some differences in the equations used to calculate the energy needed for maintenance, lactation or body condition change (e.g. deviation from normality or additivity) or, (iii) some variation in traits other than those used in the model to calculate MERQ (Luiting and Urf, 1987).

Further investigations have suggested that differences between RFI in chickens (Luiting *et al.*, 1994) and pigs (De Haer *et al.*, 1993) are caused by different maintenance costs with the higher RFI animals being more active. It is unclear whether this is also a satisfactory explanation of the differences seen in dairy cows. Gustafson *et al.* (1993) found no effect of walking a few km per day on gross energy or protein efficiency in pluriparious cows. However, the difference, in gross energetic terms, between walking and not walking in heifers was 0.39 MJ/kg energy corrected milk under a restricted feeding system.

Genetic residual feed intake

Kennedy *et al.* (1993) showed how the variance and covariance matrix between feed intake and the components traits (MERQ) can be used to calculate the properties of RFI. These authors also showed that a distinction should be made between genetic RFI and phenotypic RFI. The difference is that for genetic RFI, the feed intake is made to be genetically independent of the component traits, whereas the results discussed so far were corrected phenotypically (environmental plus genetic effects) for the component traits. The difference is that, sources of genetic variation in phenotypic RFI can still be the consequence of a genetic correlation between feed intake and the component traits, because the associations with components are phenotypically accounted for.

This is further illustrated by the results from Kennedy *et al.* (1993) and Veerkamp *et al.* (1994). Both these authors reported relatively high heritabilities for phenotypic RFI (0.14 and 0.34 respectively), but heritability estimates for genetic residual feed intake appeared to be close to zero (Table 2). One of the possible explanations for this low heritability for genetic RFI, compared with the heritability for phenotypic RFI, given by Veerkamp *et al.* (1994a) was that in their data set phenotypic RFI was still genetically correlated with liveweight change (r_g= 0.49), because the genetic and environmental correlations between feed intake and liveweight change were of opposite sign. Hence, correction of feed intake by phenotypic regression did not account sufficiently for the genetic correlation between liveweight and feed intake. So, besides the possible sources for genetic variation in RFI given above (Luiting and Urf, 1987), the genetic covariance between feed intake and the component traits is another possible source of genetic variation in phenotypic residual feed intake.

Reliable estimates of the heritability for genetic RFI and the amount of genetic variation explained by the component traits (genetic R^2) should enable us to answer the question "Is it worthwhile recording feed intake when yield, liveweight and liveweight change are known ?". The low heritabilities for genetic residual feed intake suggest that the only sources of genetic variation in feed intake come from yield, liveweight and liveweight change, with constant k-values across all animals. However, as a results of the facts that (i) the variances and covariances used by Kennedy *et al.* (1993) came from a data set in which individual feed intake was predicted from liveweight and milk yield and (ii) a bias in the estimation procedure for the estimation of the heritability for genetic RFI arises in small data sets (Veerkamp *et al.*, 1994a), the published heritability for genetic RFI are likely to be biased downwards, perhaps considerably. Therefore, there is insufficient evidence from the literature to conclude whether or not there is additive genetic variation in residual feed intake after genetically correcting for energy required for yield, maintenance and liveweight change.

Digestion and metabolism of gross energy

Clearly genetic RFI helps to indicate whether there are possible sources of genetic variation in energy utilisation, other than in the components used in the model to calculate MERQ. However, the source(s) of genetic variation in RFI are often unclear and more detailed measurements on the partitioning of gross energy are needed.

Van Es (1961) showed that little between animal variation exists in the ability to digest a given diet. Grieve *et al.* (1976) found no relationship between genetic merit for milk yield and apparent digestibilities of ration components in 24 Canadian Holstein heifers. This agreed with the results from Davey *et al.* (1983), who compared high and low genetic merit Friesians. Similarly, Graiger *et al.* (1985) found no difference between high and low merit genotypes in their ability to metabolise the gross energy of the food, or in the individual losses of energy in the faeces, urine and methane. Also, Custodio *et al.* (1983) suggested that cows of different genetic merit for milk did not differ in their ability to digest fibre and starch for milk secretion. No differences in partitioning of gross energy into digestible or metabolisable energy were found by L'Huillier *et al.* (1988) and Tyrrel *et al.* (1990) in experiments comparing Holstein and Jersey cows. In contrast, Freeman (1975) indicated that large differences in digestibility have been observed among cows and Trigg and Parr (1981) found that high genetic merit animals digested a (slightly) higher amount of the gross energy intake. On balance the conclusion that there are no true genetic differences between cows in the ability to metabolise a given feed at a constant level of feeding would seem to be a safe one.

Partial efficiencies from energy chambers

Traditionally, energy chambers are used to estimate from measurements the partial efficiencies with which ME is converted to different products. Sources of variation in the partial efficiencies, k_m, k_l and k_f, are known to exist (for a review Moe, 1981). For example typical values for k_l range from 0.54 to 0.74. Most of this variation, however, comes from experiments where the same cow (or group of cows) were fed different diets. Hence the observed variation in k-values is purely environmental. Some experiments have focused on between animal variation. For example, Van Es (1961) found a between animal coefficient of variation of 5-10% for the amount of energy needed per kg metabolic body weight for maintenance but was not persuaded that there were real differences between cows. There were large time effects which were apparently 'seasonal'.

Grainger *et al.* (1985) reported that differences between high and low genetic merit cows in the use of ME (measured as heat production at a common ME intake) did not exist or were very small. Also, Bauman *et al.* (1985) indicated on the basis of a literature review that little variation exists among animals in the partial efficiency with which ME is utilised. Nevertheless, 34 Holsteins converted relatively more energy into milk than 29 Jerseys in the second third of the lactation; there was no significant difference in the first third of the lactation (Blake *et al.*, 1986). These authors attributed this difference to the Jerseys laying down more adipose tissue and concluded that there were no notable differences in energy utilisation between the breeds. No differences were observed in the energy utilisation of 6 Holstein and 6 Jersey cows in early lactation (Tyrrel *et al.*, 1990). Contrasting results were obtained by L'Huillier *et al.* (1988) who reported the efficiency of utilisation of ME for milk and tissue to be 0.58 and 0.48 in Jerseys and Holsteins respectively. Overall there appears to be little good evidence for assuming true differences between cows in partial efficiencies

Partial efficiencies from field data

Walter and Mao (1989) used eighteen different models to estimate partial efficiencies from data collected under practical farming conditions. The were able to obtain partial efficiencies which were very similar to those efficiencies coming from energy chambers. Saama *et al.* (1991) compared gross efficiency and net efficiency of 30 pluriparious cows using two different methods. Estimates came from field records for 4 weekly periods and, in alternate weeks, from energy chambers. Field gross and net efficiency closely approximated the values in the energy chambers.

Using genetic size scaling rules Taylor *et al.* (1986) compared maintenance efficiency of mature Hereford, Aberdeen Angus, Dexter, British Friesian and Jersey cows and concluded that maintenance increased with increasing milk yield (expressed per kg mature weight). Coupled with an extensive discussion of the literature, these authors attributed this difference in maintenance requirements to large genetic differences in k_m . In contrast, Veerkamp *et al.* (1993) estimated partial energetic efficiencies for maintenance, lactation and liveweight changes, for selection line and control line cows on high and low concentrate diet. Non-significant interactions between the line or diet and k-values were backwards eliminated. Estimates for k_m were higher for the low concentrate diet and for the selection line and estimates for k_l were higher on the high concentrate diet. However, estimates for k_f were greater than one and therefore not realistic.

Variance components for partial efficiencies have been estimated by Butazonni and Mao (1989) and Svendsen and Mao (1989). They estimated k-values from several measurements within a lactation for an individual animal. Heritabilities of around 0.4 were estimated for those k-values. Also, Walter and Mao (1989) estimated a genetic correlation of 0.56 between milk yield and k_l , which would suggest that selection for milk yield will result in a higher efficiency of converting ME into milk energy. Although this method of identifying genetic variation in partial efficiency and genetic covariances between the partial efficiencies is appealing - because large data sets can be used - it is unclear to us if these genetic parameters are biased by, for example, the amount of information available for each individual animal. Measurements of the k-values are not independent and for that reason the estimated correlation between the k-values might partly be a consequence of the sampling covariance between them. More justification of the technique might be needed here.

Discussion

The genetic basis of energetic efficiency remains a live issue. In particular the proposition of Taylor et al (1986), that there is a necessary increase in scaled maintenance as yield is increased by selection, remains to be refuted. Our evidence, presented above, is that in our cows there is no support for this view.

Using the Langhill records, the current UK description available of the amount of energy needed for yield, liveweight change and maintenance (AFRC 1991) has been tested and biases have been observed. Stage of lactation, genetic group and feeding system all had clear effects on the residuals (RFI in Figure 5) indicating that the models used are not appropriate across these effects. The effects of lactation period and ration on, for example, the k-values have been investigated intensively, and discussion of these effects on the residuals has been ignored in this study (See Moe, 1981 for review). This paper has tried to identify why there is a genetic line effect, even though it is small.

From the literature it is unclear if there is any additional genetic variation in the partial efficiencies, k_m, k_l and k_f. Results from energy chambers (most often conducted by 'nutritionists') suggest no breed differences, whereas estimates from field data (most often conducted by 'geneticists') suggest there is some genetic variation in the apparent net efficiencies. When paramater estimates are used to identify sources of genetic variation, the low heritability for genetic residual feed intake also suggests that there is no variation other than in yield, liveweight and liveweight change. However, the value of 0.05 reported by Veerkamp *et al.* (1994) can be seen as a worst case scenario, because the calculations of RFI seek to minimise the genetic residual variance. Simulations based on the size of the data set as used by these authors, showed that the population value for the heritable could well be above 0.25, and hence that there might be some genetic variance in partial efficiency.

Some other factors might have influenced the identification of possible sources of variation in partial efficiencies. For example, in lactating cows it is difficult to account properly for maintenance and body tissue mobilisation. Often liveweight and liveweight changes are used to infer requirements for maintenance and body tissue mobilisation. However, it is well known that liveweight is a bad predictor of body tissue composition (Benedict, 1927 quoted in Moe *et al.* 1972). Body weight can be seen as a complex of gut fill, lipid and lipid-free empty body weight and these components can vary independently. For example, during the first weeks of lactation cows lose lipid, but gut fill increases as a consequence of higher intakes. Possible correlations with yield, might further compound the difficulties of estimating partial efficiencies. The conclusion is that it is difficult to identify any source of genetic variation in partial efficiencies, and that current literature results do not identify any strong evidence of their existence.

The most important sources of genetic variation in gross energetic efficiency, the measure of practical relevance, are likely to be the potential to yield, the capacity for feed intake, the possible extent of body tissue mobilisation and, crucially, any differences in partitioning between these components. Changes in any one of these components could lead to a complex effect on any one of the other traits, as consequence of all of the interactions that are possible. Although most of these relationships are described phenotypically in AFRC type equations, it must be emphasised here that a clear distinction should be made between a genetic change and an environmental change (e.g. nutrition or management). For example, increasing yield by feeding more concentrate, compared with increasing yield by improving genetic merit, will lead to antagonistic effects on liveweight change (Veerkamp *et al.* 1994b).

Persaud and Simm (1991) and Van Elzakker and Van Arendonk (1994) published genetic correlations between part lactation measurements of feed intake and complete lactation measurements. Svendsen *et al.* (1994) published an extensive set of estimates of the parameters describing the genetic and phenotypic relationships between several traits contributing to the composite trait, feed efficiency. These authors divided the lactation period in distinct periods and groups of cows were fed two different diets. Clearly these are steps towards the model describing the lactating dairy cow genetically. A method to evaluate the lactation period as a continuous trait instead of, for example, three distinct trimesters, is suggested by Kilpatrick *et al.* (1994). It may be possible to extend this approach to include not only the lactation curve for yield, but also relationships with other traits which vary over time and hence work towards a better genetic description (or model) of the 'infinite dimensional dairy cow' (Kilpatrick *et al.* 1994).

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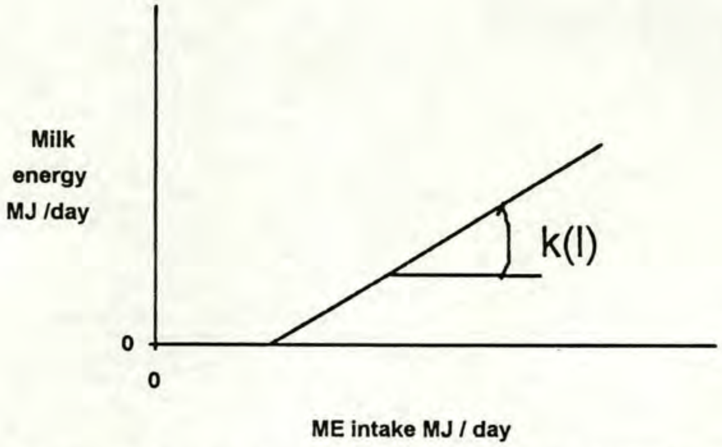

Figure 1: The assumed relationship between milk yield as energy and feed intake as energy, with no change in the cow's state for one cow.

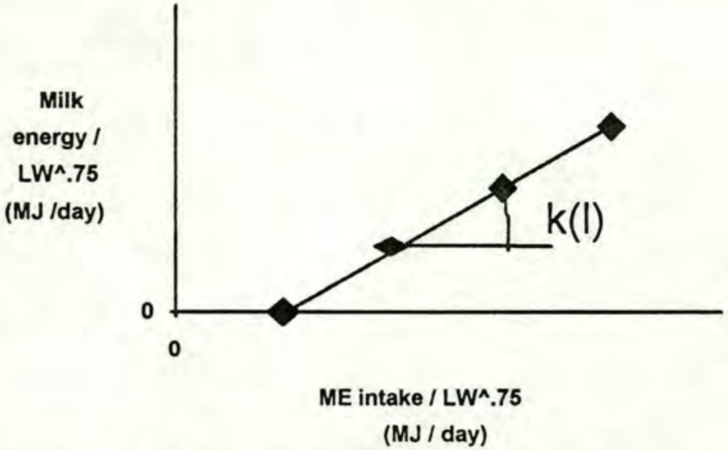

Figure 2: The assumed relationship between the scaled milk yield as energy and the scaled feed intake as energy, with no state change, across cows.

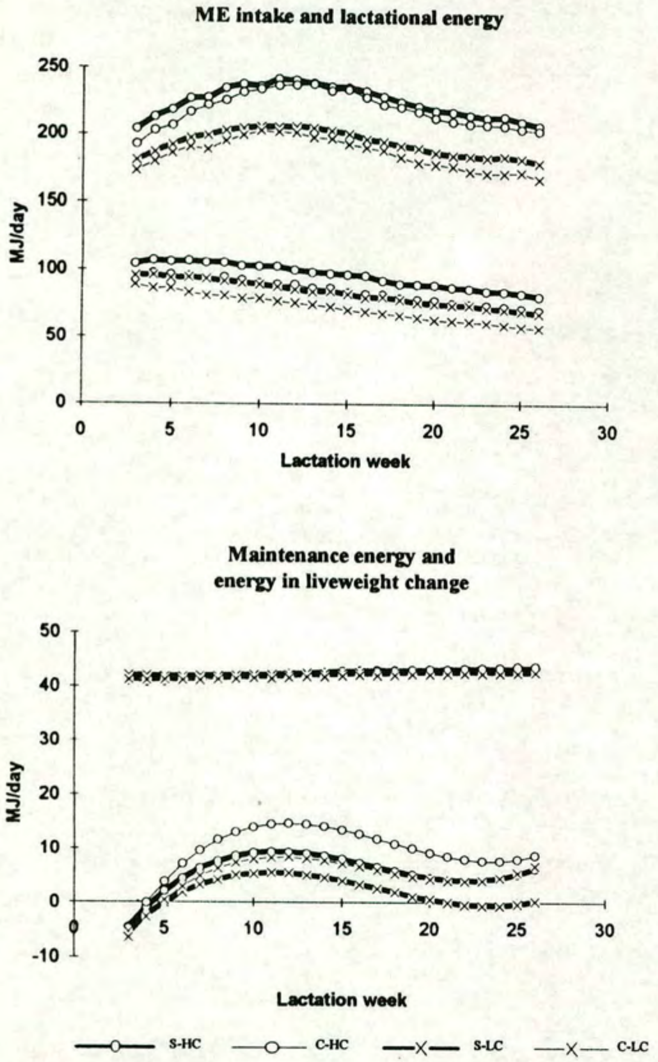

Figure 3: Metabolisable energy intake and energy in lactation (based on Tyrrel and Reid, 1965), energy for maintenance and liveweight change (AFRC, 1991), for selection and control line cows (S and C) on a high and low concentrate feeding system (HC and LC, respectively). [2]

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[2] Number of records are 102, 84, 117 and 74 for S-HC, C-HC, S-LC and C-LC, respectively.

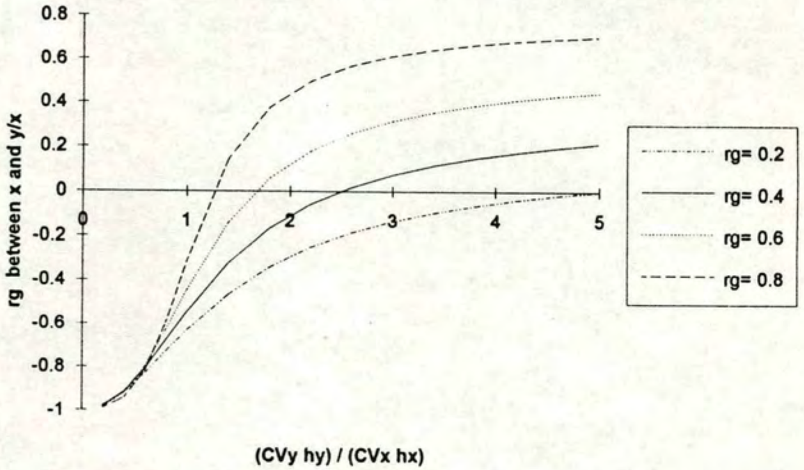

Figure 4: Predicted value for the genetic correlation between a ratio trait (y/x) and x, given the ratio between the h (squared heritabilities) and coefficients of variation (CV) for x and y, for different values of the genetic correlation between x and y.

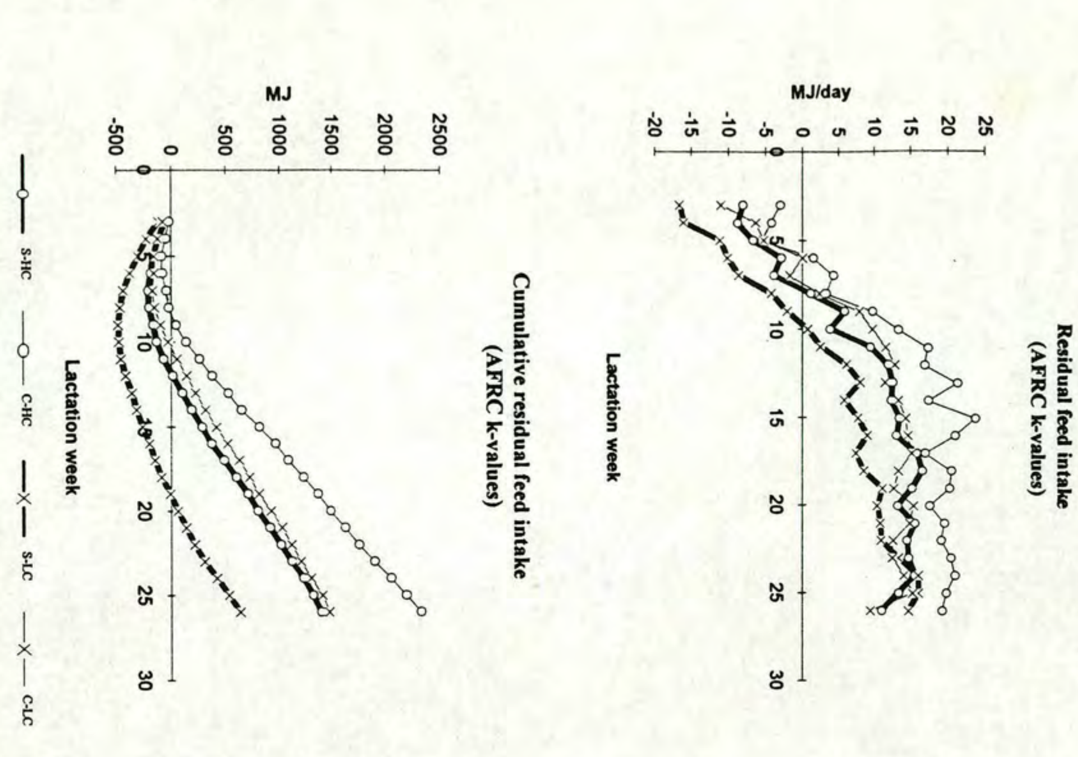

Figure 5: Residual feed intake and cumulative residual feed intake during lactation, for selection and control line cows (S and C) on a high and low concentrate feeding system (HC and LC, respectively).

Table 1: Comparison estimated and predicted variance components for gross feed efficiency.

	Observed values:							predicted:		
trait y / x	h^2_y / h^2_x	CV_y / CV_x	$r_{gx,y}$	$r_{px,y}$	$h^2_{y/x}$	$r_{gx,y/x}$	$r_{gx,y/x}$	$h^2_{y/x}$	$r_{g\,x,y/x}$	Source
LE / MEIN	0.20 / 0.37	19 / 12	0.54	0.46	0.13	0.60	-0.05	0.11	-0.07	Persaud *et al.*, 1991
MEIN/LE	0.31 / 0.47	5.4 / 11.3	0.61	0.27	0.37	0.24	-0.93	0.33	-0.93	Van Arendonk *et al.*, 1991

Table 2: Overview of heritabilities for RFI reported in the literature (from Veerkamp *et al.*, 1994).

Source[1]	h^2	# records:	period:	feeding[2]:	RFI calculation:	
			(days)		traits	method[3]
Phenotypically	calculated RFI:					
(1)	.19	360 heifers	0 - 120	fixed conc., ad lib. roughage, 2 random conc. groups	FCM, LWC, $LW^{.75}$	est. b's
(2)	.02	247 cows	0 - 300	TMR, 3 conc. groups according to yield	FCM, LWC, $LW^{.75}$	est. b's
(3)	.04	353 cows	7 - 84	fixed conc., ad lib. roughage, 2 random groups	FCM, LWC, $LW^{.75}$	fixed b's
	.00		85 - 168			
(4)	.14	> 80000 cows	1 - 305	conc. according to yield, not ad lib., several groups, no indiv. intake	FCM, LW	est. var.
(5)	.69	295 cows	1 - 250	TMR ad lib. 1 group	FCM, LWC, $LW^{.75}$	fixed b's
(6)	.38	377 lactations	1 - 182	TMR ad lib. 2 random conc. groups	LE, LWC, $LW^{.75}$	est. b's
	.32				LE, LWC, $LW^{.75}$	fixed b's
	.30				several	est. b's
	.34				LE, LWC, $LW^{.75}$	est. var.
Genetically	calculated RFI:					
(4)	.01	> 80000 cows	1 - 305	conc. according to yield, not ad lib., several groups, no indiv. intake	FCM, LW	est. var.
(6)	.05	377 lactations	1 - 182	TMR ad lib. 2 random conc. groups	LE, LWC, $LW^{.75}$	est. var.

[1] 1. Van Arendonk *et al.*, 1991; 2. Ngwerume and Mao, 1993; 3. Svendsen *et al.*, 1993; 4. Kennedy *et al.*, 1993; 5 Jensen *et al.*, 1991; 6. this study.

[2] TMR = total mixed ration; conc. = concentrate.

[3] est. b's = partial efficiencies estimated as partial regression from data.

fixed b's = partial efficiencies from literature.

est. var. = partial efficiencies from estimated variance and covariance matrix.