

GENETIC ASPECTS OF YIELD, FEED INTAKE AND FEED EFFICIENCY
IN DAIRY CATTLE FED *AD LIBITUM*

BY

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Thesis presented for the degree of
Doctor of Philosophy
University of Edinburgh
1990



DECLARATION

I declare that this thesis is my own composition
and that the research described in it is my own
work, except where otherwise stated.

Pooran Persaud

November, 1990

To my parents, brothers, sisters and
last but not least, my wife, Leela.

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ABSTRACT

Milk production, feed intake, and liveweight records were available on individual animals from a high yielding Holstein-Friesian herd in which selection had been practised on fat plus protein yield using nationally available AI sires. Unlike most other studies, animals were fed *ad libitum* thus making this data ideal for investigating genetic relationships. In total, the data comprised 475 26-week and 293 38-week (a subset of the 26-week data) lactation records.

The relationship between sires and maternal grandsires' transmitting ability (ICC), expressed as a pedigree index (sire ICC + 0.5 maternal grandsire ICC), and offspring performance for milk production traits, feed intake, and gross efficiency (milk energy (MJ)/ total energy intake (MJ)) was investigated. Regressions of fat plus protein yield, fat yield, protein yield, and milk yield, of heifers, on their corresponding pedigree index were not far from the theoretical expectation (for a full lactation) of 1. A genetic increase of 10% in fat plus protein yield of daughters of sires of high genetic merit for fat plus protein yield was accompanied by a genetic increase of 2.9% in feed intake and a 7.9% genetic increase in efficiency.

The genetic relationships among milk production, feed intake, feed efficiency and liveweight traits were investigated. Restricted Maximum Likelihood analyses were carried out, fitting an Animal Model, with repeat lactations as an additional random effect. Univariate analyses were done after approximate canonical transformation of the traits. Heritability estimates for fat plus protein yield, feed efficiency and feed intake ranged from 0.45 ± 0.22 to 0.15 ± 0.12 , 0.48 ± 0.21 to 0.13 ± 0.09 , and 0.52 ± 0.14 to 0.30 ± 0.15 , respectively. Genetic correlations between milk production traits and efficiency were generally less than 0.65. Genetic correlations between liveweight traits and efficiency were very high and negative. The results indicate that when selection is on yield, the correlated responses in efficiency may be smaller under *ad libitum* feeding,

compared with published values where cows were fed according to yield. Including liveweight in the selection criterion may give higher responses in efficiency compared to selection on yield alone. In nucleus schemes (based on Multiple Ovulation and Embryo Transfer) it may be worthwhile to include feed intake or efficiency directly in the selection criteria.

With part lactation records planned for use in MOET nucleus schemes, the relationships between part and total lactation intake and efficiency were investigated using records for successive 6 week periods. In general heritability estimates for 6-week fat plus protein yield, feed intake and efficiency were similar to those for total lactation measures, although there was a trend towards lower estimates in early lactation for yield and efficiency traits. Genetic correlations between part measures and 'total' lactation fat plus protein yield, feed intake, and efficiency ranged from 0.82 to 1.00, 0.85 to 0.98, and 0.60 to 1.00, respectively. The correlations were lowest in the first 6-week period, gradually increased up to a maximum in the third or fourth periods, and declined thereafter. The results indicate that selection on a part measure of feed intake or efficiency, taken between 15 and 20 weeks of lactation will be as effective in improving intake and efficiency as selection on total lactation measures. Other 6-week measures taken between weeks 9 to 14 and 21 to 26 will also give good prediction of total lactation intake and efficiency.

ACKNOWLEDGEMENTS

This study has been supervised by Prof. W. G. Hill and Dr. G. Simm. I am very grateful to them for their advice, guidance and constant encouragement throughout the course of this study. In particular, I would like to thank Dr. Simm for his support and patience, especially in the early part of this study.

I am grateful to Mrs. S. Brotherstone for kindly providing pedigree and sire ICC data and for advice and assistance in computational matters. I am also grateful to Dr. K. Meyer for allowing me to use her DFREML programs.

I would like to thank my friends and post graduate colleagues, especially Mr. P. M. Visscher and Mr. B. K. Beniwal, for useful discussions and encouragement during the course of this study. Mr. Visscher kindly provided the program to compute standard errors in Chapters 5 and 6.

I would also like to thank Dr. J. D. Oldham for permission to use the Langhill Data, Mr. D.R. Neilson and Mr. H. Parkinson for supervising collection of feed intake data, Dr. M. Lewis for ration formulation, and Mr. L.S. Hodgson-Jones, Mr. J. Mills and colleagues at the Langhill Dairy Farm for managing the animals.

Finally I would like to thank the IDB/ University of Guyana Project for financial support and the University of Guyana for granting me study leave.

PUBLICATIONS

Arising from this Thesis

Persaud, P., Simm, G. and Hill, W.G. 1990. Genetic parameters of feed efficiency and feed intake for dairy cattle fed *ad libitum*. *Proceedings of the 4th World Congress on Genetics Applied to Livestock Production*. Edinburgh. Vol. 14. pp 237-240.

Persaud, P., Simm, G., Parkinson, H. and Hill, W.G. 1990. Relationships between sires' transmitting ability for production and daughters' production, food intake and efficiency in a high yielding dairy herd. *Animal Production* 51: 245-253.

Persaud, P., Simm, G. and Hill, W.G. 1991. Genetic and phenotypic parameters for yield, food intake, and efficiency of dairy cows fed *ad libitum*. 1. Estimates for 'total' lactation measures and their relationship with liveweight. *Animal Production* (In press).

Persaud, P. and Simm, G. 1991. Genetic and phenotypic parameters for yield, food intake, and efficiency of dairy cows fed *ad libitum*. 2. Estimates for part lactation measures and their relationship with 'total' lactation measures. *Animal Production* (In press).

In Appendix

Simm, G., Persaud, P., Neilson, D.R., Parkinson, H. and McGuirk, B.J. 1991. Predicting food intake in dairy heifers from early lactation records. *Animal Production* (In press).

CHAPTER 1

GENERAL INTRODUCTION

Feed costs constitute the greatest single cost of dairy production, accounting for approximately 80 to 90 % of the total variable costs (MMB, 1990). In recent years the imposition of milk quotas in EC countries together with higher incentives for increased milk solids production have only served to emphasise the importance of efficient milk and milk solids production. Genetic improvement of feed efficiency (or some other objective including feed intake or feed costs e.g. profitability) is therefore justified in being one of the main objectives of dairy cattle breeding. In many dairy cattle breeding programmes, however, selection has been directed to production traits, rather than to feed efficiency. This is because the measurement of individual feed efficiency is very costly in terms of both labour and time. By contrast, production traits are easily measured and do not require expensive equipment. Furthermore, these production traits, e.g. milk yield, are themselves economically important. As a consequence, selection in dairy cattle breeding programmes has mainly been confined to milk production traits, and genetic improvement in these traits has resulted.

In conventional progeny testing schemes breeding values of sires are estimated for milk production traits but not for feed intake or efficiency. It is therefore important for breeders to know what correlated responses occur in feed intake and efficiency as selection continues for increased milk production. There is experimental evidence that shows that increases in feed intake and efficiency result when selection is for higher milk yield (Lamb *et al.*, 1977; Hind, 1979; Gibson, 1986), but there have been few investigations into these correlated responses when selection is for increased milk solids (fat plus protein) yield, particularly at high production levels. With more importance now being attached to milk solids production, particularly milk protein, it is therefore important to know if similar correlated responses are obtained when selecting for higher milk solids yield.

Given the importance of feed intake and efficiency to the profitability of dairy farming, it is surprising how little is known about genetic aspects of feed intake and

efficiency. This is, however, due mainly to the high cost of recording individual feed intake. As a consequence investigations have been done mainly on experimental farms and testing stations and rarely in field trials. Studies with experimental herds have shown variation in feed efficiency between breeds, for example among Ayrshire, Holstein, Brown Swiss, and their crosses (McDowell *et al.*, 1968; McDowell, 1982), between British Friesian and British Jersey (Gibson, 1986), and among Holstein/Friesian, Jersey, Dutch Friesian, and Dutch Red and Whites (Oldenbroek, 1988). There have, however, been fewer investigations (e.g. Mason *et al.*, 1957; Hooven *et al.*, 1968) on genetic aspects of feed efficiency at the within breed level. Results from these studies have indicated a moderate heritability for feed efficiency and a high correlated response in efficiency to selection on yield. In almost all cases, however, cows were fed according to production, and this could obscure the true biological relationship among these traits. The use of these traits in the selection criteria for the genetic improvement of dairy cattle will depend on a knowledge of these relationships. It is therefore imperative that genetic parameters for these traits are estimated under *ad libitum* feeding regimes.

Under field conditions direct selection for increased efficiency (via measurement of individual feed intake) is not practical and genetic improvement of efficiency therefore depends on the correlated response to selection on milk production traits. Further improvements in efficiency may be obtained by including measures of body size e.g. height at withers, liveweight (which are easily measured) in the selection criteria. Genetic and phenotypic parameters for efficiency and bodysize traits are, however, generally not known although a few studies have investigated the relationship between these traits.

Alternative breeding schemes for dairy cattle improvement, involving Multiple Ovulation and Embryo Transfer (MOET), have been suggested (Nicholas and Smith, 1983) and are now in operation (McGuirk, 1990). These nucleus MOET schemes will allow feed intake and hence efficiency to be measured and thus selected for directly.

This is likely to give higher responses in efficiency as compared to the correlated responses obtained in progeny testing schemes. It has been predicted that these schemes will give rates of genetic progress (in milk production) comparable to those achieved by large scale progeny testing schemes (Woolliams and Smith, 1988; Ruane and Thompson, 1989). Even though MOET schemes will facilitate direct measurement of, and selection for feed intake and efficiency, the high cost of feed recording equipment will, however, still place a limit on the progress that can be achieved in practice. An alternative selection strategy, which will reduce costs and give faster progress, will be to use early part lactation measures rather than total lactation measurements. Very few investigations, however, have been carried out into the genetic relationships between part and whole lactation feed intake and efficiency.

This study therefore has three main objectives. These are:

1. to examine and quantify the relationships between sires' predicted genetic merit for production and their daughters' production, feed intake and efficiency, in a high yielding herd;
2. to estimate genetic parameters for feed intake and efficiency, and their relationship with milk production and liveweight traits, under an *ad libitum* feeding regime; and finally
3. to estimate genetic parameters for part lactation measures of feed intake and efficiency and their relationship with total lactation measurements.

CHAPTER 2

LITERATURE REVIEW: GENETIC ASPECTS OF FEED INTAKE AND FEED EFFICIENCY

This review is divided into two main parts. In the first part the question of selecting directly for feed efficiency is addressed, while in the second, attention is paid to possible alternative selection criteria for genetically improving feed efficiency.

2.1 Measures of Feed Efficiency

Different researchers have used different measures of efficiency. That most commonly used, and for which most results relating to genetic aspects are available, is gross feed efficiency. It involves some measure of the ratio of energy produced in milk to energy consumed or its inverse (see Table 2.1). Some researchers, e.g. Oldenbroek (1988), have used a measure of economic efficiency, defined as income from milk minus feed costs. Most, if not all, dairy farmers are likely to be more interested in economic efficiency, but this will depend greatly on the prices of milk and feed, which vary widely. Although it has been found that a higher gross efficiency is associated with a higher economic efficiency (Oldenbroek, 1988; Simm and Stott, 1988), the relationship between gross efficiency and profit can vary widely, or in fact need not exist at all because the costs of metabolisable energy from forage, conserved forage, and concentrates are very different. If, however, a diet of fixed composition is offered *ad libitum*, then cost is proportional to metabolisable energy intake (Neilson, 1982). Ostergaard *et al.*, (1990) concluded that the most convenient definition to use for efficiency is the net income per kg milk produced, i.e. the difference between total income and total cost. This would, however, require information about all outputs (milk, calves, cull cows) and all inputs (feed, housing, labour, veterinary services etc.).

2.2 Definition of Feed Efficiency

In general, biological efficiency may relate to any measure of the efficiency with which a biological process is carried out to meet a biological end, in this context milk production (Spedding, 1973). In dairy cattle, the ability to convert feed into milk has been generally termed feed efficiency. Blake and Custodio (1984) define feed efficiency as

'the rate of converting dietary nutrients to milk after adjustment for nutrients supplied by catabolism or for nutrients diverted to replenish tissue reserves'. Mao *et al.*, (1990) have used a measure of net energy efficiency, defined as the ratio of milk energy to feed energy intake after correcting for maintenance energy requirements and changes in body reserve status. In practice, however, when measuring feed efficiency in dairy cattle a major problem is to account for the effects of tissue mobilisation and replenishment. This review will therefore focus on gross feed efficiency.

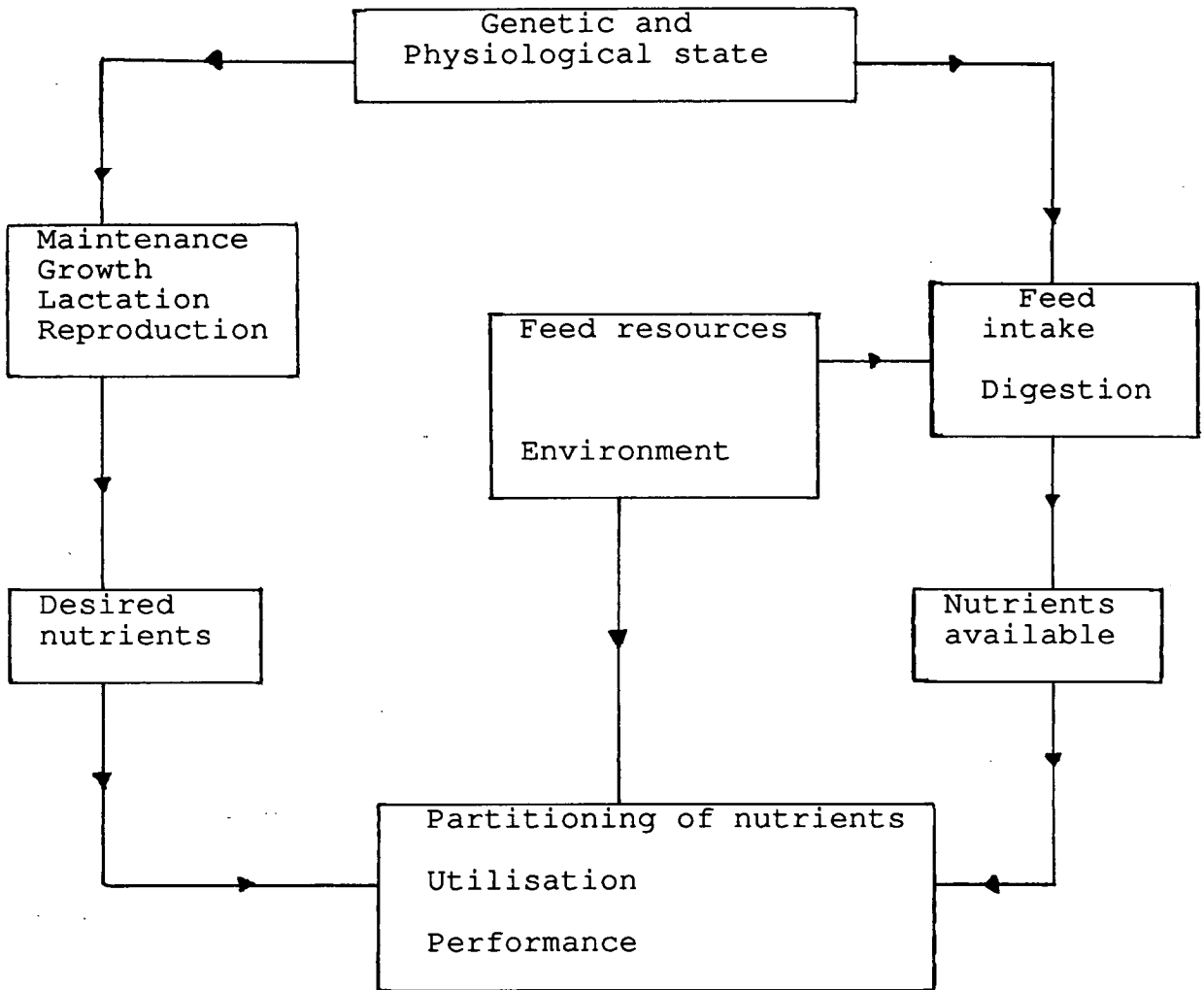
2.3 General Aspects

Feed efficiency in dairy cattle is influenced by the diet and other environmental factors and by the genetic ability of the cow to utilise these inputs for milk production. The trait is thus a composite of several characters rather than one characteristic of the cow (Blake and Custodio, 1984). A modified version of the total biological complex of feed efficiency for dairy cattle is shown in Figure 2.1.

The energy intake of dairy cows is utilised for different biological processes, mainly, milk production, maintenance, growth and reproduction. The efficiency of conversion of feed energy into milk energy is, however, affected by the amount of energy lost during the conversion and this has been shown to be closely related to the composition of the diet (Van Es and Van der Honing, 1979). Energy loss occurs during fermentation (5 to 10 per cent) (Tyrrel and Moe, 1975; Van Es, 1976; ARC, 1980), in the faeces (10 to 70 per cent), and in the urine (2 to 8 per cent) (Van Es, 1976). The utilization of the remaining metabolizable energy and the partition between maintenance, milk production, growth, and reproduction are difficult to determine (Moe and Tyrrel, 1975), but will depend to a large extent on the cow's genetic merit for milk production and environmental conditions. Based on a model described by Groen (1988), as cited by Korver (1988), it has, however, been shown that milk production and maintenance utilizes the major part, approximately 85 to 95 per cent, of the total metabolisable energy intake.

Figure 2.1

Utilisation of nutrients and performance of dairy cattle in relation to genetic state and constraints (After Korver, 1988).



2.4 Genetic Variation in Feed Efficiency

Direct selection for improved feed efficiency can only be effective if there is substantial additive genetic variation for the trait. Heritability estimates for feed efficiency obtained from the literature (Table 2.1) seem to indicate that this is so. It should, however, be noted that a moderate heritability does not necessarily imply substantial additive genetic variation, since the heritability is a ratio of the genetic to total phenotypic variance.

Differences in the heritability estimates may be due to the different measures of feed efficiency, the different breeds used, different lactation measurements, size of data and method of analysis, sampling, and environmental and management conditions (i.e. feed quality and/or quantity) peculiar to each experiment. Apart from the studies of Venge (1956), using data from 3083 cows in 174 progeny groups, Mason *et al.*, (1957), where data was from 247 progeny groups with 18 daughters each in Danish testing stations, and the Beltsville trials (Hooven *et al.*, 1968), most of these estimates have been based on small data sets. Furthermore, all of these data came from experimental herds and/or testing stations where more control can be exerted over management and feeding. In addition, it has been observed that the between sire variance, estimated from test station data, is higher than that estimated from field data (Robertson and Mason, 1956; Touchberry *et al.*, 1960), most likely due to confounding with environmental effects. In all these studies (Table 2.1) the heritability estimates of milk yield were very similar to those obtained for efficiency. This is not unexpected given the fact that efficiency is expressed as a ratio of yield to intake. These estimates for milk yield are, however, considerably higher than corresponding literature estimates obtained from analyses using large data sets (see Pearson *et al.*, 1990 for review). It therefore appears that the heritability estimates for milk yield, and consequently those for efficiency, from these experimental studies, may be inflated.

Heritability estimates for efficiency based on field data are very limited, and as

expected are lower, ranging from about 0.10 to 0.25 (Wiggans and Van Vleck, 1978; Ramirez, 1979). These field data are, however, obtained from milk recording programmes where roughage intake is measured on a herd basis and individual concentrate intake is frequently imprecisely measured (Kennedy, 1984).

Despite these limitations, the results from these studies demonstrate that there is a genetic component for gross feed efficiency. It therefore seems likely that direct selection for improved feed efficiency is feasible and relatively good genetic progress can be expected.

2.5 Genetic Improvement of Feed Efficiency

From heritability estimates in Table 2.1 it appears possible to select directly for, and hence obtain improvement in, feed efficiency. Given the high cost of recording feed intake, however, the obvious question is 'is it worthwhile to do so?', and if not, then how should improvement in efficiency be achieved. A reasonable answer may be obtained by examining the relationships between efficiency and milk yield, and the other biological components of gross efficiency.

2.5.1 Selection on Milk Yield

Results from several studies have shown a high correlation, both phenotypic and genetic, between milk yield and efficiency, with the latter tending to be higher than the former (Table 2.2). These correlations indicate that a high correlated response in efficiency will accompany selection for increased milk yield. Assuming mass selection, for example, the correlated response in efficiency when selection is for yield relative to that from direct selection for efficiency, is equal to $r_g h_y/h_x$ (Falconer, 1989), where r_g is the genetic correlation between the two traits and h_y and h_x are the square root of the heritabilities of milk yield and efficiency, respectively. This formula assumes equal selection intensities for both traits and examples of these relative correlated responses have been given by Freeman (1967) (Table 2.3). As seen from Table 2.3, the magnitude

Table 2.1

Summary of heritability estimates for feed efficiency of milk production.
Corresponding estimates for milk yield are in brackets.

Measure of Efficiency	h^2	SE	Reference
FU/kg Butterfat	0.40 (0.54)	- -	Venge, 1956
FCM/FU	0.48 (0.57)	0.07 (0.08)	Mason <i>et al.</i> , 1957
FCM/100 FU	0.12 (0.12)	0.02 -	Syrstad, 1966
FCM/ENE	0.46 (0.58)	0.18 (0.18)	Hooven <i>et al.</i> , 1968
60-day TDN/FCM	0.63 (0.63)	0.09 (0.11)	Hickman and Bowden, 1971
FCM/ENE	0.56 (0.56)	0.07 (0.06)	Hooven <i>et al.</i> , 1972
4 % FCM/ENE	0.46 (0.52)	0.10 (0.10)	Miller <i>et al.</i> , 1972
ME/DE	0.47 -	0.23 -	Lamb <i>et al.</i> , 1977

FU = feed units.
ME = milk energy.
DE = digestible energy.
FCM = fat corrected milk.
ENE = estimated net energy.
TDN = total digestible nutrients.

Table 2.2

Summary of correlations between milk yield and feed efficiency.

Measure of Efficiency	r_g	SE	r_p	Reference
FCM/FU	0.95	0.08	0.84	Mason <i>et al.</i> , 1957
FCM/100FU	0.88	0.06	0.95	Syrstad, 1966
FCM/ENE	0.92	0.04	0.66	Hooven <i>et al.</i> , 1968
ME/FE	-	-	0.86	Dickinson <i>et al.</i> , 1969
FCM/Mcal ENE	0.93	0.01	0.82	Hooven <i>et al.</i> , 1972
ME/GE, %	0.36	-	0.72	Grieve <i>et al.</i> , 1976
ME/DE, %	0.29	-	0.60	Grieve <i>et al.</i> , 1976
ME/DE	0.95	0.07	-	Lamb <i>et al.</i> , 1977
FPCM/EI	0.95	-	0.69	Korver, 1982
SCM/Mcal NE	0.42	-	0.75	Custodio <i>et al.</i> , 1983
Milk/NE	-	-	0.35	Smothers <i>et al.</i> , 1986
Milk/FE	-	-	0.82	Gibson, 1986
Milk/FE	-	-	0.75	Oldenbroek, 1988

1 FU = 0.7 starch equivalent.
 DE = digestible energy.
 GE = gross energy.
 NE = net energy.
 ME = milk energy
 FE = feed energy
 EI = energy intake
 SCM = solids corrected milk.
 FPCM = fat-and-protein corrected milk.

Table 2.3

Expected relative correlated response in gross feed efficiency when selection is for increased milk yield (After Freeman, 1967).

Heritability		Correlated response / Direct response		
		Genetic correlation		
Milk	Efficiency	0.8	0.9	0.95
0.20	0.2	0.80	0.90	0.95
	0.3	0.65	0.74	0.76
0.25	0.2	0.89	1.00	1.06
	0.3	0.73	0.82	0.87
0.30	0.2	0.98	1.10	1.16
	0.3	0.80	0.90	0.95

Note: The calculation assumes mass selection and equal selection intensities for milk yield and efficiency.

of the relative correlated responses in feed efficiency depends on the heritability for feed efficiency and this is likely to vary depending on management and environmental effects. Also indirect selection is expected to be superior to direct selection only if the heritability of milk yield is substantially higher than that of feed efficiency, if the genetic correlation is high, or if a substantially higher selection intensity can be applied to milk than to feed efficiency. From estimates in Table 2.1, the former does not appear to be true. In practice, however, the effective selection intensity will be greater for milk yield than for feed efficiency, since it is easier to measure the former on a larger number of cows. Consequently higher genetic gain may be obtained via indirect selection for milk yield rather than direct selection for feed efficiency. A major part of the improvement in milk production of dairy cattle comes from the selection of progeny tested bulls. Therefore the relationship between indirect (efficiency) and direct (milk yield) response will approach the genetic correlation, as the progeny groups increase in size. Almost all the estimates of correlations in Table 2.2 have, however, been obtained from experiments in which cows have been fed concentrate or grain according to yield. This system of feeding could have induced a high correlation between milk yield and efficiency. Korver (1988) has suggested that this problem may be reduced by recording data only in the early part of lactation during which cows have a negative energy balance and are fed less adequately according to production.

These results suggest that it may be more practical to improve feed efficiency by indirect selection for increased milk production. This conclusion is, however, based on estimated correlations under a particular feeding regime. There is a need to estimate this correlation under *ad libitum* feeding regime, and also to test such conclusions by direct selection experiments.

2.5.2 Feed Intake

In the first part of lactation, the high yielding dairy cow's energy requirements cannot be met by feed intake thus resulting in a negative energy balance. As a result tissue reserves are mobilized for milk production. Results from several studies (e.g. Dickinson *et al.*, 1969; Grieve *et al.*, 1976; Custodio *et al.*, 1983) have indicated that increases in gross energy efficiency of high genetic merit cows are not due to a better dietary utilization, but rather to a higher degree of tissue catabolism. This is also supported by the observation that genetically high yielding cows use up more of their body reserves than genetically low yielding ones (Cunningham, 1984; Gibson, 1986). Van Es and van der Honning (1979) concluded that the energetic efficiency can be improved if milk is synthesised from nutrients rather than from adipose tissue. More nutrients can be made available by increasing the density of the diet but this is limited by the fact that 30 per cent of the diet needs to be of long roughage for normal rumen function (Korver, 1988). Also several studies in which the energy intake was increased during early lactation (Broster *et al.*, 1969; Van der Honing *et al.*, 1981; De Visser *et al.*, 1982), showed an increase in milk yield, but did not show any obvious reduction in the negative energy balance.

An alternative to increasing nutrient intake would be to genetically increase feed intake. A genetic increase in feed intake, especially in early lactation would reduce the energy deficit and thus result in an improvement in feed efficiency. This approach to increase production and/or efficiency via a genetic increase in feed intake (capacity) is now receiving increased attention (Pearson *et al.*, 1990; Svandsen *et al.*, 1990; Madsen *et al.*, 1990). Genetic improvement of efficiency via direct selection on intake may be preferable to direct selection on efficiency as in the latter case the relative response in the component traits (i.e. yield and intake) are not actually known.

Table 2.4
Heritability estimates for measures of feed intake.

Measure of Feed Intake	h^2	SE	Reference
Total ENE	0.36	0.14	Hooven <i>et al.</i> , 1968
60 day TDN	0.78	0.08	Hickman and Bowden, 1971
31 to 60 day ENE	0.24	0.05	Hooven <i>et al.</i> , 1972
Total ENE	0.26	0.06	Hooven <i>et al.</i> , 1972
Forage	0.19	0.09	Miller <i>et al.</i> , 1972
Grain	0.26	0.09	Miller <i>et al.</i> , 1972
Total ENE	0.42	0.10	Miller <i>et al.</i> , 1972
First 20 weeks	0.16	-	Gravert, 1985
1 to 100 days	0.42	-	Leuthold <i>et al.</i> , 1989
101 to 200 days	0.54	-	Leuthold <i>et al.</i> , 1989
201 to 305 days	0.07	-	Leuthold <i>et al.</i> , 1989
90 day energy	0.12 ⁺⁺	-	Moore <i>et al.</i> , 1990
90 to 305 day energy	0.16 ⁺⁺	-	Moore <i>et al.</i> , 1990
2 to 6 week roughage	0.55	0.22	Svendsen <i>et al.</i> , 1990
7 to 12 week roughage	0.25	0.20	Svendsen <i>et al.</i> , 1990

ENE Estimated net energy
 TDN Total digestible nutrients
 ++ Estimates based on milk recording (field) data.

It appears that selection on milk yield would not automatically increase feed intake of dairy cows in early lactation (Hooven *et al.*, 1972; Gravert, 1985), but heritability estimates of feed intake (Table 2.4) appear to be moderate indicating that selection for increased intake in early lactation is possible. The possibility of selecting for increased feed intake, within present breeding schemes is, however, almost impossible due to the high costs of measuring individual feed intake. Nicholas and Smith (1983) and Gibson (1987) concluded that it is possible to include feed intake in a selection index for dairy cattle in nucleus breeding schemes because feed intake would only have to be measured on a limited number of potential bull dams or sisters.

In the UK, Genus (formerly the Farm Services Division of the Milk Marketing Board of England and Wales (MMB)), is currently developing a MOET nucleus breeding scheme (formerly owned and operated by Premier Breeders) within which they will record individual feed intakes (McGuirk, 1990). The high cost of feed recording facilities will, however, place a limit on the number of animals that can be recorded. More animals may be recorded and the generation interval reduced by measuring intake and hence efficiency over a shorter period, early in lactation. This would only be feasible if these early part measures are sufficiently heritable and well correlated with total lactation measures. Apart from that of Hooven *et al.*, (1972), however, there seems to be little or no investigation into genetic relationships between part and whole-lactation feed intake and efficiency.

Performance testing schemes (for sires) may also provide an opportunity to measure and select directly for increased intake, and one such study has been reported by Korver *et al.*, (1987), in which feed intake is being measured on young AI bulls between 4 and 12 months of age at central testing stations. The benefit of measuring feed intake in such a scheme would depend on the relationship between feed intake of young growing bulls and that of their daughters during lactation. Haapa and Syvavarvi (1987), however, concluded that this relationship was not clear. At present, investigations are continuing in

Denmark and The Netherlands to assess this relationship (Ostergaard *et al.*, 1990).

2.5.3 Body Size

In addition to milk yield and feed intake, body weight plays an important role in biological efficiency of milk production. Selection for increased body size seems to be antagonistic to feed efficiency (Ramirez, 1979; Yerex *et al.*, 1988). Hooven *et al.*, (1968) obtained a genetic correlation of $-0.17(\pm 0.26)$ while Oldenbroek (1988) obtained a "cow correlation" of -0.29 between body weight and feed efficiency. By contrast, Mason *et al.*, (1957) indicated that selection for increased yield and hence efficiency would result in a slight increase in body size (heart girth and height at withers being used as measures of size), while Gibson (1986) observed no significant differences in body weight or size between genetically high and low yielding groups. The conclusion from the literature is thus not clear. These results are even more difficult to interpret given that most European black and white dairy populations increasingly have some proportion of North American Holstein genes and that historically Holsteins were selected for increased size. Nevertheless, assuming the same yield, one would expect that larger and heavier dairy cows would have a lower feed efficiency because of increased maintenance requirements. However larger dairy cows may also have a greater feed intake (appetite) and any increase in milk energy production may offset the increased maintenance requirements thus resulting in an overall increase in feed efficiency. The relationship between milk yield or feed efficiency and body size is, however, not expected to be linear and, as Robertson (1973) indicated, dairy cows of intermediate size would likely have the greatest efficiency if no allowance is made for body size when feeding according to yield.

With this background, what then is the possibility for genetically improving feed efficiency in dairy cows using body measurements? Gravert (1985) reported that chest circumference is an accurate predictor of feed intake, while Mason *et al.*, (1957) found that wither height, a more permanent measure of size, is favourably associated with yield and efficiency. Mason *et al.*, (1957) concluded that, in the absence of efficiency

measurements, it would be best to select on yield, taking into consideration height at withers. They further concluded that, using the correlation they obtained, it could be demonstrated (mathematically), that the ratio of yield over height would correspond closely to the best index. Gibson (1986), however, found that the ratio of yield to body weight did not predict efficiency any better than did yield itself.

The relationship between body size and feed efficiency is complicated because it varies with breeds and their growth rates, the energetic composition of gain, age, stage of lactation, and level of management. Nevertheless the inclusion of body size traits in the selection criteria for genetic improvement of dairy cattle, especially under field conditions (where individual feed recording is not feasible), is likely to result in higher correlated responses in efficiency than those presently obtained. Further investigations into the relationships between efficiency and body size traits are therefore warranted.

2.5.4 Maintenance Requirements

Considerable variation has been found for maintenance requirements (per unit metabolic size) between different species and at different ages (Reid, 1974; Ried *et al.*, 1980). However, reviews by Freeman (1975) and Bauman *et al.*, (1984) have concluded that relatively little variation exists among cows fed similar rations in maintenance requirements per kg metabolic weight. Taylor *et al.*, (1986) computed a phenotypic coefficient of variation of 6.4 per cent for maintenance requirements per unit metabolic weight, while Van Es (1961) adjusted maintenance requirements to constant body weight and obtained estimates of among cow coefficients of variation of 4 to 8 per cent (dry dairy cows), using respiration chambers. Davey *et al.*, (1983) found no difference in apparent maintenance requirements between high and low genetic group Friesians, although Anderson (1980) obtained a heritability of 0.31 for maintenance requirements in beef bulls, using a small data set. In spite of the fact that most of these studies were based on small number of animals, the evidence so far indicates some variation for maintenance requirements. To what degree this variation is genetic, is however, still not clear.

Furthermore the extent to which this source of variation may be utilised in the genetic improvement of efficiency may be limited given the difficulty of accurately measuring this trait.

2.5.5 Digestion, Absorption, and Utilization of Metabolisable Energy

It is possible to improve feed efficiency through changes in digestion, nutrient absorption, or the utilization of metabolizable energy. These can be realised through manipulation of the diet or by the pattern of nutrients supplied to the tissues (Bauman *et al.*, 1984). Little genetic variation has, however, been observed for these factors (Van Es, 1961; Davey *et al.*, 1983). Gravert (1985) has suggested that factors such as saliva production and the intensity of rumination may have an influence on intake and hence efficiency, but there has been little or no attempt to investigate the variation in these factors. Genetic variation in other components of efficiency, such as susceptibility to disease appear to be small: for example, heritability estimates for mastitis and ketosis range from 0.01 to 0.05 (Norman and Van Vleck, 1972; Henricson *et al.*, 1977; Hansen *et al.*, 1979; Philipsson *et al.*, 1980; Solbu, 1984). More recent estimates, however, indicate a moderate heritability for these traits (Lin *et al.*, 1989). Also recent estimates of economic loss associated with these health/disease traits are substantial (Smith, Oltenacu and Erb, 1985 as cited by Lin *et al.*, 1989). Further investigations into genetic aspects of these traits may therefore be worthwhile.

2.5.6 Residual Feed Consumption

Residual feed consumption (RFC) refers to the variation in feed intake after adjustment for maintenance and production requirements (Luiting and Urff, 1987). Usually maintenance and production requirements are expressed as a function of metabolic body weight and product composition, respectively. Most work with RFC has been done with poultry and estimates of heritability in laying hens range from 0.05 to 0.40 (Luiting, 1987). Moderate heritability estimates have also been reported for this trait in cattle (Koch *et al.*, 1963; Korver *et al.*, 1987). These estimates indicate differences

between animals in the utilisation of metabolisable energy for maintenance and production and seem to contradict the conclusions of other workers (e.g. Van Es, 1961; Davey *et al.*, 1983) who have observed little variation for metabolisable energy utilisation. The variance of this trait could, however, be inflated by variance arising from (a) inaccurate estimation functions with regard to the independent variables, (b) independent variables not included in the model, (c) individual variation of the parameters of the model, and (d) random error i.e. error of measurement (Luiting and Urff, 1987). These features of RFC will certainly reduce its potential as a trait of importance for the genetic improvement of efficiency.

2.5.7 Heterosis

Little research has been done to evaluate the effects of heterosis on feed efficiency in dairy cattle. One of the few investigations found in the literature seems to be that reported by Freeman (1975 and 1979), in which purebred Holsteins (H), Ayrshires (A) and Brown Swiss (S) cattle were compared with their crosses. Heterosis of about 4 to 5 % was observed for the A x H and S x H crosses, with the three-breed crosses showing more heterosis than the two-breed ones. When expressed as a difference from the Holstein mean, the A x S, S x H and three-breed crosses were generally more efficient, although they had slightly lower milk production. The effect of heterosis on overall economic efficiency is, however, likely to be greater since characters such as reproduction show appreciable amounts of heterosis.

2.6 Conclusion

Heritability estimates from the literature indicate that genetic improvement in feed efficiency via direct selection, is possible. Variation between these heritability estimates may partly be a result of the different methods of measuring feed efficiency, differences in the feeding regimes used, and differences in the method of data analysis. There is therefore still a need for further investigations.

From estimates of genetic correlations it seems more practical to improve feed efficiency indirectly by selecting on milk yield. These correlation estimates are, however, based mainly on management systems where animals were fed according to yield. Estimates of genetic correlations under *ad libitum* feeding regimes are scarce.

A genetic increase in feed intake during early lactation offers a possibility to improve feed efficiency.

The establishment of nucleus MOET schemes now provides the opportunity to select directly for feed intake and/or efficiency. Furthermore the use of part lactation records in such schemes has potential advantages in reducing costs and giving faster progress. Investigation into genetic aspects of feed intake and feed efficiency and their relationship with part lactation measures is therefore warranted.

In view of the relative ease of measuring body size traits, further investigations into their relationship with efficiency should be carried out in order to conclude on their potential for use in the genetic improvement of efficiency.

Genetic variation in biological components of efficiency such as digestion, absorption and utilisation of metabolisable energy appear to be small, thus offering little prospect for genetically improving efficiency.

Investigations into genetic aspects of feed efficiency in dairy cattle are severely limited by the cost of measuring feed intake. This has resulted in small experiments done over part or a single lactation in many cases. No attention has been given to feed efficiency over the "productive life" of the dairy cow.

The study described in this thesis will focus on some of the problems and needs highlighted in this review.

CHAPTER 3

DATA, DATA RECORDING AND PREPARATION

3.1 Introduction

In 1973 a long-term breeding project involving 200 pedigree British Friesian cows was initiated at the Edinburgh School of Agriculture's Langhill Farm. The aims of the project when it was first set up were:

1. To demonstrate the rate of genetic improvement in fat and protein yields which could be achieved through the use of top AI bulls.
2. To examine the consequences of this selection policy on overall profitability.
3. To develop management strategies for high-yielding dairy cows.

The improvement programme was developed jointly by the Edinburgh School of Agriculture and the AFRC Animal Breeding Research Organisation (presently AFRC Institute of Animal Physiology and Genetics Research) and the project is supported by the Holstein Friesian Society of Great Britain and Ireland (HFS), the MMB, and the Scottish Milk Marketing Board (SMMB). The selection objective of the breeding programme is 305 day lactation fat and protein yields. More recently, the emphasis in this project has changed to examining the consequences of selection for high fat plus protein yields on overall efficiency and profitability in different feeding systems.

3.2 Experimental Protocol

3.2.1 Selection Policy

Pedigree Holstein-Friesian AI bulls were selected for use at Langhill on the basis of their Improved Contemporary Comparison (ICC) for weight of fat plus protein. No attention was paid to type traits, although bulls in the AI stud have already been screened on daughter type. Attention was, however, paid to the reliability of sire proofs: bulls were required to have at least 25 effective daughters in 10 or more herds with less than 50 per cent of the daughters in any two herds. Once selected, a bull was used at random over all cows and heifers, except that a bull was not mated to a close relative. Bulls known to cause calving difficulty problems were not used on heifers.

Over the last ten years an increasing number of Canadian Holstein bulls have been used. Bulls without a reliable UK proof, were selected on the basis of their predicted Canadian breeding value for fat plus protein yield converted to ICCs. In 1976 a control herd was established and, up to 1986, cows in this herd were bred at random using semen from one of 50 bulls which entered the MMB or SMMB progeny tests in 1976. Animals from both the selection and control herds were managed identically. Figure 3.1 shows how the ICCs of bulls used at Langhill have changed over the years.

Selection was also practised within the herd. Each year the top 50 per cent (approximately) of heifers, ranked on a predicted cow genetic index (CGI) ($0.5 \text{ sire ICC} + 0.5 \text{ dam ICC}$ for kg fat plus protein (from the dam CGI)), were selected to enter the selection herd. Some attention was also paid to expected date of calving.

3.2.2 General Management

About 75 % of the herd at Langhill calves between September and December. As a result of this wide spread in calving, cows were housed into four groups according to their calving date. During this winter housing period, which usually lasted up to April, all cows were fed, *ad libitum*, a complete mixed diet. During the summer cows were rotationally grazed over six paddocks. Drinking water was offered *ad libitum* from self filling water troughs.

The cows were milked twice daily at 05.00 and 15.00 hours, through a 16:16 herringbone parlour, with automatic cluster removal and milk transfer.

All calves and cows were identified by ear tags and later by freeze branding. Information on health, reproduction and reason for disposal was also recorded.

3.2.3 Feeding Policy

The complete diet was formulated from grass silage, wet brewers' grains (draff) and a compound balancer meal mixed and fed to appetite from a mixer wagon. In some years

potatoes and sugar beet pulp were also used in formulating the ration. The balanced concentrate meal was formulated on a least cost basis to contain approximately 13 MJ ME/kg DM, 18 per cent crude protein (60 per cent degradability), together with all the required minerals and vitamins according to the Agricultural Research Council (ARC, 1980) recommendations. The ratio of silage to concentrate in the mix was determined by dietary specification for energy density (ME concentration) which takes account of silage quality and the stage of lactation of the cows.

In addition to feeding the complete diet *ad libitum*, 0.8 kg per day of concentrate was fed in the parlour in most years to encourage entry of the cows.

For diet formulation purposes the cows were divided into three groups, namely, early lactation, mid lactation, and late lactation. The ratio of silage to concentrate in the mix was varied according to the silage quality so that the complete diet reached target ME concentrations of 11.8-12.0, 11.4-11.6 and 11.0-11.2 MJ/kg DM in early, mid and late lactation respectively. The diet formulation was changed for all animals in a group when the group reached an average of about 100 days of lactation and about 200 days of lactation (with a range of about ± 30 days for individual cows). Usually concentrate:silage dry matter ratios in the complete diet were around 50:50 for early, 35:65 for mid, and 25:75 for late lactation rations. Table 3.3 is given, as an example, to show the complete diet formulation and composition at the different stages of lactation for the 1987/88 winter feeding period. In formulating the rations the main objective was to maximise the intake of silage at all stages of lactation, taking into consideration the dry matter content and nutritive value of the silage and the intake potential of the cows.

Individual intake of a complete mixed diet of silage, draff (brewers grain) and a compound balancer meal was measured on up to 86 cows per annum using Calan-Broadbent electronic gates (Broadbent, McIntosh and Spence, 1970). Both first calvers and cows were trained, for 6-8 weeks pre-calving, to use these gates. About 7-10

days before the expected day of calving cows were housed in straw-bedded courts. Within a week of calving cows were introduced into individual feeding gates within cubicles bedded with sawdust in a loose house.

3.3 Data Recording

3.3.1 Animals

The study involved first and subsequent lactation Friesian/Holstein cows over nine winter feeding periods starting from September 1979. In the first four years of the study, feed intake was recorded up to the 28th week of lactation for most cows while in the following years this was extended up to the 40th and 45th week for most cows. As a result of this, and also because of the higher frequency of missing records (from later calving animals) at the end of the recording period, it was decided to truncate records up to the 26th and 38th week. This resulted in two data sets: Data Set 1 containing records up to the 26th week only and Data Set 2, which is a subset of Data Set 1, comprising lactation records up to the 38th week. The number of lactation records in each year of the investigation in the two data sets are shown in Tables 3.1 and 3.2. In total, Data Set 1 included 475 lactations representing 251 animals while Data Set 2 had 293 lactations representing 168 animals.

3.3.2 Milk Yield and Composition Analysis

Milk yields were recorded on a weekly basis as the sum of Tuesday afternoon and Wednesday morning milkings.

Milk composition analysis was done monthly in the first year and every fortnight thereafter except in the last year when it was done weekly. Samples of milk (250 ml) were collected from the Tuesday afternoon and the Wednesday morning yield to give a representative sample of the milk at each milking. The analyses were done by the Central Testing Laboratory, the SMMB and the West of Scotland Agricultural College.

Butterfat and protein were determined with a milkosan 300 infra red analyser (Foss Electric UK Ltd), the analyses being standardised by the Gerber method for butterfat and the Kjeldahl method for protein estimation.

3.3.3 Feeding and Feed Recording

Cows were offered a 'complete' diet dispensed into individual feed bins once daily, with an allowance for refusals of 100 g/kg (10 per cent) of mean daily intake in the previous week. The weight of fresh diet offered and refused was recorded on four consecutive days (Monday through Thursday) each week, to the nearest 0.1 kg. This four day recording was found to be representative of the total feed intake for the week (Kabuga, 1986). From the dry matter (DM) determinations (see feed analysis) carried out on samples of diet and refusals collected from individual bins on each of the 4 days, mean daily dry matter intakes for each week of the investigation were calculated, i.e.

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

where DMI = mean daily dry matter intake(kg/cow)

FF = fresh food offered(kg/cow/day)

DMFF = dry matter of FF

FR = feed refusal(kg/cow/day)

DMFR = dry matter of FR

3.3.4 Feed Analysis

The silage and diet were sampled at weekly intervals throughout the investigation and analysed for dry-matter concentration (DM g/kg), crude protein (CP g/kg), modified acid detergent fibre (MADF g/kg), ash (g/kg), and *in vitro* organic matter digestibility (IVDOM g/kg). Ammonia nitrogen (N g/kg total nitrogen) and pH were also determined on the silages. Table 3.4 is given, as an example, to show the composition of the silages and diets used for 1983/84 feeding period.

Table 3.1
 Number of animals in each lactation in each year for data set 1.

Year		Lactation number					Total
Number	Date	1	2	3	4	>4	
1	1979/80	—	11	6	9	11	37
2	1980/81	—	7	13	4	13	37
3	1981/82	—	9	11	9	8	37
4	1982/83	23	—	6	5	4	38
5	1983/84	26	14	—	—	—	40
6	1984/85	21	17	17	9	19	83
7	1985/86	29	14	14	10	15	82
8	1986/87	30	19	7	10	18	84
9	1987/88	12	10	5	1	9	37
Total		141	101	79	57	97	475

Table 3.2

Number of animals in each lactation in each year for data set 2.

Year		Lactation number					Total
Number	Date	1	2	3	4	>4	
5	1983/84	13	6	—	—	—	19
6	1984/85	21	16	17	9	17	80
7	1985/86	28	14	13	10	15	80
8	1986/87	30	19	7	10	18	84
9	1987/88	9	8	4	1	8	30
Total		101	63	41	30	58	293

Figure 3.1: Change in genetic merit of sires for fat plus protein yield.

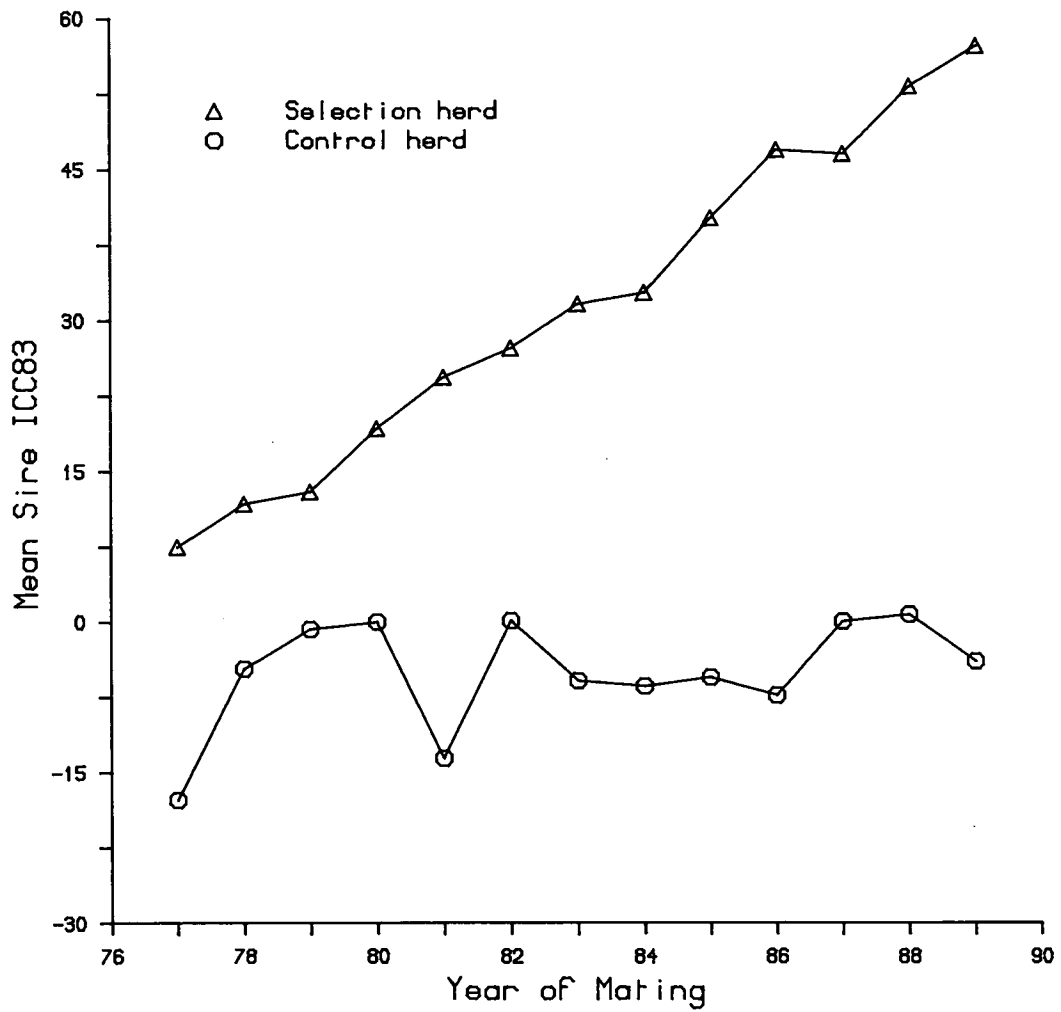


Table 3.3
Complete diet formulation for 1987/88 winter feeding period.

		Stage of Lactation		
		Early	Mid	Late
Diet formulation: (DM basis)	Silage	0.47	0.62	0.72
	Draff	0.05	0.05	0.06
	Meal	0.48	0.33	0.22
Diet composition:	DM g/kg	330	264	253
	CP g/kg DM	165	181	158
	ME MJ/kg DM	11.9	11.5	11.3

Table 3.4
Composition of grass silages and complete diet in year 1983/84.

Number of samples ⁺	Silage		Complete diet	
	33		33	
	Mean	SD	Mean	SD
Dry matter (DM) concentration	226	26	365	40
<i>Composition of DM</i>				
Crude protein (g/kg)	158	19	169	8
Modified acid detergent fibre (MADF) (g/kg)	331	17	212	15
Ash (g/kg)	82	9	77	8
<i>In vitro</i> digestible organic matter (g/kg)	662	14	771	14
Estimated metabolisable energy (MJ/kg)	10.4	0.2	11.3	0.3
Ammonia nitrogen (g/kg total N)	96	41		
pH	3.86	0.26		

+ refers to weekly samples

3.3.5 Liveweight

Within 48 hours after calving the liveweight of all cows was recorded. Thereafter weighing was on a weekly basis at approximately the same time of day on each occasion. In order to partially offset the problem of gut fill, the liveweight of a particular week was taken as the mean of the weight in the current week and of those in the preceding and succeeding weeks. Liveweight change over a given period is calculated as the difference between the last and the first weight over that period. If the weight in the last week of the period was missing then the weight in the preceding week was used.

3.4 Data Handling

As indicated before, lactations were either truncated at 26 or 38 weeks. All data from cows with prolonged periods of illness, or from cows which showed abnormal milk yields or feed intake following a period of illness, were discarded. A small number of animals had no data available for the first or last week or two of the recording period. This was because the intake recording was not started until at least 4 or 5 animals had calved each year, and some late calving animals were turned out to grass before week 26 or 38 of lactation. Also, a small number of animals had missing feed intake or milk yield data in other weeks of the recording period, due to temporary removal from the trial due to illness.

Although milk composition analyses were done monthly in the first year, fortnightly in the next seven years and weekly in the last year, there were a few fat and protein values missing. In addition, for the weeks where there was a missing milk record there was no composition analysis.

In order to make maximum use of the recorded information it was decided to predict these missing records. Lactations in which a lot of weekly records were missing were removed from the original data set. In this regard 11 lactations were discarded.

3.4.1 Prediction of Dry Matter Intake

A polynomial was fitted by linear regression to the available weekly dry matter intake data for each lactation, for each cow, where a feed intake record was missing i.e.

$$Y = A + B(WK) + C(WK)^2 + \dots$$

where Y = dry matter intake.

WK = week number(1 to 26 or 38).

A,B,C = constants

Additional terms i.e. cubic etc. were then added to or removed from the polynomial until the equation with the least residual mean squares was obtained. In each case the parameters A,B,C etc. were optimized so that the best values (for which the model has least squares fit) were obtained. This was done individually for each lactation for each cow. It was found that the polynomial which included the cubic term gave the best fit to the data. The parameters in this final equation were used to predict the missing weekly dry matter intake values.

In addition to predicting missing intake records, the dry matter intake curves for each lactation for each cow were also plotted. Some cows had very consistent patterns of intake over weeks, whilst others varied greatly. A few records which deviated substantially were discarded. Records were rejected if they were greater than 2 to 3 standard deviations from their expected value based on the values in the preceding and succeeding weeks. This subjective interpretation was used in deciding which threshold (i.e. 2 or 3 standard deviations) to use for rejection of records because of the great variation in intake in some lactations. These rejected weekly records were then predicted as described above.

Dry matter intake curves for each lactation for each cow were also plotted for Data Set 2. After examining the plots and applying the same criteria as for rejection of records

in Data Set 1, a few weekly records were also rejected. These weekly intake records were then predicted as described above.

In total, less than 4 per cent of the weekly dry matter intake records were predicted for Data Set 1. Of these, more than half (approx. 52 per cent) of them were for the first week of lactation. Similarly, less than 4 per cent of the weekly feed intake records were also predicted in Data Set 2. A summary of the number of mean daily dry matter intake records missing, discarded, and predicted in the two data sets are given in Table 3.5.

3.4.2 Prediction of Milk Yield

After fitting polynomials by regression to the weekly milk yields for each lactation for each cow, and checking actual against predicted milk yield for animals with fully recorded lactations, it was observed that the quadratic polynomial gave the best fit to the first 12 weeks of lactation, while the later part of the lactation curve was best predicted by linear equations, after dividing it into 10 week periods. No single polynomial (up to the 4th power) was able to give a good fit to the whole 26 or 38 week lactation data. Based on this, it was therefore decided to do the following:

(1) Missing milk records between weeks 1 to 12 were predicted by fitting a quadratic equation to the available data for the first 15 weeks of the lactation in which the record was missing, i.e.

$$Y = A + B(WK) + C(WK)^2$$

where Y = milk record between weeks 1 and 12.

WK = week number(1 to 15).

A,B,C = constants.

(2) Records missing in the later part of lactation (i.e. after week number 12) were predicted by dividing the data (after week 12) into ten week periods (12 to 22, 20 to 30,

28 to 38) and fitting a linear regression to each ten week period for each part of a lactation where a record was missing, i.e.

$$Y = A + B(WK)$$

where Y = milk record between weeks 12 and 38.

WK = week number(12-22,20-30,28-38).

A, B = constants.

For Data Set 1 (26 week lactation), the data for predicting missing records were split into 10 to 20 and 18 to 26 week periods. In each case the parameters were optimized so that the best values (for which the model has least squares fit) were obtained.

Milk yield records for individual lactations were plotted for each cow, as for the dry matter intake records for both Data Set 1 and Data Set 2. In some cases substantially deviant values were observed and these were rejected based on the same criteria as those for weekly dry matter intake records (i.e. rejected records were greater than 2 to 3 standard deviations from their expected value, based on the preceding and succeeding week records). The rejected milk yield records were predicted in the same way as the missing weekly milk yield records.

In total, less than 3 per cent of weekly milk yield records were predicted for Data Set 1. Of these, 66 per cent were for the first week of lactation. Similarly, less than 4 per cent of weekly milk records were predicted for Data Set 2. Table 3.5 summarises the number of weekly milk yield records missing, discarded, and predicted.

Table 3.5

A summary of the number of weekly milk yield and dry matter (DM) intake records missing, discarded and predicted.

	Missing	Number of records		Percentage
		Discarded	Predicted	of total
Data set 1				
Milk yield	281	44	325	2.6
DM intake	448	38	486	3.9
Data set 2				
Milk yield	373	3	376	3.4
DM intake	378	5	383	3.4

Table 3.6

Ratios of mean weekly fat and protein concentrations to total mean fat and protein concentrations, respectively, for all animals for lactation 1, lactation 2, and lactations greater than 2.

Week	Lactations					
	1	2	>2	1	2	>2
	Fat ratios			Protein ratios		
1	1.05	1.24	1.12	1.08	1.14	1.12
2	1.00	1.04	1.18	1.05	1.05	1.05
3	0.96	0.98	1.03	0.98	0.96	0.98
4	0.98	0.95	1.03	0.97	0.96	0.96
5	0.93	0.93	0.94	0.95	0.93	0.94
6	0.90	0.89	0.96	0.96	0.94	0.94
7	0.93	0.91	0.94	0.95	0.94	0.95
8	0.95	0.94	0.90	0.97	0.96	0.95
9	0.92	0.91	0.94	0.98	0.96	0.96
10	0.91	0.91	0.90	0.97	0.98	0.97
11	0.93	0.90	0.91	0.98	0.98	0.97
12	0.95	0.93	0.93	0.98	0.98	0.98
13	0.93	0.94	0.94	1.00	0.99	1.01
14	0.95	0.93	0.97	0.99	0.98	1.00
15	0.95	0.93	0.94	1.01	0.98	0.99
16	0.99	0.97	0.99	0.99	0.99	1.00
17	0.97	0.94	0.97	1.00	1.02	1.01
18	0.98	0.95	0.97	1.02	0.99	1.02
19	0.96	0.97	0.95	1.04	1.02	1.01
20	0.98	1.00	0.98	1.03	0.99	1.02
21	0.99	0.99	0.98	1.02	1.02	1.01
22	0.99	0.99	1.00	1.01	1.00	1.03
23	1.01	0.99	0.97	1.02	1.03	1.00
24	1.02	1.04	1.00	1.02	1.01	1.03
25	1.03	1.02	1.01	1.02	1.05	1.01
26	1.03	1.04	1.00	1.02	1.01	1.03
27	1.05	1.04	1.00	1.02	1.02	1.00
28	1.08	1.08	1.03	1.04	1.01	1.02
29	1.06	1.02	1.02	1.01	1.02	1.03
30	1.08	1.03	1.06	1.02	1.01	1.01
31	1.03	1.10	1.03	1.00	1.02	0.99
32	1.08	1.06	1.06	1.00	1.00	1.01
33	1.06	1.10	1.07	0.99	1.01	1.01
34	1.10	1.07	1.08	1.00	0.99	1.00
35	1.08	1.15	1.07	0.97	1.06	1.01
36	1.10	1.10	1.07	0.99	0.97	1.01
37	1.13	1.11	1.11	0.96	1.02	1.01
38	1.14	1.14	1.08	0.99	1.00	1.02

3.4.3 Prediction of Fat and Protein Concentrations

Individual lactation curves for both fat and protein concentrations (g/kg milk) appeared to have no consistent pattern. This was in contrast to the fat and protein (concentration) curves obtained from the pooled fat and protein records (i.e. all lactations). It was therefore decided to utilise information from both the overall data set and the individual lactation in predicting the missing values. The procedure for prediction of missing weekly fat and protein concentration is outlined below:

(1) The mean weekly fat and protein concentration for all animals were expressed as a proportion of the total fat and protein concentration means, respectively, for all animals. This is referred to as the weekly weighting factor (WWF), and is calculated separately for lactation 1, lactation 2, and lactations greater than 2 (Table 3.6).

$$WWF = \mu_w / \mu_t$$

where WWF = ratios of mean weekly fat and protein concentrations to total mean fat and protein concentrations respectively for all animals for lactation 1, lactation 2, and lactations greater than 2.

μ_w = weekly mean fat or protein concentrations for lactation 1, lactation 2, and lactations greater than 2.

μ_t = overall mean fat or protein concentrations for lactation 1, lactation 2, and lactations greater than 2.

(2) After calculating the weekly weighting factors an individual weighting factor (IWF) was calculated for each lactation for each cow. This was done by summing up the appropriate lactation WWF for those weeks where a fat concentration record was present in each lactation for each cow and then dividing by the number of fat records in each lactation for each cow respectively. Similarly, IWF was calculated for the protein concentration, for each lactation for each cow.

$$IWF = \sum WWF / N$$

where IWF = individual weighting factor for fat or protein concentration for each lactation for each cow.

WWF = as defined above.

N = number of fat or protein records for an individual lactation.

(3) If a fat and/or protein concentration record was missing in a particular lactation, then the mean fat and/or mean protein concentration for that particular lactation was corrected for that missing record. This was done by multiplying the mean fat and/or mean protein concentration for that particular lactation by the inverse of the individual weighting factor for the fat and/or protein concentration, respectively, for the same lactation.

$$CM = \mu_1 \times 1 / IWF$$

where CM = corrected fat concentration or protein concentration mean for each lactation for each cow where a fat or protein record is missing.

μ_1 = fat concentration mean or protein concentration mean for each lactation for each cow where a fat and/or protein record is missing.

IWF = individual weighting factor for either fat or protein concentration for each lactation for each cow where a fat and/or protein record is missing.

(4) The missing fat or protein concentration for a given week in a particular lactation was then predicted as the product of the corrected mean (CM) for that particular lactation and the WWF for the appropriate lactation number and for that particular week.

$$P = CM \times WWF$$

where P = predicted fat or protein concentration for a specific record in a particular lactation.

CM = as defined above.

WWF = as defined above.

Approximately 3 per cent fat and protein concentrations were predicted.

3.4.4 Estimation of Milk Energy

Milk energy (MJ/kg milk) was calculated from the weekly milk fat and protein concentrations using the equation derived by Tyrrell and Reid (1965), i.e.

$$E = 40.72 F + 22.65 P + 102.77$$

where E = gross energy value of milk (Kcal/lb).

F = milk fat concentration (%).

P = milk protein concentration (%).

The coefficient of variation between the energy value predicted by this equation and that measured by bomb calorimetry was 2.31 per cent at the mean. When this equation was converted from kilocalories per pounds (kcal/lb) to megajoules per kilogrammes (MJ/kg) it became:

$$E = 0.376 F + 0.209 P + 0.948$$

This final equation was used to estimate the milk energy for each week for each lactation, using the fat and protein concentrations (g/kg milk).

3.4.5 Estimation of Energy Intake

Metabolisable energy (ME) intake was estimated on a weekly basis for the complete diet except for the last year when this was done on a monthly basis. Estimates of ME were used to calculate the metabolisable energy intake of the animals for each week in each year. In cases, where no feed analysis was available for the later part of the lactation, the mean ME for the last five weeks in that particular year was used.

In addition to the complete diet, concentrate was fed in the parlour during milking. From year 2 to year 8, this was fed at a rate of 0.8 kg (fresh weight) per milking (1.6 kg per day). In the first year concentrates was fed at the same rate but only for the first eight

weeks of lactation. The concentrates had on average 87 per cent DM, an ME of 13 MJ/kg DM, and 20 per cent crude protein (CP). Thus 18.096 MJ of ME and 278 g of CP were obtained from the concentrates each day. In the last year (1987/88) concentrates was fed at the rate of 0.4 kg per milking (0.8 kg fresh weight per day) except in weeks 1,2,3 and 12 when nothing was fed. The ME and CP of this concentrate varied monthly. The ME intake was calculated on a weekly basis as follows:

$$EI = (DMI \times ME) + MEC$$

where EI = energy intake.

DMI = dry matter intake (kg).

ME = metabolisable energy of DMI (MJ/kg).

MEC = metabolisable energy of concentrates (MJ).

3.4.6 Estimation of Gross Efficiency

In this study gross or biological efficiency is defined as the energy in milk produced per unit of feed energy consumed. Cumulative gross efficiency was calculated as follows:

$$GEF = (\sum ME/N_1) / (\sum EI/N_2)$$

where GEF = average cumulative gross efficiency for a given period.

$\sum ME$ = total milk energy over a given period.

$\sum EI$ = total energy intake over the same period.

N_1 = number of milk energy records over the same period.

N_2 = number of energy intake records over the same period.

CHAPTER 4

RELATIONSHIP BETWEEN SIRES' TRANSMITTING ABILITY AND THEIR DAUGHTERS' PRODUCTION, INTAKE AND EFFICIENCY

4.1 Introduction

One of the original aims of the Langhill Dairy Cattle Breeding project was to show that sires' transmitting abilities, estimated from dairy progeny testing schemes, were a reliable guide to their daughters' performance. A sire's transmitting ability or ICC (MMB, 1979), predicts one half of the breeding value of that bull from his progeny merit. The regression of daughters' full lactation production on sire ICC is therefore expected to be 1. Cunningham (1984) failed, however, to obtain a significant positive relationship between sire ICCs and their daughters' production, using data from the Langhill project.

In field progeny testing schemes, sires' transmitting abilities or breeding values can be predicted for milk production traits, but not for feed intake or for efficiency of milk production. Alternative breeding schemes involving Multiple Ovulation and Embryo Transfer (Nicholas and Smith, 1983) have been suggested and are now in operation. These MOET schemes will allow feed intake to be measured and efficiency of milk production to be selected for directly. Such schemes are not, however, likely to replace field progeny testing schemes completely in the near future. As breeders continue to select on production traits using sires of high genetic merit for production, the important question then is, 'what correlated response occurs in gross efficiency and in feed consumption?' or put another way 'what is the relationship between sire's breeding value for production and daughters' efficiency and feed intake? '.

Experimental evidence has shown that progeny of bulls of high breeding value for liquid milk production produce more milk, consume more feed, but are more efficient for milk production than progeny of low breeding value bulls (Lamb *et al.*, 1977; Hind, 1979; Gibson, 1986). Few studies have, however, investigated the relationship between sire ICCs for solids production (fat plus protein) and gross efficiency for milk production and feed intake, particularly in high producing herds.

The objectives of this study are to examine, in a high yielding herd, (1) the

relationship between sires' predicted genetic merit and their daughters' production, and (2) the relationship between sires' predicted genetic merit for fat plus protein yield and their daughters' feed intake and efficiency.

4.2 Materials and Methods

4.2.1 Data

The study involved data from two data sets: Data Set 1 containing 475 lactation records on 251 animals up to the 26th week only and Data Set 2, a subset of Data Set 1, comprising 293 lactation records on 168 animals up to the 38th week. Details of the data and data recording are given in Chapter 3.

4.2.2 Statistical Methods

Regression analysis was carried out on milk yield, fat yield, protein yield, fat plus protein yield, dry matter intake, gross efficiency, calving and mean liveweights, and liveweight change. Liveweight change for a given period was computed as the difference between the last and first weights for the period. Preliminary analysis was carried out using the statistical package Genstat V Mark 4.03 (Lawes Agricultural Trust, 1980). Both data sets 1 and 2 were split into first lactations (heifer), and later lactations (cows) and the analysis was carried out on heifers, cows, and all lactations pooled (all data).

The following fixed effects were fitted in the model of analysis: (1) Lactation number. This was grouped from 1 to 4, group 1 for first lactation animals, group 2 for second lactation animals, group 3 including lactations 3 to 5 and group 4 including lactations 6 to 9. (2) Year of calving, from 1979 to 1987. (3) Month of calving, from September to November. Five late August calving animals were grouped with the September calving cows while thirteen early December calving animals were grouped with the November cows. No recorded animals calved outside these months.

Preliminary analysis showed that age at calving was not significant ($P > 0.05$), nor

did it remove a substantial proportion of the variance when included in the models for heifers, cows or pooled lactation data.

A pedigree index was computed for each animal as: pedigree index = sire ICC + 0.5 maternal grandsire ICC, using the latest available ICCs computed by the MMB using a sire and maternal grandsire Best Linear Unbiased Prediction (BLUP) model (Quaas *et al.*, 1979; MMB, 1979). It should be noted that the pedigree index computed here is a prediction of breeding value and is in contrast to the index recently introduced by the HFS, which is a prediction of transmitting ability. Also, since this prediction was based on maternal grandsire ICC rather than the dam CGI, it did not use data from within the herd (except in so far as Langhill data were used by the MMB to compute ICCs). Replacement heifers were selected to enter the selection herd on the basis of predicted genetic merit for fat plus protein yield (predicted cow genetic index from 1983). The data included a small number of cows from the genetic control group. To ascertain whether or not the pedigree index took sufficient account of the difference between selected and control groups, two models were fitted: one with all the fixed effects plus the pedigree index, the other as for the first but including an additional genetic group effect. There was very little difference between the residual mean squares when the two models were compared, and the effect of genetic group fitted after the pedigree index was not significant (Table 4.1). For example, the t values for genetic group effects were $|t| < 1.31$ for heifers in data set 1 and $|t| < 1.26$ for cows in data set 2 for the yield, intake and efficiency traits analysed. Therefore no genetic group effect was included in the model for analysis so as to maximise the precision of estimates of regression of performance on pedigree indices.

In analysing the data for the cows and pooled lactations, standard errors were likely to be underestimated because more than one lactation was included for some cows. To take account of this within-cow correlation a random effect for individual cows was fitted

Table 4.1

Residual mean squares (r.m.s.) and t value for genetic groups (t) after fitting lactation number, year and month of calving, together with pedigree index or with index plus genetic groups (Index 2), taking, as examples, heifers in data set 1 and pooled lactations in data set 2.

Dependant variate	Independent variables	Heifers - Set 1		All data - Set 2	
		r.m.s.	t	r.m.s.	t
Fat+protein yield (kg)	Index	2054		7311	
	Index 2	2057	-0.88	7306	1.10
Fat yield (kg)	Index	746		2807	
	Index 2	746	-1.04	2810	0.84
Protein yield (kg)	Index	374		1212	
	Index 2	375	-0.81	1211	1.10
Milk yield (kg)	Index	473345		1255998	
	Index 2	474168	-0.88	1253179	1.20
Dry matter Intake (kg)	Index	46575		158646	
	Index 2	46275	-1.30	159188	-0.20
Efficiency (KJ/MJ)	Index	2.38		2.75	
	Index 2	2.40	-0.41	2.74	1.25

using model 1 of the Derivative-Free Restricted Maximum Likelihood program (DFREML) (Meyer, 1988). This is an individual animal model (IAM) with cows being the only random effect, apart from the error term, but no pedigree relationships were included in the analysis. The regression coefficients and standard errors were obtained in a post-estimation step after the variance components had been determined. The final model used for the analysis was:

$$Y_{ijklmn} = \mu + a_i + L_j + C_k + M_l + bI_m + e_{ijklmn}$$

where, Y_{ijklmn} = record with effects and subscripts specified as follows;

μ = overall mean;

a_i = random effect of animal i, common to each lactation;

L_j = fixed effect of lactation number j (j = 1,2,3,4);

C_k = fixed effect of year of calving k (k = 1,...,9);

M_l = fixed effect of month of calving l (l = 1,2,3);

I_m = pedigree index for cow m, fitted as a covariate;

b = linear regression on pedigree index;

e_{ijklmn} = random error term, specific to each lactation.

As a check for heterogeneity of variance, traits were transformed to logarithms and the analyses repeated. The results from these analyses were consistent with those from the untransformed data.

4.3 Results

Figures 4.1 to 4.6 show the pattern of yield, intake, liveweight and efficiency over the first 38 weeks of lactation for heifers and cows. For cows, peak milk yield occurred about weeks 3 to 5 while peak intake occurred about weeks 9 to 12. Corresponding peak values for heifers occurred slightly later i.e. weeks 7 to 9 for yield and weeks 13 to 15 for intake. Figures 4.3 and 4.4 indicate large variation in fat and protein yield from week to

week. This is partly due to the fact that apart from the last year, milk analysis was not done on a weekly basis. Both cows and heifers appeared to be losing body weight in early lactation. However, the loss is greater for cows than for heifers (Figure 4.5) and this may be partly responsible for the relatively higher efficiency of cows in early lactation as compared to heifers (Figure 4.6).

Table 4.2 gives the means and standard errors of the performance traits (adjusted for the fixed effects in the model) for heifers, cows, and all lactations pooled, for data sets 1 and 2. Over all lactations, the mean 38-week milk yield \pm standard error was 6610 ± 91 kg with 501 ± 7 kg fat plus protein. Over the same period the average dry matter intake was 4460 ± 32 kg and the mean cumulative gross efficiency 0.39 ± 0.004 . Cows had higher intakes, were more productive, and also more efficient than heifers (0.37 ± 0.006 for heifers versus 0.39 ± 0.006 for cows). This difference in efficiency between heifers and cows was much greater over the shorter 26-week lactation period, indicating that cows were mobilising tissue reserves in early lactation. The means and ranges for the pedigree indices are given in Table 4.3; note that those for fat yield and protein yield are very highly correlated. The standard deviations of pedigree indices are about 0.4 of the phenotypic standard deviation of yield for heifers in data set 1, and about 0.2 for cows in data set 2.

The regression of heifer production traits on their corresponding pedigree index were all near 1 (0.71 ± 0.20 to 0.99 ± 0.31) (Table 4.4). Those in the longer 38 week period were higher than those in the 26 week period, but standard deviations of the traits concerned were also higher. The regression coefficients for cows were all lower than the corresponding ones for heifers in both data sets, while those for the pooled lactations were generally lower than those for heifers but higher than those for cows.

The regression of milk yield, fat plus protein yield, dry matter intake, and gross efficiency on pedigree indices for fat, protein, and fat plus protein yield were all positive

for heifers, cows, and the pooled lactations for data set 1 (Table 4.5) and data set 2 (Table 4.6). As expected, the regressions on pedigree index for protein yield gave the highest coefficients. The regression for the different traits were similar in both data sets with the exception of those involving cows in set 1, although standard errors were high.

The regression of absolute liveweights on pedigree index for fat plus protein yield were all positive (Table 4.7). Similar regressions for liveweight change over the first 12, 26, and 38 weeks of lactation were all negative.

Regression coefficients were also expressed as a ratio of herd mean (Table 4.8, 4.9, and 4.10), and as a ratio of phenotypic standard deviation (Tables 4.11, 4.12, and 4.13). When expressing the regression coefficients as a ratio of herd mean the indices were also scaled by the mean 305 day lactation yield (for Langhill) of their corresponding trait. Expressing the regression coefficients as a ratio of the means minimises the differences in residual variation at the different level of production (i.e. heifer, cow), and is almost equivalent to a logarithmic transformation of the traits. Similarly, expressing the coefficients in phenotypic standard deviation units tends to reduce the variance within each level of performance and hence allows a more standard comparison across the two data sets and over different levels of performance. These standardisations resulted in the regression coefficients of heifers being proportionately higher than those of cows, and consequently those of the pooled lactation, when compared to the untransformed regression coefficients. This is expected as the means and variances are higher at higher levels of production, i.e. heifer versus later lactations. Corresponding regressions of traits on pedigree indices for fat, protein, and fat plus protein yield, were very similar when regression coefficients were scaled by herd mean.



Figure 4.1: Pattern of milk yield for heifers and cows.

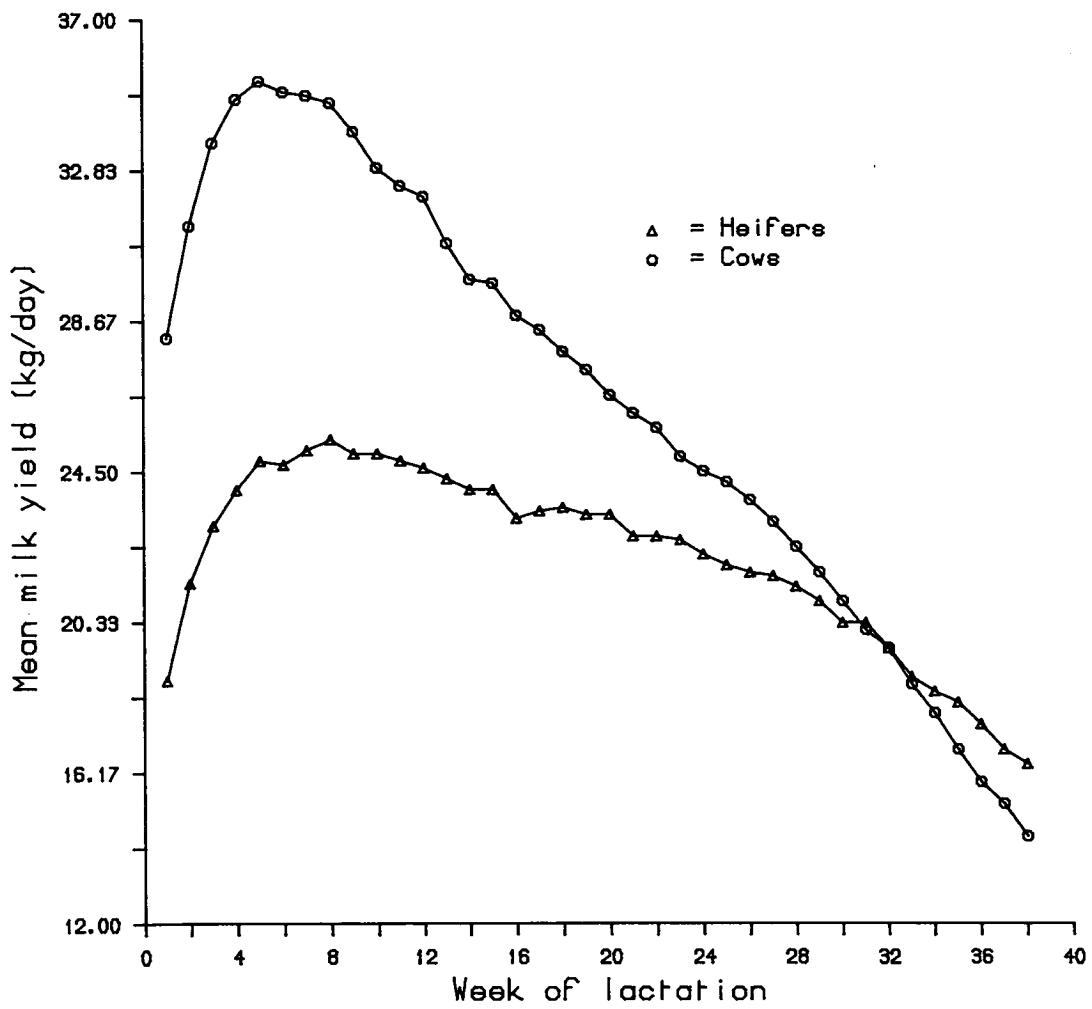


Figure 4.2: Pattern of intake for heifers and cows.

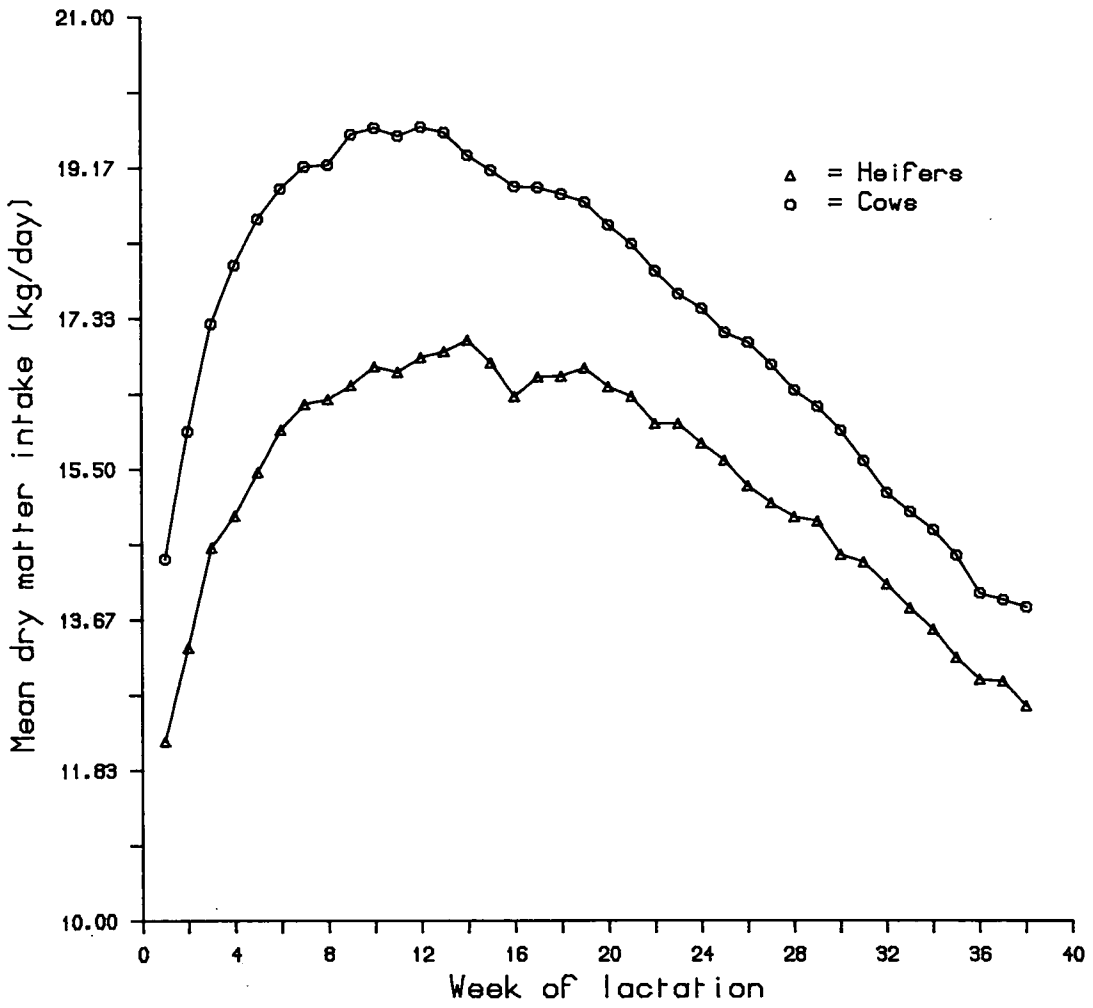


Figure 4.3: Mean fat yield by week of lactation

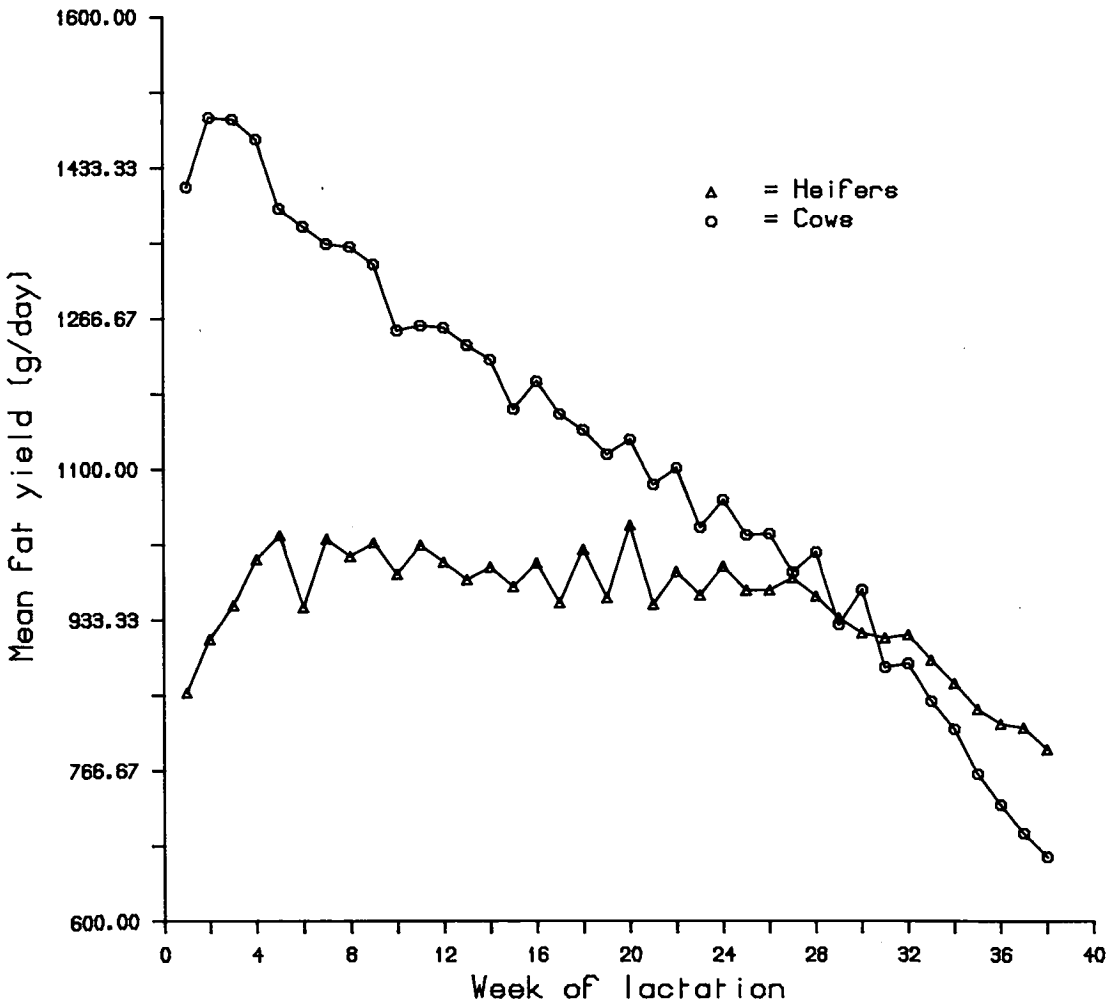


Figure 4.4: Mean protein yield by week of lactation.

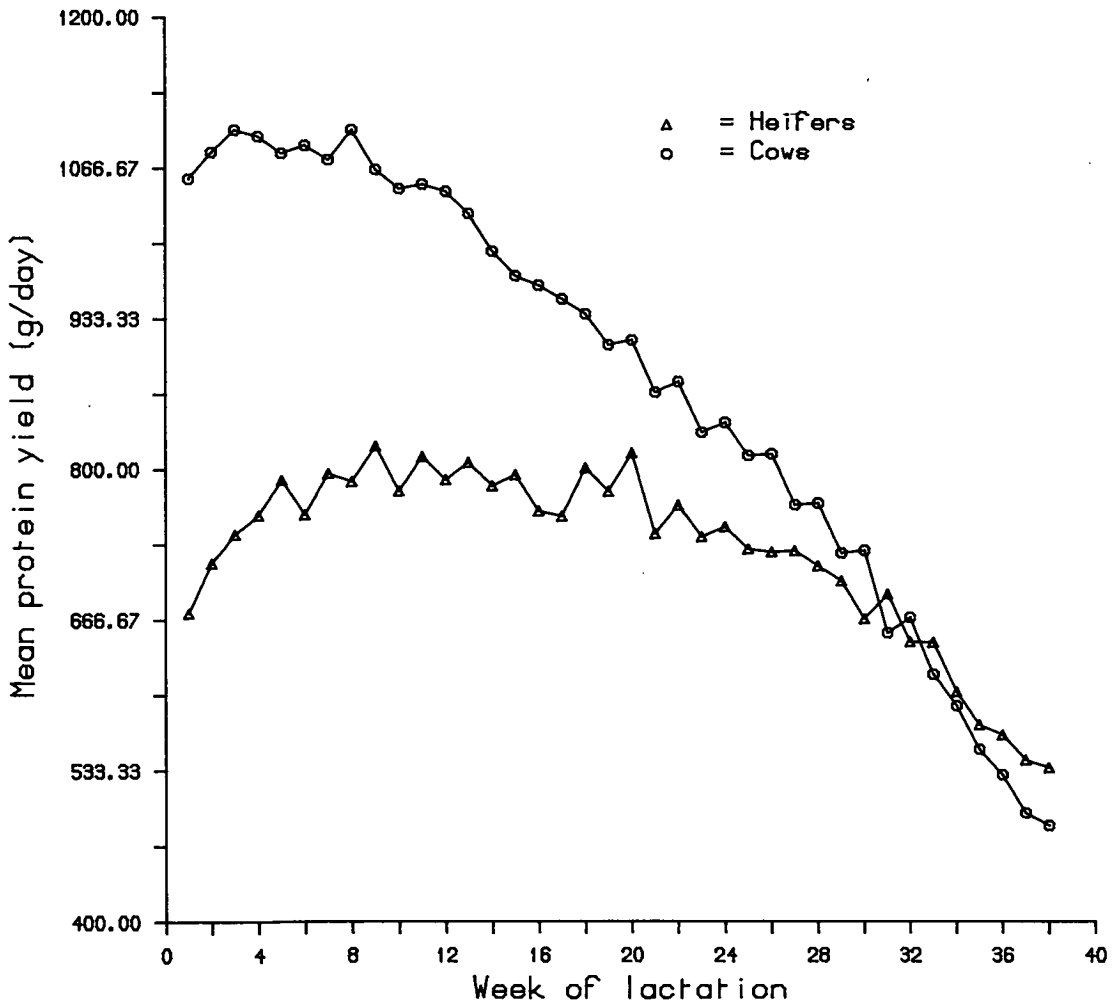


Figure 4.5: Mean liveweight by week of lactation.

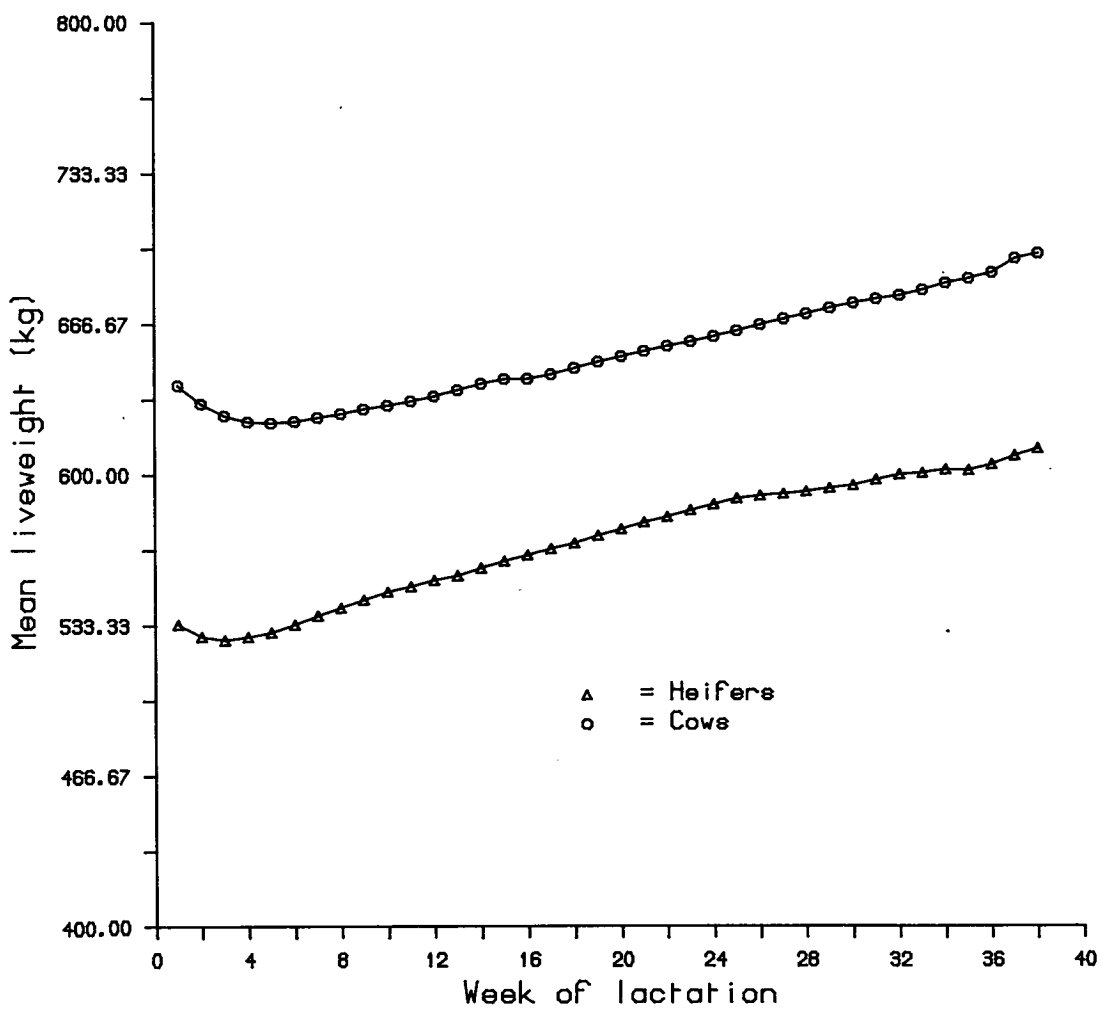


Figure 4.6: Efficiency by week of lactation.

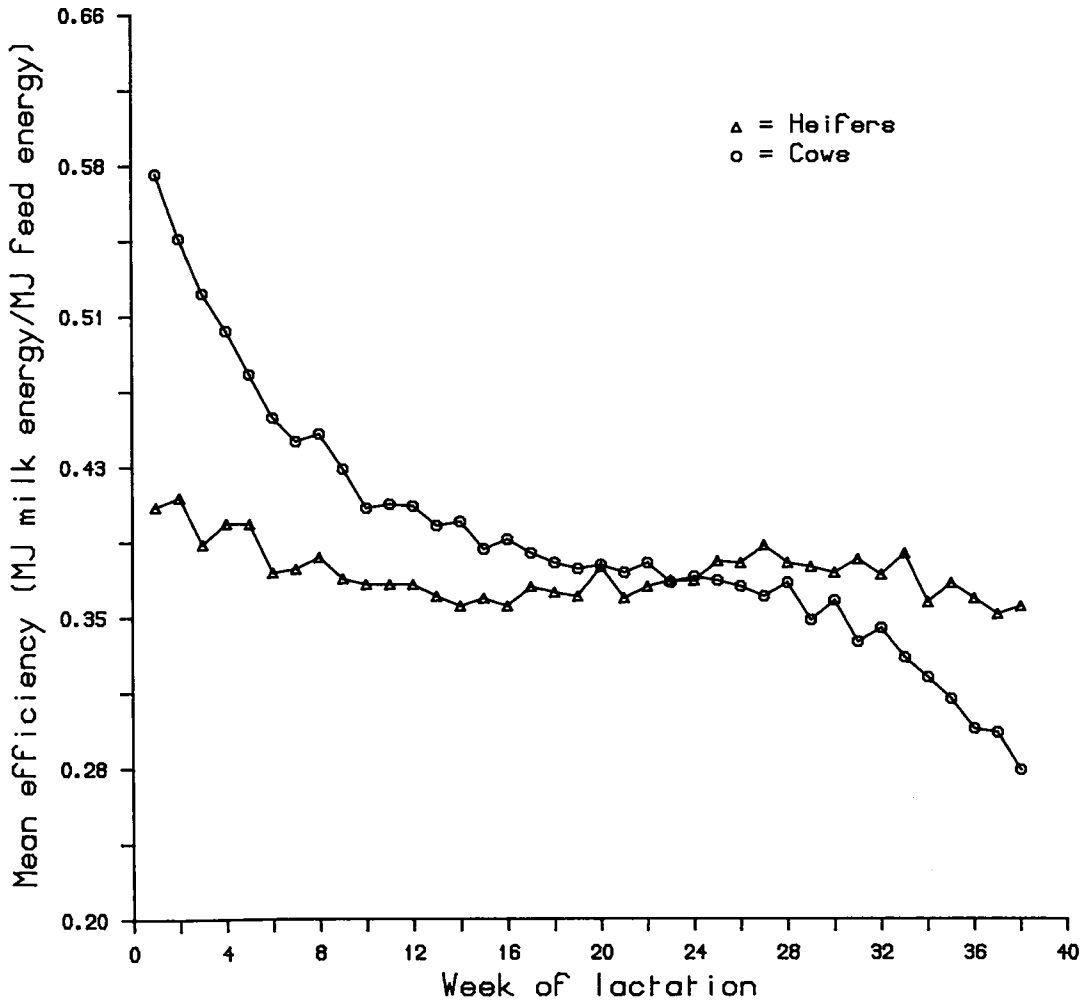


Table 4.2

Means and standard error of performance and liveweight traits,
adjusted for lactation number, year and month of calving.

Trait (kg)	Heifers		Cows		All data	
	Mean	SE	Mean	SE	Mean	SE
Set 1: 26 weeks						
Number of records	(141)		(334)		(475)	
Milk yield	4178.0	67.6	5209.6	56.5	4939.7	43.1
Fat yield	176.9	2.7	217.6	2.8	207.4	2.0
Protein yield	138.7	1.9	174.8	1.8	165.9	1.3
Fat + protein yield	315.7	4.4	392.4	4.4	373.3	3.2
Dry matter intake	2901.0	20.3	3373.2	22.8	3251.6	16.3
Efficiency ⁺⁺	371.0	4.7	402.4	3.8	395.0	2.9
Calving liveweight	532.5	4.3	639.8	3.8	614.5	2.8
Mean liveweight	553.1	4.1	641.0	3.6	619.3	2.7
Set 2: 38 weeks						
Number of records	(101)		(192)		(293)	
Milk yield	5725.9	127.0	6808.4	133.5	6611.6	91.3
Fat yield	253.4	5.1	285.8	6.6	282.8	4.2
Protein yield	190.4	3.6	224.5	4.3	218.7	2.8
Fat + protein yield	443.8	8.5	510.3	10.6	501.5	6.9
Dry matter intake	4050.0	37.9	4538.5	48.8	4461.8	31.6
Efficiency ⁺⁺	372.6	6.0	387.2	6.2	385.9	4.2
Calving liveweight	532.1	5.0	636.5	6.1	610.4	3.9
Mean liveweight	566.2	5.1	645.0	6.3	628.9	4.1

⁺⁺ Efficiency expressed as (MJ/MJ x 10³)

Table 4.3
Means, standard deviations, and ranges of pedigree indices.

Pedigree Index (kg)	Mean	SD	Maximum	Minimum
Set 1: 26 weeks				
Milk yield	239	329	1123	-509
Fat yield	8.6	12.3	37.8	-19.8
Protein yield	6.4	8.1	26.6	-15.4
Fat + protein yield	15.0	20.0	64.4	-35.2
Set 2: 38 weeks				
Milk yield	324	344	1123	-509
Fat yield	12.4	12.4	37.8	-19.0
Protein yield	8.6	8.4	26.6	-13.5
Fat + protein yield	21.0	20.5	64.4	-29.2

Table 4.4

Regressions of milk production traits on their corresponding pedigree indices (sire ICC + 0.5 maternal grandsire ICC)

Trait	Heifers		Cows		All data	
	b	SE	b	SE	b	SE
Set 1: 26 weeks						
Number of records	(141)		(334)		(475)	
Milk yield (kg)	0.75	0.19	0.47	0.20	0.64	0.15
Fat yield (kg)	0.72	0.20	0.39	0.27	0.55	0.20
Protein yield (kg)	0.74	0.21	0.57	0.27	0.67	0.19
Fat+protein yield (kg)	0.71	0.20	0.43	0.27	0.57	0.20
Set 2: 38 weeks						
Number of records	(101)		(192)		(293)	
Milk yield (kg)	0.99	0.31	0.71	0.34	0.99	0.26
Fat yield (kg)	0.91	0.35	0.68	0.45	0.87	0.33
Protein yield (kg)	0.95	0.35	0.88	0.46	1.04	0.33
Fat+protein yield (kg)	0.89	0.35	0.74	0.45	0.90	0.33

Table 4.5

Regressions of milk yield, fat plus protein yield, dry matter intake and efficiency ($\times 10^3$) on pedigree indices for fat, protein, and fat plus protein yield, for data set 1.

Traits	Index	Heifers		Cows		All data	
		b	SE	b	SE	b	SE
Number of records		(141)		(334)		(475)	
Milk yield (kg)	Fat	17.81	5.22	10.27	5.56	15.11	4.37
	Protein	29.03	7.39	24.13	8.25	28.31	6.26
	Fat+protein	11.47	3.11	8.02	3.42	10.54	2.64
Fat + protein yield (kg)	Fat	1.17	0.34	0.62	0.43	0.91	0.32
	Protein	1.63	0.49	1.11	0.65	1.35	0.47
	Fat+protein	0.71	0.20	0.43	0.27	0.57	0.20
Dry matter intake (kg)	Fat	2.92	1.61	3.70	2.28	4.27	1.66
	Protein	4.78	2.30	5.50	3.43	5.94	2.43
	Fat+protein	1.89	0.95	2.35	1.41	2.62	1.01
Efficiency (MJ/MJ)	Fat	1.106	0.365	0.255	0.373	0.611	0.288
	Protein	1.491	0.525	0.630	0.561	0.991	0.491
	Fat+protein	0.658	0.219	0.204	0.231	0.400	0.175

Table 4.6

Regressions of milk yield, fat plus protein yield, dry matter intake and efficiency ($\times 10^3$) on pedigree indices for fat, protein, and fat plus protein yield, for data set 2.

Traits	Index	Heifers		Cows		All data	
		b	SE	b	SE	b	SE
Number of records		(101)		(192)		(293)	
Milk yield (kg)	Fat	20.06	8.74	17.76	9.48	22.66	7.42
	Protein	36.40	12.30	36.60	13.89	41.99	10.52
	Fat+protein	13.58	5.20	12.77	5.75	15.61	4.44
Fat + protein yield (kg)	Fat	1.43	0.58	1.06	0.74	1.40	0.54
	Protein	2.13	0.82	2.03	1.09	2.25	0.78
	Fat+protein	0.89	0.35	0.74	0.45	0.90	0.33
Dry matter intake (kg)	Fat	4.01	2.65	2.40	3.46	3.76	2.55
	Protein	7.16	3.77	4.81	5.14	6.28	3.68
	Fat+protein	2.69	1.58	1.70	2.11	2.47	1.54
Efficiency (MJ/MJ)	Fat	0.879	0.417	0.599	0.448	0.822	0.342
	Protein	1.249	0.597	1.134	0.663	1.327	0.492
	Fat+protein	0.535	0.250	0.415	0.273	0.532	0.206

Table 4.7

Regressions of liveweight (LW) and liveweight change traits, over the first 12, 26, and 38 weeks of lactation (1-12, 1-26, and 1-38, respectively) on pedigree index for fat plus protein yield.

Traits (kg)	Heifers		Cows		All data	
	b	SE	b	SE	b	SE
			Set 1: 26 weeks			
Calving LW	0.36	0.20	0.42	0.23	0.43	0.18
Mean LW	0.22	0.20	0.31	0.23	0.23	0.18
LW Change 1-26	-0.13	0.18	-0.16	0.18	-0.18	0.14
LW Change 1-12	-0.18	0.14	-0.07	0.16	-0.16	0.12
			Set 2: 38 weeks			
Calving LW	0.51	0.21	0.38	0.27	0.48	0.19
Mean LW	0.42	0.21	0.20	0.28	0.23	0.21
LW Change 1-12	-0.10	0.17	-0.14	0.20	-0.21	0.14
LW Change 1-38	-0.11	0.24	-0.22	0.25	-0.26	0.18

Table 4.8

Regressions of milk production traits on their corresponding pedigree index (sire ICC + 0.5 maternal grandsire ICC), with traits and indices expressed as a ratio of the herd mean.

Traits (kg/mean)	Heifers		Cows		All data	
	b	SE	b	SE	b	SE
Set 1: 26 Week						
Number of records	(141)		(334)		(475)	
Milk yield	1.40	0.35	0.70	0.30	1.02	0.24
Fat yield	1.34	0.37	0.58	0.40	0.87	0.31
Protein yield	1.35	0.38	0.82	0.39	1.03	0.29
Fat + protein yield	1.31	0.37	0.63	0.40	0.89	0.31
Set 2: 38 Week						
Number of records	(101)		(192)		(293)	
Milk yield	1.33	0.42	0.80	0.38	1.18	0.31
Fat yield	1.18	0.46	0.76	0.50	1.02	0.38
Protein yield	1.25	0.46	0.97	0.51	1.22	0.39
Fat + protein yield	1.16	0.46	0.82	0.50	1.05	0.38

Table 4.9

Regression of milk yield, fat plus protein yield, dry matter intake and efficiency on pedigree indices (sire ICC + 0.5 maternal grandsire ICC) for fat, protein and fat plus protein yields, for data set 1, with traits and indices expressed as a ratio of the herd mean.

Traits (kg/mean)	Index (kg/mean)	Heifers		Cows		All data	
		b	SE	b	SE	b	SE
Number of records		(141)		(334)		(475)	
Milk yield	Fat	1.40	0.41	0.64	0.35	1.01	0.29
	Protein	1.76	0.45	1.17	0.40	1.46	0.32
	Fat+protein	1.60	0.43	0.89	0.38	1.25	0.31
Fat + protein yield	Fat	2.18	0.63	0.93	0.64	1.44	0.51
	Protein	2.98	0.89	1.60	0.94	2.07	0.72
	Fat+protein	1.31	0.37	0.63	0.40	0.89	0.31
Dry matter intake	Fat	0.33	0.18	0.36	0.22	0.44	0.17
	Protein	0.42	0.20	0.42	0.26	0.47	0.19
	Fat+protein	0.38	0.19	0.41	0.25	0.48	0.18
Efficiency	Fat	0.99	0.33	0.21	0.30	0.51	0.24
	Protein	1.03	0.36	0.40	0.35	0.64	0.27
	Fat+protein	1.04	0.35	0.29	0.33	0.59	0.26

Table 4.10

Regression of milk yield, fat plus protein yield, dry matter intake and efficiency on pedigree indices (sire ICC + 0.5 maternal grandsire ICC) for fat, protein, and fat plus protein yields, for data set 2, with traits and indices expressed as a ratio of herd mean.

Traits (kg/mean)	Index (kg/mean)	Heifers		Cows		All data	
		b	SE	b	SE	b	SE
Number of records		(101)		(192)		(293)	
Milk yield	Fat	1.13	0.49	0.84	0.45	1.13	0.37
	Protein	1.59	0.54	1.33	0.51	1.63	0.41
	Fat+protein	1.36	0.52	1.07	0.48	1.39	0.39
Fat + protein yield	Fat	1.86	0.75	1.18	0.83	1.64	0.63
	Protein	2.80	1.08	2.24	1.20	2.63	0.91
	Fat+protein	1.16	0.46	0.82	0.50	1.05	0.38
Dry matter intake	Fat	0.33	0.22	0.17	0.25	0.28	0.19
	Protein	0.45	0.24	0.27	0.29	0.36	0.21
	Fat+protein	0.39	0.21	0.22	0.27	0.33	0.20
Efficiency	Fat	0.78	0.37	0.51	0.38	0.71	0.29
	Protein	0.86	0.41	0.74	0.43	0.88	0.33
	Fat+protein	0.84	0.39	0.62	0.41	0.81	0.31

Table 4.11

Regression of milk production traits on their corresponding pedigree indices (sire ICC + 0.5 maternal grandsire ICC), with traits expressed in units of 0.01 phenotypic standard deviations.

Traits (/ 0.01 σ_p)	Heifers		Cows		All data	
	b	SE	b	SE	b	SE
Set 1: 26 Week						
Number of records	(141)		(334)		(475)	
Milk yield	0.10	0.03	0.05	0.02	0.07	0.02
Fat yield	2.34	0.65	0.96	0.66	1.28	0.46
Protein yield	3.54	1.01	2.09	0.99	2.18	0.62
Fat + protein yield	1.42	0.40	0.66	0.41	0.80	0.28
Set 2: 38 Week						
Number of records	(101)		(192)		(293)	
Milk yield	0.09	0.03	0.06	0.03	0.08	0.02
Fat yield	2.02	0.78	1.13	0.75	1.48	0.56
Protein yield	3.07	1.13	2.23	1.16	2.54	0.81
Fat + protein yield	1.21	0.47	0.76	0.46	0.93	0.34

Table 4.12

Regressions of milk yield, fat plus protein yield, dry matter intake and efficiency on pedigree indices (sire ICC + 0.5 maternal grandsire ICC) for fat, protein, and fat plus protein yields, for data set 1, with traits expressed in units of 0.01 phenotypic standard deviations.

Traits (/ 0.01 σ_p)	Index (kg)	Heifers		Cows		All data	
		b	SE	b	SE	b	SE
Number of records		(141)		(334)		(475)	
Milk yield	Fat	2.38	0.70	1.18	0.64	1.56	0.45
	Protein	3.89	0.99	2.78	0.95	2.93	0.65
	Fat+protein	1.55	0.42	0.92	0.39	1.09	0.27
Fat + protein yield	Fat	3.80	1.10	1.52	1.06	2.12	0.74
	Protein	7.80	2.34	4.08	2.39	4.38	1.53
	Fat+protein	1.42	0.40	0.66	0.41	0.80	0.28
Dry matter intake	Fat	1.04	0.57	1.04	0.64	1.09	0.42
	Protein	1.70	0.82	1.55	0.97	1.51	0.62
	Fat+protein	0.67	0.34	0.66	0.40	0.67	0.26
Efficiency	Fat	2.09	0.69	0.43	0.63	1.02	0.48
	Protein	2.81	0.99	1.07	0.95	1.65	0.70
	Fat+protein	1.24	0.41	0.35	0.39	0.67	0.29

Table 4.13

Regression of milk yield, fat plus protein yield, dry matter intake and efficiency on pedigree indexes (sire ICC + 0.5 maternal grandsire ICC) for fat, protein, and fat plus protein yields, for data set 2, with traits expressed in units of 0.01 phenotypic standard deviations.

Traits (/ 0.01 σ_p)	Index (kg)	Heifers		Cows		All data	
		b	SE	b	SE	b	SE
Number of records		(101)		(192)		(293)	
Milk yield	Fat	1.85	0.80	1.42	0.76	1.72	0.56
	Protein	3.35	1.13	2.90	1.11	3.19	0.80
	Fat+protein	1.25	0.48	1.02	0.46	1.19	0.34
Fat + protein yield	Fat	3.17	1.29	1.76	1.23	2.38	0.92
	Protein	6.89	2.65	5.14	2.76	5.50	1.91
	Fat+protein	1.21	0.47	0.76	0.46	0.93	0.34
Dry matter intake	Fat	1.00	0.66	0.53	0.77	0.75	0.51
	Protein	1.79	0.94	1.07	1.14	1.24	0.73
	Fat+protein	0.67	0.37	0.38	0.47	0.49	0.30
Efficiency	Fat	1.76	0.83	1.02	0.76	1.44	0.60
	Protein	2.50	1.19	1.92	1.12	2.33	0.86
	Fat+protein	1.07	0.50	0.70	0.46	0.93	0.36

4.4 Discussion

Sire ICCs or transmitting abilities are calculated from first lactation (305 day) production records using BLUP. The regression of complete lactation heifer production traits (milk, fat, and protein yields) on their corresponding pedigree index should therefore be 1. In this analysis these regression coefficients range from 0.71 ± 0.20 to 0.75 ± 0.19 for heifers with 26 week recording, and are higher for the longer 38 week recording period (Table 4.4), but values are similar when scaled by herd mean (Table 4.8) or standard deviation (Table 4.11), as would be expected if the correlation between part- and whole-lactation production is high. The regression of production traits on the corresponding pedigree indices for cows alone are much lower (0.39 ± 0.27 to 0.57 ± 0.27) than those for heifers (Table 4.4). This could be due, in part, to a non-unit genetic correlation between first and later lactations, decreasing with increasing lactation number (Maijala and Hanna, 1974), although other estimates of this correlation are high (Meyer, 1984).

The low regressions for cows in data set 1 may also, in part, have been due to the fact that in the first two years of the experiment older cows with a wide range of lactation number were used, and this may have weakened the association with sire ICC. By contrast, in data set 2, where these cows are not present, the regression coefficients are much higher. As a check, the analyses for cows and pooled lactations in data set 1 were repeated, omitting data for the cows in the first two years of the experiment, and results are shown in Table 4.14. The regression coefficients are much higher and comparable to those in data set 2, substantiating the hypothesis that the older cows were responsible for the low regression coefficients. In fact when the analysis was repeated using data from the first two years of the experiment only, the regression coefficients were effectively zero. Much of the data used by Cunningham (1984) came from these older cows.

The standard errors of the regression coefficients for cow lactations are higher than those for heifers, even though the heifer data set comprised only about half the number of

records of those in the cow data analysis. The poorer correlation of later lactation records with sire ICCs would result in an increase in the variance about regression, and consequently in an increase in the standard errors. Some evidence for this is seen in Table 4.14, where the standard errors are approximately equal to those in Tables 4.4 and 4.5, although 74 lactations (cows from the first two years) were removed from the analysis.

The regressions of liveweight traits on pedigree index for fat plus protein yield (Table 4.7) indicate that larger and/or heavier cows are more productive, while the regression coefficients for liveweight change (weight gain) indicate that higher gain is associated with lower yields i.e. more energy is partitioned for growth and therefore less for production. Although the standard errors were high, these results agree well with those from other studies (Miller *et al.*, 1973; Gibson, 1986).

In this experiment sires were selected on the basis of high transmitting abilities for fat plus protein yields. The positive regressions on pedigree index for fat plus protein yield (Tables 4.5 and 4.6) indicate that sires of high genetic merit for fat plus protein yield produce daughters with higher feed intakes, but also higher gross efficiency for milk production. Expressed as a proportion of their respective means, a 10% genetic increase in fat plus protein yield was accompanied by a 2.9% increase in feed intake and a 7.9% genetic increase in efficiency (Table 4.9). The correlations between the pedigree indices for fat plus protein yield, fat yield and protein yield were almost 1 (as can be seen from the near additivity of standard deviations in Table 4.2). The results were therefore very similar when traits were regressed on either indices of fat or protein yield with the coefficients scaled by herd mean. For example, a 10% genetic increase in fat or protein yield resulted in a 2.5% or 3.1% increase in feed intake and a 7.4% or 7.6% increase in efficiency, respectively (Tables 4.8 and 4.9). These correlated responses are in agreement with the positive genetic correlations estimated between fat plus protein yield and feed intake and efficiency using the same Langhill data (see Chapter 5) In general, similar conclusions can be drawn from the results of Hind (1979) and Gibson (1986). Gibson

(1986) found that for every 10% genetic increase in milk yield, there was a 7.3% increase in efficiency between genetically high and low yielding Friesian progeny, but did not give values for feed intake, while Hind (1979) found, on a subset of data from the same experiment, that a 10% increase in milk yield resulted in a 3.7% increase in feed intake and a 5.6% increase in efficiency. The relatively high increases in efficiency in this study may be due to the high level of production of the Langhill herd and to the fact that part lactation records were used in this study. It is known that high yielding dairy cows have a greater tendency to deplete body reserves and partition energy to milk yield in early lactation, replenishing reserves later in lactation or in the dry period. If this is so, then the correlated response in efficiency would be expected to be smaller while those in feed intake would be expected to be larger over the period from calving to calving. In this study the correlated responses in feed intake over the longer 38 week period (Table 4.10) are slightly, but not significantly, higher (0.29 v. 0.34) and those in efficiency, slightly lower (0.79 v. 0.72) compared to responses in the shorter 26 week period. These results suggest that although the correlated response over a calving to calving period may be higher for feed intake and lower for efficiency than the results reported here, they are not expected to be substantially different.

The results obtained in this study supports the fact that sire ICCs are a reliable guide to their daughter's performance and also clearly demonstrate that the use of sires of high genetic merit for fat plus protein yield results in substantial increases in gross efficiency for milk production. Similar responses will be obtained using sires of high genetic merit for fat or protein yield.

Table 4.14

Regression of milk production traits, dry matter intake, and efficiency ($\times 10^3$) on pedigree indices (sire ICC + 0.5 maternal grandsire ICC) for milk, fat, protein, and fat plus protein yield, for cows and all data pooled, for data set 1, when data for the first two years (1979/80 and 1980/81) are excluded from the analysis.

		Cows		All data	
Number of records		(260)		(401)	
Trait	Index	b	SE	b	SE
Milk yield (kg)	Milk	0.51	0.22	0.69	0.16
Fat yield (kg)	Fat	0.57	0.29	0.67	0.20
Protein yield (kg)	Protein	0.61	0.29	0.71	0.20
Fat+protein yield(kg)	Fat+protein	0.56	0.29	0.66	0.20
Milk yield (kg)	Fat	14.28	6.01	18.10	4.57
	Protein	25.79	8.87	29.77	6.54
	Fat+protein	9.76	3.67	11.84	2.75
Fat+protein yield (kg)	Fat	0.92	0.47	1.11	0.33
	Protein	1.29	0.70	1.46	0.48
Dry matter intake (kg)	Fat	2.91	2.31	3.83	1.62
	Protein	4.30	3.44	5.27	2.35
	Fat+protein	1.82	1.42	2.34	0.98
Efficiency (MJ/MJ)	Fat	0.650	0.399	0.880	0.298
	Protein	0.946	0.595	1.204	0.432
	Fat+protein	0.406	0.245	0.533	0.180

CHAPTER 5

GENETIC AND PHENOTYPIC PARAMETERS FOR FEED INTAKE AND EFFICIENCY AND THEIR RELATIONSHIP WITH MILK PRODUCTION AND LIVELWEIGHT TRAITS

5.1 Introduction

The most important goal in dairy cattle breeding is to improve economic efficiency of production. Feed or gross efficiency is one of the main components of overall efficiency and its genetic improvement is therefore an important objective of dairy cattle breeding programmes. While direct selection is impractical in field progeny testing schemes, present nucleus breeding schemes, e.g. the Genus (part of the MMB) MOET scheme, facilitates direct measurement of, and hence selection for, feed intake and efficiency.

Several investigations into the genetic aspects of feed intake and efficiency indicate a moderate heritability for both traits and have predicted a high correlated response in gross efficiency to selection on yield (see reviews by Kennedy, 1984, and Korver, 1988). In almost all cases, however, cows were fed according to yield. The high correlation between yield and efficiency could be a consequence of feeding concentrate or grain according to production (Freeman, 1975; Korver, 1988), and it has been suggested that this correlation is lower when animals are fed *ad libitum* (Gravert, 1985).

Under field conditions, improvement in efficiency depends on the correlated response to selection on milk production traits. Further improvements may be obtained by including measures of body size in the selection criteria, and this has been predicted to give substantial improvement in economic efficiency (Dempfle, 1986). Estimates of genetic and phenotypic parameters required to calculate such selection criteria are lacking, however, although the relationship between body size and efficiency has been investigated in a few studies (Mason *et al.*, 1957; Hooven *et al.*, 1968; Gibson, 1986; Lee *et al.*, 1989).

The aim of this study was to estimate the heritabilities of feed intake and efficiency and their genetic correlation with milk production and liveweight traits under an *ad libitum* feeding regime.

5.2 Materials and Methods

5.2.1 Data

Two data sets were available for analyses: the first containing 475 lactation records on 251 animals up to the 26th week only, and the second, a subset of the first, comprising 293 lactation records on 168 animals up to the 38th week of lactation. More details of the data and on milk and feed recording and analyses are given in Chapter 3.

5.2.2 Statistical Methods

Restricted Maximum Likelihood (REML) (Patterson and Thompson, 1971) analyses were conducted on feed efficiency, feed intake, milk yield, fat plus protein yield, calving liveweight and mean liveweight, using a derivative-free REML package (Meyer, 1988). The data were divided into heifer and later lactations and REML analyses carried out on traits, individually (univariate analyses), for heifer, cow and pooled data for both 26- and 38-week lactation periods. The model of analysis included the additive genetic merit of all animals as a random effect, and incorporated information on genetic relationships between all animals including those without records e.g. sires. The common environmental effect due to animals having more than one record was fitted as an additional random effect. The model was:

$$y = Xb + Za + Wc + e$$

where y = the vector of observations,

b = the vector of fixed effects,

X = the incidence matrix for fixed effects,

a = the vector of random animal (additive genetic) effects,

c = the vector of additional random (common environment) effects,

W, Z = the incidence matrices for random effects, and

e = the vector of random residual errors.

The fixed effects fitted included: (1) lactation number, which was grouped from 1 to 4, group 1 for first lactation animals, group 2 for second lactation animals, group 3 including lactations 3 to 5 and group 4 including lactations 6 to 9; (2) year of calving, from 1979 to 1987; and (3) month of calving, from September to November. Sires were intensely selected, but the variance of ICC of fat plus protein was twice as high as expected from a random sample of bulls, probably because the sires used spanned a long time period and included control bulls. To account for this time trend and consequent increase in variance, sires from the selection herd were grouped according to the year their daughters first calved in the herd, with another group for the control sires. Sires whose daughters first calved between 1979/80 to 1981/82, 1982/83 to 1984/85 and 1985/86 to 1987/88 were assigned to groups 1, 2, and 3, respectively. These four sire groups were then fitted as fixed effects in the model.

Univariate REML analyses were conducted on each trait and on their sums. Before summing, traits were scaled by their approximate phenotypic standard deviations. Estimates of variances from analyses of individual traits and pairs of traits were then used to estimate the covariance between pairs of traits, i.e. $Cov(x,y) = \{(V(x+y) - V_x - V_y)/2\}$ where $Cov(x,y)$ is the covariance between traits x and y, $V(x+y)$ is the variance of the sum of traits x and y, and V_x and V_y are the variances of trait x and trait y respectively. Genetic correlations (r_g) between traits were computed as:

$$r_{gxy} = Cov_g(x,y) / (V_{gx} V_{gy})^{0.5}$$

where $Cov_g(x,y)$ is the genetic covariance between traits x and y, and V_{gx} and V_{gy} are the genetic variances for the two traits. Phenotypic correlations were computed similarly.

In this study, both sires and cows were selected for increased fat plus protein yields. Estimates of heritability and genetic variances from the univariate REML analyses were therefore expected to be biased as no account was taken of the reduction of variance due to selection. In order to account for selection and also increase the precision of estimates, a multivariate REML analysis was attempted. Problems were, however, encountered with

convergence, probably due to the high correlations amongst the traits, combined with the small number of records. A canonical transformation of the traits was attempted, as an alternative to the multivariate REML analysis.

The canonical transformation is a linear transformation of the original variables to new or canonical variables such that the covariances amongst all traits are zero, with each trait having unit residual variance. Usually this transformation is used to reduce the computational requirements in estimating variance and covariance components by a multivariate REML analysis. By transforming the original traits to independent canonical traits, an n -variate analysis is reduced to n corresponding univariate analyses (Meyer, 1985). A univariate REML analysis of these canonical variates gives the same results as the straightforward multivariate REML analysis (Meyer, 1985; Jensen and Mao, 1988).

The canonical transformation involves diagonalising both the genetic and residual (co)variance matrices, i.e. the off diagonal elements are zero. In this analysis three covariances were involved: additive genetic (G), environment common to all lactations (C), and to specific lactations (E), so it was therefore not possible to do a canonical transformation. Instead an approximate canonical transformation, based on diagonalising G and C+E (co)variance matrices, was carried out. The procedure is outlined below.

1. Estimates of variances and covariances from the univariate analyses (as described above) were used to compute an approximate canonical transformation matrix. This was then used to transform the original traits to new (approximate canonical) variates.
2. Univariate REML analyses were then carried out on these transformed variates and their sums, yielding variances and covariances on the transformed scale.
3. The variances and covariances of the transformed variates were then back transformed to re-estimate variances and covariances on the original scale.
4. Steps 1, 2, and 3 were then repeated until the covariances on the transformed scale were effectively zero.

An example of the transformation, involving four traits, is given in Table 5.1. Using

the variances and covariances from cycle 1 on the original scale, estimates are obtained on the transformed scale (cycle 1). These are then back-transformed to yield estimates on the original scale (cycle 2). The process is then repeated, using estimates of cycle 2 on the original scale as starting parameters. After two cycles, the covariances amongst the traits on the transformed scale are already near zero, i.e. G and C+E (co)variance matrices are nearly diagonal. Although, when taken individually, C and E are not diagonal, the covariances and correlations are nevertheless low. This is shown in Table 5.2 where the covariances for C and E are generally less than ± 0.1 , and, with the exception of traits 1 and 2, the correlations are generally within the range ± 0.05 to ± 0.15 . It is therefore obvious that the transformation based on diagonalising G and C+E is advantageous, although it is not clear whether it is optimal. Calculations suggest that estimates of G are at least 97% efficient (Thompson and Hill, 1990).

Estimates of variances and covariances on the original scale (after back transformation) were used to compute heritabilities, genetic and phenotypic correlations. Repeatabilities were computed as the ratio of the sum of the genetic and common environmental variance to the total phenotypic variance. Standard errors of the heritability estimates were estimated from univariate analyses of individual traits by a quadratic approximation to the log likelihood using a number of point estimates above and below the maximum likelihood heritability value. Standard errors of the genetic correlations were not estimated given the complex method of calculating the correlations.

For the heifer analyses, canonical transformation was carried out, except for the smaller 38-week heifer data set, in which most of the residual (co)variance matrices were not positive definite, i.e. negative roots were obtained.

Table 5.1

Examples of estimates of variances and covariances by univariate REML analyses of traits and sums of traits from successive iterates using original data (cycle 1) and transformed data (cycle 1 and 2). Traits 1, 2, 3, and 4 are 26-week, milk yield, feed intake, fat plus protein yield and calving liveweight respectively, each trait scaled by their approximate phenotypic standard deviation.

Variates	Original			Transformed	
	Cycle 1	(2)**	(3)**	1	2
Variance/ Covariance					
(Common Environment + Residual) Components					
1,1	0.526902	0.529119	0.522523	0.992435	0.992282
1,2	0.223711	0.187516	0.188665	-0.013845	-0.002619
1,3	0.506175	0.477312	0.475709	-0.034097	0.004910
1,4	0.150079	0.149274	0.144423	-0.015746	0.007509
2,2	0.361204	0.353686	0.355508	0.965522	0.987856
2,3	0.219866	0.202587	0.208393	-0.186565	0.035148
2,4	0.088969	0.084401	0.078585	-0.049170	-0.008287
3,3	0.513226	0.506505	0.505689	2.617056	1.002729
3,4	0.173353	0.156904	0.154196	0.355695	0.008049
4,4	0.675906	0.695833	0.692808	1.136488	0.988224
Genetic Components					
1,1	0.134808	0.133519	0.139769	0.000002	0.000001
1,2	0.095484	0.093384	0.093109	-0.016284	0.001877
1,3	0.110089	0.103305	0.108090	0.097259	0.014729
1,4	-0.096793	-0.085568	-0.085381	0.055843	-0.015049
2,2	0.205526	0.212088	0.212163	0.490205	0.514532
2,3	0.114435	0.131388	0.127725	-0.038915	-0.024691
2,4	0.070292	0.062164	0.069738	-0.028506	0.009957
3,3	0.134469	0.143815	0.137804	2.780075	1.081132
3,4	-0.130553	-0.098084	-0.097155	0.366543	-0.005080
4,4	0.324207	0.301671	0.297261	0.810283	0.720249

** Estimated by back transformation of transformed variates of cycles 1 and 2, respectively.

Table 5.2

Examples of estimates of variances, covariances, and correlations, on approximate canonical scale, of C (common environment effect), E (residual effect), and C+E from univariate REML analyses of the original traits and their sums from cycle 2 in Table 5.1.

	Common Environment (C)	Residual (E)	C+E
Variances			

1	0.218288	0.774258	0.992282
2	0.271096	0.716099	0.987856
3	0.513689	0.493234	1.002729
4	0.518866	0.469278	0.988224
1+2	0.701278	1.273512	1.974899
1+3	0.737884	1.275360	2.004830
1+4	0.798624	1.198959	1.995524
2+3	0.871416	1.189574	2.060882
2+4	0.921093	1.034625	1.959507
3+4	1.160770	0.853071	2.007052
Covariances			

1,2	0.105947	-0.108422	-0.002619
1,3	0.002954	0.003934	0.004910
1,4	0.030735	-0.022288	0.007509
2,3	0.043315	-0.009879	0.035148
2,4	0.065565	-0.075376	-0.008287
3,4	0.064107	-0.054720	0.008049
Correlations			

1,2	0.435524	-0.145608	-0.002659
1,3	0.008820	0.006366	0.004922
1,4	0.091325	-0.036975	0.007583
2,3	0.116072	-0.016623	0.035483
2,4	0.174817	-0.130026	-0.008387
3,4	0.124173	-0.113738	0.008086

Even with the larger 26-week heifer data set, a maximum of only three traits could be transformed simultaneously, and convergence was slow. This problem is not unexpected given the high correlation amongst the traits and the small number of records (Hill and Thompson, 1978; Meyer, 1985).

Results are presented for both the univariate analysis and univariate analysis after approximate canonical transformation of the traits.

5.3 Results

Means and standard deviations for the performance and liveweight traits are given in Table 5.3. Average liveweights were over 550 kg for heifers and over 640 kg for cows. As expected, cows were heavier than heifers at calving although mean feed intakes and efficiencies were similar for both groups. Mean liveweight over the longer 38-week period was generally higher than that over the shorter 26-week period, indicating that both heifers and cows were depositing fat and/or growing in later lactation.

Estimates of heritabilities, genetic and phenotypic correlations from univariate analyses are given in Tables 5.4, 5.5, and 5.6 for the heifer, cow, and pooled lactations, respectively. Estimates of heritability and correlations (absolute value) are generally slightly higher than corresponding estimates obtained from the transformed data. Because of this similarity, only results from the transformed data are discussed.

Repeatabilities for milk production traits and efficiency ranged from 0.45 to 0.65, while those for feed intake and liveweight traits were slightly higher, ranging from 0.55 to 0.80 (Table 5.7). Estimates were similar for the cow and pooled data analyses, with those in the longer 38-week period being consistently higher than those in the 26-week period.

Estimates of heritability, genetic and phenotypic correlations from the heifer, cow and pooled data, after transformation of the traits, are given in Tables 5.8, 5.9, and 5.10,

respectively. Heritability estimates over the 26-week period, for efficiency, feed intake and milk yield were 0.48 ± 0.21 , 0.44 ± 0.23 and 0.49 ± 0.20 for heifers and 0.13 ± 0.09 , 0.37 ± 0.11 and 0.20 ± 0.08 for the pooled data, respectively. Estimates were similar for the cow data analysis and over the longer 38-week period, although standard errors were higher as there were fewer records. Genetic correlations between efficiency and milk production traits ranged from 0.50 to 0.65 although those for heifers were slightly higher. Corresponding phenotypic correlations were all between 0.80 to 0.90 for the different data sets. Genetic correlations between feed intake and milk production traits were similar to those between efficiency and the milk production traits. For both efficiency and feed intake, genetic correlations with milk production traits were lower and phenotypic correlations were higher in the 38-week period than in the 26-week period. Genetic correlations between efficiency and liveweight traits were all negative and very high, and in some cases, near to 1, except those for heifers. Phenotypic correlations were also negative but much smaller. Correlations between feed intake and liveweight traits were all positive and moderate, with the genetic correlations being higher, ranging from 0.30 to 0.45 for the pooled data.

5.4 Discussion

Published heritability estimates for feed efficiency and feed intake range from 0.12 to 0.63 and 0.03 to 0.45 respectively (Freeman, 1975; Korver, 1988). This large variation among estimates may be due in part to differences in the definition of efficiency and in management and environmental conditions peculiar to each experiment. The heritability estimates for efficiency obtained in this study are within the range quoted in the literature, although those for the pooled data set are on the lower side. Heritability estimates for yield of milk and of fat plus protein are also lower than published values. Hooven *et al.*, (1972), however, obtained slightly lower heritability estimates for part lactation efficiency as compared to total lactation efficiency.

Table 5.3

Raw means and standard deviations of performance and liveweight traits.

Trait (kg)	Heifers		Cows		All data	
	Mean	SD	Mean	SD	Mean	SD
	Set 1: 26 weeks					
Number of records	(141)		(334)		(475)	
Milk yield	4227	747	5297	869	4979	967
Fat + protein yield	319.0	50.0	400.8	65.2	376.5	71.6
Dry matter intake	2925	282	3375	355	3242	393
Efficiency ⁺⁺	370.9	53.0	408.8	59.0	397.6	60.0
Calving liveweight	533.2	45.3	640.6	65.3	608.7	77.5
Mean liveweight	554.6	44.1	641.0	57.7	615.3	66.9
	Set 2: 38 weeks					
Number of records	(101)		(192)		(293)	
Milk yield	5876	1087	7025	1255	6629	1317
Fat + protein yield	450.7	73.6	530.4	96.9	502.8	97.3
Dry matter intake	4070	400	4614	450	4427	504
Efficiency ⁺⁺	374.6	50.0	393.8	59.0	387.2	57.0
Calving liveweight	533.4	41.3	639.5	63.0	602.9	75.7
Mean liveweight	569.0	43.8	651.8	58.7	623.2	66.8

⁺⁺ Efficiency expressed as (MJ/MJ x 10³)

Table 5.4

Univariate estimates of Heritability \pm SE (on diagonal), Genetic Correlations (above diagonal) and Phenotypic Correlations (below diagonal) for feed efficiency (EFF), dry matter feed intake (DMI), milk yield (MY), fat plus protein yield (FP), calving liveweight (CLW) and mean liveweight (MLW) for 26- and 38-week lactation periods, for heifer data.

		EFF	DMI	FP	MY	CLW	MLW
EFF	26	0.44 (0.21)	0.09	0.87	0.78	-0.42	-0.81
	38	0.48 (0.29)	-0.11	0.77	0.79	-0.55	-0.74
DMI	26	0.09	0.45 (0.23)	0.53	0.70	0.63	0.32
	38	0.17	0.99 (0.52)	0.55	0.50	0.01	-0.33
FP	26	0.86	0.56	0.40 (0.22)	0.96	-0.14	-0.58
	38	0.86	0.61	0.55 (0.30)	0.78	-0.37	-0.65
MY	26	0.87	0.45	0.91	0.47 (0.20)	0.01	-0.38
	38	0.87	0.49	0.89	0.57 (0.23)	-0.07	-0.34
CLW	26	-0.09	0.33	0.08	0.11	0.81 (0.24)	1.00*
	38	-0.09	0.28	0.06	0.15	0.73 (0.31)	1.00*
MLW	26	-0.44	0.24	-0.25	-0.23	0.84	0.81 (0.29)
	38	-0.48	0.13	-0.30	-0.28	0.77	0.31 (0.38)

* Estimates greater than 1.00

Table 5.5

Univariate estimates of Heritability \pm SE (on diagonal), Genetic Correlations (above diagonal) and Phenotypic Correlations (below diagonal) for feed efficiency (EFF), dry matter feed intake (DMI), milk yield (MY), fat plus protein yield (FP), calving liveweight (CLW) and mean liveweight (MLW) for 26- and 38-week lactation periods, for cow data.

		EFF	DMI	FP	MY	CLW	MLW
EFF	26	0.22 (0.12)	-0.26	0.74	0.50	-1.00*	-0.79
	38	0.24 (0.18)	-0.18	0.77	0.59	-0.81	-0.56
DMI	26	-0.04	0.29 (0.15)	0.44	0.43	0.10	0.35
	38	0.11	0.52 (0.23)	0.48	0.49	0.21	0.58
FP	26	0.80	0.54	0.23 (0.13)	0.78	-0.87	-0.47
	38	0.86	0.59	0.29 (0.18)	0.94	-0.57	-0.26
MY	26	0.78	0.47	0.90	0.13 (0.11)	-0.74	-0.24
	38	0.84	0.53	0.93	0.15 (0.18)	-0.99	-0.38
CLW	26	-0.08	0.18	0.03	0.04	0.30 (0.16)	1.00*
	38	-0.16	0.10	-0.10	-0.11	0.54 (0.34)	1.00*
MLW	26	-0.40	0.22	-0.20	-0.21	0.82	0.38 (0.17)
	38	-0.52	0.10	-0.38	-0.38	0.77	0.36 (0.31)

* Estimates greater than ± 1.00 .

Table 5.6

Univariate estimates of Heritability \pm SE (on diagonal), Genetic Correlations (above diagonal) and Phenotypic Correlations (below diagonal) for feed efficiency (EFF), dry matter feed intake (DMI), milk yield (MY), fat plus protein yield (FP), calving liveweight (CLW) and mean liveweight (MLW) for 26- and 38-week lactation periods, for pooled data.

		EFF	DMI	FP	MY	CLW	MLW
EFF	26	0.14 (0.09)	-0.06	0.67	0.67	-1.00*	-0.91
	38	0.05 (0.12)	-0.11	0.56	0.62	-1.00*	-0.86
DMI	26	-0.01	0.36 (0.11)	0.69	0.57	0.27	0.29
	38	0.16	0.51 (0.14)	0.70	0.56	0.44	0.73
FP	26	0.82	0.55	0.21 (0.10)	0.82	-0.62	-0.40
	38	0.86	0.61	0.16 (0.12)	0.73	-0.63	-0.07
MY	26	0.85	0.52	0.94	0.20 (0.08)	-0.46	-0.31
	38	0.89	0.58	0.95	0.18 (0.11)	-0.73	-0.21
CLW	26	-0.06	0.21	0.05	0.07	0.32 (0.11)	1.00*
	38	-0.11	0.17	-0.02	-0.02	0.25 (0.20)	1.00*
MLW	26	-0.40	0.23	-0.19	-0.21	0.65	0.43 (0.13)
	38	-0.49	0.12	-0.34	-0.35	0.76	0.30 (0.20)

* Estimates greater than ± 1.00 .

Table 5.7
 Repeatabilities for milk production, feed intake, efficiency,
 and liveweight traits.

Traits	26 Week		38 Week	
	Cow data	Pooled data	Cow data	Pooled data
Milk (kg)	0.41	0.47	0.61	0.63
Fat plus protein (kg)	0.52	0.51	0.68	0.64
Feed intake (kg)	0.66	0.63	0.70	0.67
Efficiency (MJ/MJ)	0.43	0.41	0.63	0.60
Calving liveweight (kg)	0.66	0.58	0.67	0.56
Mean liveweight (kg)	0.79	0.76	0.78	0.79

Note: Pooled data refers to heifer data plus cow data.

Table 5.8

Estimates of Heritability \pm SE (on diagonal), Genetic Correlations (above diagonal) and Phenotypic Correlations (below diagonal) for feed efficiency (EFF), dry matter feed intake (DMI), milk yield (MY), fat plus protein yield (FP), calving liveweight (CLW) and mean liveweight (MLW) for 26-week lactation period, for heifer data, after canonical transformation.

	EFF	DMI	FP	MY	CLW	MLW
EFF	0.48 (0.21)	0.06	0.87	0.74	-0.39	-0.73
DMI	0.09	0.44 (0.23)	0.49	0.65	0.61	0.38
FP	0.86	0.56	0.45 (0.22)	0.95	-0.07	-0.49
MY	0.86	0.45	0.90	0.49 (0.20)	0.06	-0.33
CLW	-0.08	0.33	0.09	0.12	0.81 (0.24)	0.99
MLW	-0.43	0.25	-0.24	-0.22	0.83	0.80 (0.29)

Table 5.9

Estimates of Heritability \pm SE (on diagonal), Genetic Correlations (above diagonal) and Phenotypic Correlations (below diagonal) for feed efficiency (EFF), dry matter feed intake (DMI), milk yield (MY), fat plus protein yield (FP), calving liveweight (CLW) and mean liveweight (MLW) for 26- and 38-week lactation periods, for cow data, after approximate canonical transformation.

		EFF	DMI	FP	MY	CLW	MLW
EFF	26	0.18 (0.12)	-0.28	0.65	0.56	-0.97	-0.74
	38	0.30 (0.18)	-0.29	0.69	0.56	-0.63	-0.62
DMI	26	-0.04	0.30 (0.15)	0.54	0.49	0.03	0.29
	38	0.10	0.52 (0.23)	0.44	0.42	0.20	0.41
FP	26	0.80	0.56	0.22 (0.13)	0.78	-0.78	-0.42
	38	0.84	0.59	0.29 (0.18)	0.88	-0.55	-0.32
MY	26	0.78	0.48	0.90	0.13 (0.11)	-0.68	-0.25
	38	0.84	0.52	0.92	0.16 (0.18)	-0.59	-0.42
CLW	26	-0.05	0.15	0.04	0.05	0.28 (0.16)	0.97
	38	-0.16	0.09	-0.10	-0.09	0.51 (0.34)	0.99
MLW	26	-0.40	0.23	-0.20	-0.21	0.79	0.35 (0.17)
	38	-0.52	0.09	-0.38	-0.38	0.74	0.43 (0.31)

Table 5.10

Estimates of Heritability \pm SE (on diagonal), Genetic Correlations (above diagonal) and Phenotypic Correlations (below diagonal) for feed efficiency (EFF), dry matter feed intake (DMI), milk yield (MY), fat plus protein yield (FP), calving liveweight (CLW) and mean liveweight (MLW) for 26- and 38-week lactation periods, for pooled data, after approximate canonical transformation.

		EFF	DMI	FP	MY	CLW	MLW
EFF	26	0.13 (0.09)	-0.05	0.60	0.61	-0.94	-0.82
	38	0.13 (0.12)	-0.41	0.44	0.52	-0.99	-0.81
DMI	26	0.02	0.37 (0.11)	0.74	0.54	0.28	0.34
	38	0.14	0.52 (0.14)	0.65	0.47	0.33	0.46
FP	26	0.81	0.56	0.20 (0.10)	0.75	-0.51	-0.31
	38	0.86	0.60	0.15 (0.12)	0.71	-0.45	-0.22
MY	26	0.80	0.46	0.89	0.20 (0.08)	-0.42	-0.31
	38	0.85	0.53	0.91	0.20 (0.11)	-0.70	-0.33
CLW	26	-0.04	0.20	0.07	0.07	0.31 (0.11)	0.96
	38	-0.03	0.16	-0.03	-0.02	0.24 (0.20)	1.00*
MLW	26	-0.38	0.24	-0.17	-0.20	0.75	0.40 (0.13)
	38	-0.50	0.11	-0.34	-0.35	0.79	0.34 (0.20)

* Estimate greater than 1.00

Estimates from the heifer and cow data analyses were higher than those from the pooled data, but standard errors were also higher. Repeatabilities of efficiency, which represent the upper limit for the heritabilities, were very similar for both cow and pooled data sets and in fact were not much different from the estimates of 0.45 to 0.60 obtained for milk yield. Heritability estimates for feed intake, on the other hand, were higher than most reported values, and this may be due in part to the feeding regime, which allowed full expression of appetite. Under *ad libitum* feeding, however, Gravert (1985) obtained an estimate of 0.16 for feed intake in the first 20 weeks of lactation using a total of 96 records from 32 pairs of monozygous twins, while Oldenbroek (1988) obtained a repeatability of 0.39, using a total of 265 lactations of 165 cows from four different breeds. These estimates indicate that the genetic variation in feed intake may not be as high as observed in this study, especially as the estimate from the monozygous twins are likely to be biased upwards by common environment and non additive genetic variance. With the small number of animals and records involved, however, these estimates would be expected to have high standard errors.

From Table 5.3, it can be seen that the variance of feed intake is much higher in later lactations than in the first lactation. Combining data from different lactations, as in the pooled data analysis, can therefore give rise to problems of heterogeneity of variance; but a logarithmic transformation of the data gave similar estimates to those from the untransformed data. In addition, estimates from the separate heifer and cow data analyses were quite similar to those from the pooled data analysis, although standard errors were high. These observations suggest that it is unlikely that the heritability estimates from the pooled data could be substantially biased as a result of heterogeneity of variance.

The heritability estimates from this study, especially over the shorter 26-week period, indicate that selection for increased feed intake is possible. Higher intakes will reduce the negative energy balance in early lactation, thereby reducing catabolism of body reserves and thus improving efficiency.

Model calculations have shown that selection on milk yield is expected to give between 70 and 95% of the response in efficiency from direct selection on efficiency, when selection intensities are equal for the two traits (Freeman, 1967). These responses were predicted assuming a genetic correlation between milk yield and efficiency of 0.75 to 0.95. Except for the heifer analysis (over 26 weeks), and contrary to most other studies, corresponding genetic correlations in this study were lower. In addition the genetic correlations were also lower than the corresponding phenotypic correlations. Using the genetic parameters estimated from the pooled data, the expected correlated responses in efficiency, from indirect selection on fat plus protein yield, are 74 and 47% of those expected from direct selection, for the 26- and 38-week lactation periods respectively.

The moderate, positive genetic correlation between liveweight and feed intake and higher negative genetic correlation between liveweight and milk production traits indicate that heavier animals consumed more but were less productive and consequently less efficient than the lighter animals. In other studies (Hooven *et al.*, 1968; Oldenbroek, 1988), where selection was for increased yields, liveweight was found to be highly positively genetically correlated with feed intake and moderately positively genetically correlated with milk production resulting in a small to moderate negative genetic correlation between efficiency and liveweight. The unexpectedly high negative genetic correlation obtained in this study, may partly be explained by the fact that heavier animals or animals which gained more weight used a higher proportion of feed energy for maintenance and growth compared to lighter animals. In addition, and contrary to other studies, the heavier animals also produced less. This may be a consequence of the *ad libitum* feeding used in this study. In addition, this high negative genetic correlation may be due in part, to sampling, as the number of records analysed were small. A check on the correlation between cow effects (genetic plus common environmental effect) i.e. cow correlation, between efficiency and calving liveweight, showed that this was only -0.41

as compared to a genetic correlation of -0.94. In this case the covariance due to the common environmental effect was -0.006 i.e. the lower cow correlation was not due to a relatively high positive covariance between common environmental effects. The much smaller cow correlation is similar to that of -0.29 obtained by Oldenbroek (1988), between efficiency and average bodyweight. These results indicate that the genetic correlation estimated may be too high, since the cow covariance is the upper limit for the genetic covariance. If one assumed the genetic correlation between efficiency and liveweight were near unity, as obtained in this analysis, then liveweight should be a very good predictor of efficiency: i.e. liveweight in, say, lactation one should be able to predict (based on G + C) efficiency in another lactation almost as well as efficiency in lactation one. Using the 26-week pooled data, it was found that the ability of liveweight in one lactation to predict efficiency in another lactation was about 0.20, i.e. about half the repeatability of efficiency. This further supports the suggestion that the genetic correlation obtained in this analysis is inflated. In spite of this, bodyweight may be worth considering as a selection criterion for the genetic improvement of feed efficiency. Using parameters estimated from this study and comparing different selection criteria, selection on an index of fat plus protein yield and liveweight is predicted to be much more accurate than mass selection on fat plus protein yield or efficiency (Table 5.6). Selection on breeding value for liveweight or index of fat plus protein and liveweight is about 85 to 95% as accurate as selection on breeding value for efficiency. The high accuracy obtained when selecting on breeding value for liveweight or index including liveweight is undoubtedly due to the high genetic correlation between efficiency and liveweight, and, as discussed earlier, this may be due to chance, as the number of records analysed were small.

For a progeny test with n effective daughters, the accuracy r is given as:

$$r = \{nh^2 / [4 + (n - 1)h^2]\}^{0.5}$$

Hence for a bull with a moderately reliable test, i.e. ($n = 35$) the accuracy of selection for

efficiency, when selection is on fat plus protein yield, are 0.48 and 0.33 for the 26- and 38-week periods, respectively (Table 5.11). Comparable accuracies, when selection is on index of fat plus protein and mean liveweight or fat plus protein and calving liveweight are 0.86 and 0.99. Even assuming a heritability of 0.25 for fat plus protein yield and a genetic correlation of 0.7 with efficiency, selection on the index is still predicted to be higher, compared to selection for fat plus protein yield, based on progeny testing (Table 5.11). The accuracy of selection for efficiency when efficiency is measured directly (progeny test), is much higher, i.e. 0.74.

In practice, however, this accuracy is unlikely to be achieved, as a relatively smaller number of daughters will be recorded for feed intake, i.e. n is likely to be much smaller than 35. These results suggest that greater improvement in efficiency can be obtained by selecting on an index of yield and liveweight rather than on efficiency or yield alone. It must, however, be emphasised that the number of records analysed in this study was small.

In conclusion, the results obtained in this study indicate that the correlated responses in efficiency given selection on milk production under *ad libitum* feeding are likely to be smaller than those predicted in other studies where cows were fed according to yield. In MOET nucleus schemes, where it is feasible to record feed intake, it may be worthwhile to consider direct selection for efficiency. In other situations selection on an index of yield and liveweight may give higher responses in efficiency, compared to selection on yield alone. Given the relative ease of measuring body size traits more research into their relationship with efficiency is warranted. More specifically the relationship between efficiency and body size traits such as stature and chest circumference, which are less influenced than liveweight by temporary changes in cow state (i.e. pregnancy, variation in gut fill) should be further investigated.

Table 5.11

Accuracy of selection for efficiency when selection is on phenotype, or breeding value based on progeny testing, or on perfect estimate of breeding value, of individual traits or index, with measurements over 26- or 38-week lactation periods.

Selection Criterion		EFF	FP	MLW	CLW	ID1	ID2	ID3	ID4
Phenotype	26	0.36	0.27	0.52	0.52	0.55	0.61	0.55	0.63
	38	0.36	0.17	0.47	0.49	0.47	0.51	0.54	0.65
Progeny test	26	0.74	0.48	0.73	0.81	-	-	-	-
	38	0.74	0.33	0.71	0.82	-	-	-	-
		0.58 ⁺⁺	0.59 ^a	0.26 [*]	0.25 [*]				
Breeding value	26	1.00	0.60	0.82	0.94	0.90	0.95	1.00	1.00
	38	1.00	0.44	0.81	0.99	0.86	0.99	1.00	1.00

EFF = Feed efficiency
 FP = Fat plus protein yield
 MLW = Mean liveweight
 CLW = Calving liveweight
 ID1 = Index of FP and MLW
 ID2 = Index of FP and CLW
 ID3 = Index of FP, MLW and EFF
 ID4 = Index of FP, CLW and EFF

Note: number of effective daughters used for progeny test is 35.

⁺⁺ number of effective daughters equal to 15.
^a assume heritability is 0.25 and genetic correlation with efficiency is 0.7
^{*} assume genetic correlation with efficiency is -0.3

CHAPTER 6

GENETIC AND PHENOTYPIC RELATIONSHIPS BETWEEN PART AND 'TOTAL' LACTATION INTAKE AND EFFICIENCY

6.1 Introduction

The recent establishment of nucleus breeding schemes, e.g. that of Genus, which have been predicted to give improvements in milk production traits comparable to those of a large progeny testing scheme (Woolliams and Smith, 1988; Ruane and Thompson, 1989), now provides the opportunity for recording and hence selecting for increased feed intake and efficiency. The high cost of feed recording facilities will, however, still place a limit on the progress that can be achieved in practice. Progress can be increased by using an early part lactation measure of feed intake and efficiency as the selection criterion, rather than total lactation measurements.

Selection based on part lactation records will result in a reduction of the time required for, and hence cost of, recording traits and housing animals. In addition to a lower generation interval, a higher selection intensity can be achieved as more animals can be recorded with a fixed number of facilities. Furthermore, the problem of bias in sire evaluations resulting from the culling of heifers before the end of lactation will also be reduced. This selection strategy would, however, be feasible only if early part lactation measures of feed intake and efficiency were sufficiently heritable and well correlated with total lactation measurements. Although there is good evidence to suggest that this is so for milk production traits (Danell, 1982a; Wilmink, 1987), there is little or no information of this kind relating to feed intake or efficiency.

The aim of this study was to estimate the heritabilities of part lactation feed intake and efficiency and their relationship with total lactation feed intake and efficiency.

6.2 Materials and Methods

6.2.1 Data

The two data sets used in Chapter 5 were also used in this analysis. Data set 1, contained 475 lactation records on 251 animals up to the 26th week the lactation, while

data set 2, a subset of the first, comprised of 293 lactation records on 168 animals up to the 38th week of lactation. It was decided to exclude data for the first two weeks as intakes and production were very variable, and also because some records were predicted (see chapter 3). After dropping the first two weeks, the data were divided into 6-week periods, i.e. from weeks 3 to 8, 9 to 14, 15 to 20, 21 to 26, 27 to 32, and 33 to 38. Total fat plus protein yield, feed intake, and cumulative efficiency were then computed for each period for both data sets 1 and 2. This resulted in four, 6-week lactation measurements for each trait in data set 1, and six for each trait in data set 2. In addition, fat plus protein yield, feed intake, and cumulative efficiency were calculated for the whole 26-week and 38-week lactation periods for data sets 1 and 2, respectively.

6.2.2 Statistical Methods

Univariate REML analyses were conducted on each part measurement and their sums, for each trait, using a derivative-free REML package (Meyer, 1988). Before summing, traits were divided by their approximate phenotypic standard deviation. The model of analysis included the additive genetic merit of all animals as a random effect, and incorporated information on genetic relationships between all animals, including those without records. The common environmental effect due to animals having more than one record was fitted as an additional random effect. The model was:

$$y = \mathbf{X}b + \mathbf{Z}a + \mathbf{W}c + e$$

where y = the vector of observations,

b = the vector of fixed effects,

\mathbf{X} = the incidence matrix for fixed effects,

a = the vector of random animal (additive genetic) effects,

c = the vector of additional random (common environment) effects,

\mathbf{W}, \mathbf{Z} = the incidence matrices for random effects, and

e = the vector of random residual errors.

Fixed effects included lactation number, year and month of calving, and a sire grouping and were the same as described in chapter 5.

Estimates of variances from analyses of individual traits and sums of traits were then used to compute the covariance between pairs of traits, as described in chapter 5. An approximate canonical transformation, identical to that used and described in chapter 5, was then carried out, using the part lactation traits as different traits. Estimates of variances and covariances, obtained after this transformation, were used to compute heritabilities, genetic and phenotypic correlations. Repeatabilities and standard errors of the heritability estimates were estimated as in chapter 5.

6.3 Results

Unadjusted means and coefficients of variation ($\times 100$) for the 6-week and 'whole' lactation measures, for each trait, from data sets 1 and 2, are given in Tables 6.1 and 6.2, respectively. Means and coefficients of variation for the same traits were similar for equivalent periods in the two data sets. Both fat plus protein yield and efficiency declined with advancing period of lactation, while feed intake peaked in the second period (weeks 9 to 14) and then gradually declined in later lactation. The fact that efficiency peaked earlier than feed intake may be due to the catabolism of fat reserves in the early part of lactation. The coefficient of variation for fat plus protein yield declined as lactation progressed, with that over the whole 38-week period being similar to that over the second 6-week period. Unlike yield, however, the coefficient of variation for efficiency and feed intake tended to increase in the latter part of lactation, with the coefficients for the 38-week efficiency and intake being lower than the coefficients for any of their respective 6-week measures.

Repeatabilities for fat plus protein yield, efficiency, and feed intake, for the different periods from data set 2, ranged from 0.5 to 0.6, 0.4 to 0.5, and 0.5 to 0.6, respectively (Table 6.3). Estimates for the same periods from data set 1 were slightly

lower. The lowest repeatabilities for all three traits were obtained in the first period (weeks 3 to 8), while the highest were obtained over the whole 38-week period.

Estimates of heritabilities (\pm standard errors), genetic and phenotypic correlations between the 6-week measures and 26-week lactation fat plus protein yield, feed intake, and efficiency are given in Tables 6.4, 6.5, and 6.6, respectively. Corresponding estimates between 6-week and 38-week lactation measurements are given in Tables 6.7, 6.8, and 6.9. Heritability estimates for 6-week measures for fat plus protein yield ranged from 0.08 ± 0.10 to 0.17 ± 0.12 with the lower estimates in early lactation (Table 6.7); estimates for efficiency were similar, ranging from 0.08 ± 0.14 to 0.25 ± 0.11 (Table 6.9), while those for feed intake ranged from 0.15 ± 0.09 to 0.49 ± 0.15 (Table 6.8). Over the whole lactation (38 weeks) estimates for fat plus protein yield, efficiency, and feed intake were 0.16 ± 0.12 , 0.13 ± 0.09 , and 0.51 ± 0.14 , respectively (see also Chapter 5, Table 5.10). Heritability estimates for equivalent part lactation measures of fat plus protein yield and efficiency in data set 1 were slightly higher (Tables 6.4 and 6.6), while those for feed intake were slightly lower (Table 6.5). Estimates for fat plus protein yield, efficiency, and feed intake, over the 26 week period were 0.20 ± 0.09 , 0.12 ± 0.09 , and 0.35 ± 0.12 , respectively.

Genetic correlations between the 6-week measures and 38-week lactation measurements were generally high for all traits, ranging from 0.60 to 1.03, for example, for efficiency and 0.85 to 0.98 for feed intake, with the lowest correlations occurring with measurements in the first period. In general, the correlations increased up to the third or fourth period and declined thereafter. The highest genetic correlations between 38-week fat plus protein yield, efficiency and intake were with measurements in periods four (1.00), three (1.03), and three (0.98), respectively. A few estimates of genetic correlations in the smaller data set 2 were greater than 1.00, and this may have been due to sampling as the number of records analysed were small, and because the method of analysis using pairs of traits did not impose bounds on the correlations. Phenotypic correlations were

slightly lower, for example, ranging from 0.73 to 0.89 for efficiency and 0.68 to 0.87 for feed intake, but followed the same pattern as the genetic correlations, i.e. increasing up to the third or fourth period then declining. Genetic correlations between individual 6-week and 26-week lactation measurements were slightly lower (fat plus protein yield and efficiency) or similar (feed intake), compared to genetic correlations between measurements taken over the same periods and 38-week measurements. The highest genetic correlation between 26-week fat plus protein yield, efficiency, and intake were with measurements taken in periods two (0.99), three (0.91), and three (0.99), respectively. Phenotypic correlations were slightly lower than the corresponding genetic correlations and were similar to those obtained for the same periods in the 38-week data set.

6.4 Discussion

In this study the relationships between successive 6-week measurements and 26- and 38-week lactation fat plus protein yield, efficiency, and feed intake, were investigated. The analysis was carried out on the larger 26-week lactation data set, partly to compare with, and hence act as a check on, the results obtained on the smaller, but more appropriate, 38-week lactation data set. The relationships between 6-week measurements over the same period and 26- or 38-week lactation fat plus protein yield, efficiency, and feed intake, were very similar. This would be expected as data set 2 is a subset of data set 1, but would also be expected if the correlation between 26- and 38-week lactation periods was high. Therefore only results from the 38-week data analyses, which are closer to total lactation measurements, are discussed here.

In previous studies on part lactation milk fat or protein yields, the highest heritabilities have been obtained at or near mid-lactation while the lowest have been found in early lactation (Auran, 1976a; Danell, 1982a; Wilmink, 1987).

Table 6.1

Means and coefficient of variation x 100 (C.V) for part lactation
fat plus protein yield, feed intake and efficiency (n=475)

Trait	Fat+Protein (kg)		Feed intake (kg)		Efficiency (MJ/MJ)	
	Mean	C.V	Mean	C.V	Mean	C.V
3 - 8	96.03	21.1	744.1	13.9	0.442	18.2
9 - 14	90.08	18.7	796.7	13.2	0.390	17.5
15 - 20	83.22	17.0	773.0	13.3	0.370	17.8
21 - 26	75.79	16.1	722.9	13.5	0.362	18.0
1 - 26	376.47	19.6	3241.6	12.1	0.398	15.1

Table 6.2

Means and coefficient of variation x 100 (C.V) for part lactation fat plus protein yield, feed intake and efficiency (n=293)

Trait	Fat+Protein (kg)		Feed intake (kg)		Efficiency (MJ/MJ)	
	Mean	C.V	Mean	C.V	Mean	C.V
3 - 8	94.82	21.6	735.3	13.6	0.441	18.6
9 - 14	89.67	18.8	781.5	12.6	0.395	17.3
15 - 20	83.82	17.4	758.8	13.1	0.377	17.5
21 - 26	77.37	16.4	713.0	13.0	0.371	17.9
27 - 32	69.53	16.7	653.1	13.3	0.363	18.9
33 - 38	56.57	16.8	584.4	14.5	0.328	26.2
1 - 38	502.80	19.3	4427.0	11.4	0.387	14.7

Table 6.3
**Repeatabilities of part lactation fat plus protein yield,
 feed intake and efficiency.**

Period (Weeks)	Fat+Protein		Feed intake		Efficiency	
	Set 1	Set 2	Set 1	Set 2	Set 1	Set 2
3 - 8	0.41	0.52	0.42	0.52	0.29	0.40
9 - 14	0.43	0.57	0.54	0.61	0.33	0.48
15 - 20	0.45	0.53	0.51	0.50	0.36	0.43
21 - 26	0.46	0.57	0.45	0.53	0.46	0.54
27 - 32	-	0.56	-	0.45	-	0.54
33 - 38	-	0.46	-	0.27	-	0.50
1 - 26	0.51	-	0.63	-	0.41	-
1 - 38	-	0.64	-	0.68	-	0.60

Table 6.4

Heritabilities (\pm SE) (on diagonal), genetic (above diagonal) and phenotypic (below diagonal) correlations between 6-week periods and 26-week lactation fat plus protein yield.

Weeks	3-8	9-14	15-20	21-26	1-26
3-8	0.16 (0.09)	0.73	0.56	0.57	0.80
9-14	0.73	0.15 (0.09)	0.98	0.98	0.99
15-20	0.65	0.83	0.23 (0.09)	1.00	0.95
21-26	0.56	0.75	0.88	0.24 (0.09)	0.96
1-26	0.84	0.92	0.92	0.88	0.20 (0.09)

Table 6.5

Heritabilities (\pm SE) (on diagonal), genetic (above diagonal) and phenotypic (below diagonal) correlations between 6-week periods and 26-week lactation feed intake.

Weeks	3-8	9-14	15-20	21-26	1-26
3-8	0.29 (0.10)	0.88	0.95	0.97	0.94
9-14	0.75	0.23 (0.11)	0.96	0.84	0.95
15-20	0.55	0.78	0.25 (0.11)	0.96	0.99
21-26	0.34	0.61	0.79	0.22 (0.12)	0.97
1-26	0.82	0.90	0.89	0.81	0.35 (0.12)

Table 6.6

Heritabilities (\pm SE) (on diagonal), genetic (above diagonal) and phenotypic (below diagonal) correlations between 6-week periods and 26-week lactation efficiency.

Weeks	3-8	9-14	15-20	21-26	1-26
3-8	0.10 (0.09)	0.59	0.25	0.04	0.70
9-14	0.73	0.12 (0.08)	0.80	0.66	0.89
15-20	0.57	0.76	0.12 (0.08)	0.92	0.91
21-26	0.42	0.61	0.80	0.11 (0.09)	0.74
1-26	0.82	0.89	0.88	0.79	0.12 (0.09)

Table 6.7

Heritabilities (\pm SE) (on diagonal), genetic (above diagonal) and phenotypic (below diagonal) correlations between 6-week periods and 38-week lactation fat plus protein yield.

Weeks	3-8	9-14	15-20	21-26	27-32	33-38	1-38
3-8	0.08 (0.10)	0.78	0.63	0.67	0.62	0.54	0.82
9-14	0.75	0.10 (0.11)	0.99	0.97	0.90	0.63	0.98
15-20	0.65	0.85	0.13 (0.11)	1.01	0.99	0.83	0.99
21-26	0.59	0.79	0.88	0.15 (0.11)	0.99	0.82	1.00
27-32	0.52	0.71	0.78	0.90	0.17 (0.12)	0.87	0.97
33-38	0.40	0.61	0.71	0.81	0.91	0.14 (0.12)	0.82
1-38	0.76	0.90	0.93	0.94	0.90	0.83	0.16 (0.12)

Table 6.8

Heritabilities (\pm SE) (on diagonal), genetic (above diagonal) and phenotypic (below diagonal) correlations between 6-week periods and 38-week lactation dry matter intake.

Weeks	3-8	9-14	15-20	21-26	27-32	33-38	1-38
3-8	0.49 (0.15)	0.99	0.97	0.94	0.90	0.89	0.85
9-14	0.71	0.40 (0.15)	1.02	0.90	0.89	0.91	0.95
15-20	0.49	0.75	0.46 (0.15)	0.97	0.94	0.93	0.98
21-26	0.42	0.62	0.79	0.29 (0.14)	0.97	0.93	0.97
27-32	0.35	0.57	0.68	0.85	0.19 (0.11)	0.96	0.95
33-38	0.32	0.46	0.52	0.60	0.76	0.15 (0.09)	0.95
1-38	0.68	0.82	0.87	0.87	0.85	0.74	0.51 (0.14)

Table 6.9

Heritabilities (\pm SE) (on diagonal), genetic (above diagonal) and phenotypic (below diagonal) correlations between 6-week periods and 38-week lactation efficiency.

Weeks	3-8	9-14	15-20	21-26	27-32	33-38	1-38
3-8	0.12 (0.09)	0.88	0.85	0.36	0.06	0.13	0.60
9-14	0.77	0.10 (0.12)	0.91	0.86	0.82	0.80	0.93
15-20	0.59	0.77	0.08 (0.14)	1.01	0.90	0.85	1.03
21-26	0.47	0.61	0.83	0.15 (0.12)	0.92	0.87	0.90
27-32	0.38	0.53	0.71	0.84	0.10 (0.14)	0.94	0.83
33-38	0.24	0.44	0.61	0.70	0.82	0.25 (0.11)	0.81
1-38	0.74	0.85	0.89	0.87	0.84	0.73	0.13 (0.09)

The pattern of heritabilities obtained in this study for successive 6-week measurements of fat plus protein yield is in agreement with these reports, although the estimates are lower (and the standard errors are higher). However, the repeatabilities, which are the upper limit for the heritabilities, are well within the range quoted in the literature for milk or fat yield (Maijala and Hanna, 1974). Heritability estimates for part lactation measures of feed efficiency (Table 6.9) were not different from those obtained for fat plus protein yield, although repeatabilities were slightly lower, ranging from 0.40 to 0.55, the lower estimates occurring in early lactation. In an experiment where cows were fed according to yield, Hooven *et al.*, (1972) reported higher heritabilities for part lactation efficiency, but estimates for part lactation fat corrected milk yield were considerably higher than most literature estimates. For example, in the second and fourth month of lactation the heritabilities for efficiency were 0.44 ± 0.07 and 0.44 ± 0.07 , while those for milk yield were 0.48 ± 0.06 and 0.58 ± 0.07 , respectively. Estimates for part lactation feed intake were generally high with some indication of a decrease in heritability in later lactation (Table 6.8). These estimates are not very different from those of Hooven *et al.*, (1972), who also obtained lower estimates in later lactation. The high heritabilities for early lactation feed intake are however, in contrast to that of 0.16 obtained by Gravert (1985) for the first 20 weeks of lactation. However, this estimate would be expected to have a high standard error as data from only 96 lactations were used in the analysis.

Unlike milk production traits, heritability estimates for part lactation efficiency and feed intake are very few. Despite the high standard errors (due to a relatively small number of records) the estimates obtained in this study indicate that part lactation efficiency and feed intake measurements are sufficiently heritable to allow selection on part lactation records.

Genetic and phenotypic correlations between 6-week and 38-week lactation fat plus protein yield were very high, with the former being lower than the latter. The lowest and highest correlations were obtained with measurements in the first and fourth periods,

respectively, but correlations in adjacent third and second periods were also high. These results are also in agreement with those of Danell (1982a) and Wilmink (1987), and indicate that selection on total lactation fat plus protein yield could be replaced by a part measure taken over the second, third, or fourth 6-week period.

The genetic correlations between part and 38-week lactation efficiency indicate that efficiency measured over the third 6-week period will give the best prediction of the total lactation efficiency, while efficiency measured over the first 6-week period will give the worst prediction. Similarly, intake measured over the third 6-week period gave the highest genetic correlation with 38-week lactation intake, although, apart from the first period, the correlations with other 6-week intakes were also very high. The high genetic correlations obtained in this study are similar to those of Hooven *et al.*, (1972), who obtained genetic correlations of 1.00 and 1.06 between total lactation efficiency and intake, with efficiency and intake measured between 121 and 150 days of lactation, respectively. The results obtained here indicate that selection on a 6-week measure of efficiency and feed intake taken in the third period should be as effective as selection on total lactation measures, for improving efficiency and feed intake.

Other researchers investigating these part whole relationships at the phenotypic level have also made similar conclusions. For example, Gibson (1987), analysing data from 221 British Friesian and Jersey cows, with feed intake recorded from calving to calving, concluded that measurements taken near mid-lactation gave the best prediction of total lactation feed intake and efficiency. Simm *et al.*, (1991; see also Appendix), using a subset of data from this study (heifers only), examined the relationship between weekly feed energy intake for the first 12 weeks of lactation, and intake up to 38 weeks of lactation. They concluded that for a fixed period of intake, measurements taken later in lactation gave the best prediction of 38 week intake.

It is obvious that the earlier part lactation records are taken and used for selection

purposes the greater would be the potential benefits. However, the genetic correlations suggest that part measures in early lactation (period 1) will not be as good in predicting total lactation measures compared to part measures taken slightly later (periods 2, 3, and 4). In practice longer periods of part measures may be used. However, estimates of genetic correlations between period 1 plus period 2 (i.e. 12 week period) and 38-week lactation fat plus protein yield, feed intake and efficiency, computed from estimates of variances and covariances, were 0.93, 0.98, and 0.92, respectively. The accuracy of selection (computed as the product of the genetic correlation and square root of the heritability of the part measure) for 38-week measures using measurements in periods 1, 2, and 1 plus 2 were 0.23, 0.31, and 0.29 for fat plus protein yield, 0.60, 0.60, and 0.70 for feed intake, and 0.21, 0.29, and 0.30 for efficiency, respectively, indicating that a longer period of recording in early lactation will give little or no advantage in predicting total lactation measurements, compared to a 6-week measurement in the second or third period. It is clear that there will be a trade off between generation interval and accuracy of prediction, and this must be considered when deciding which part lactation measure to use.

In conclusion, the genetic correlations obtained in this study indicate that a measure of efficiency and intake, taken between 15 to 20 weeks of lactation will give a very good prediction of 38-week lactation efficiency and feed intake, respectively; other 6-week measurements taken between weeks 9 to 14 or 21 to 26 will also give good estimates of 38-week lactation efficiency and intake. Heritability estimates for these 6-week measurements appear to be moderate. Taken together, these results suggest that selection on a part measure of efficiency or feed intake between 15 to 20 weeks of lactation will be equally effective in improving efficiency or intake compared to selection on total lactation efficiency or feed intake. Future research is necessary to determine the optimum selection strategy for MOET nucleus herds given that early lactation measurements (i.e. before week 12) are proposed (e.g. in the current Genus scheme) to minimise the

generation interval, but that higher heritabilities and correlations exist for later lactation measurements.

CHAPTER 7

GENERAL DISCUSSION AND CONCLUSIONS

7.1 Correlated Responses in Feed Intake and Efficiency

The first aim of this study was to investigate the correlated responses in feed intake and efficiency when selection is for increased fat plus protein yield. Previous studies (e.g. Hind, 1979) have shown increases in feed intake and efficiency when selection is for increased milk yield. With selection emphasis in dairy cattle production now moving towards higher milk solids production, it is essential to quantify what, if any, correlated response occur in feed intake and efficiency. The results presented in Chapter 4 indicate that selecting for higher milk solids (fat, protein or fat plus protein) yield will result in an increase in feed intake but also a substantially higher increase in gross efficiency.

The data used in this study were, however, only for the first 26 and 38 weeks of lactation, and it is therefore important to know if these correlated responses will be maintained over the whole lactation or more importantly over the whole calving to calving period. Emmans and Neilson (1984) have suggested that 'short run' and 'long run' biological efficiencies will be poorly correlated. The results given in Tables 4.9 and 4.10 show that a 1% increase in fat plus protein yield of heifers, will be accompanied by a 0.29 % increase in feed intake and 0.79 % increase in feed efficiency over the first 26 weeks of lactation; over the first 38 weeks of lactation corresponding correlated responses for intake and efficiency are 0.34 % and 0.72 %, respectively. These results suggest that although the correlated responses in feed intake are expected to increase and those in efficiency to decrease, over a longer period than that studied here, they are not, however, expected to be substantially different. In fact, this suggestion is supported by Gibson (1986) who obtained a correlated response of 0.73 %, in efficiency, for a 1 % increase in milk yield, using data from calving to calving period.

The reduction in efficiency in the latter part of lactation is due to the replenishment of body reserves, which have been mobilised in early lactation as a consequence of the inability of feed energy intake to meet production requirements. This feature of tissue mobilisation and replenishment is characteristic of high yielding dairy cows and, is

supported by the negative regressions of liveweight change on sire ICC for fat plus protein yield (Table 4.7) i.e. cows that lose weight over the lactation period are more productive and possibly more efficient compared to animals that gain weight.

7.2 Genetic Parameters

Investigations into the genetic aspects of feed intake and efficiency have been limited to a few small experiments. Nevertheless results from these studies have indicated a moderate heritability for efficiency with estimates for feed intake being lower. Estimates of genetic correlations between yield and efficiency from these studies have been very high, ranging from 0.80 to 0.90, and based on these correlations, it has been concluded that selection for higher yields will result in high correlated responses in efficiency. Almost all these studies have, however, been carried out using data obtained from experiments where animals have been fed according to yield, and this may have led to an automatic correlation between yield and efficiency (Freeman, 1975; Korver, 1988).

The data in this study came from the Langhill dairy herd where animals are fed a balanced high energy complete diet *ad libitum*. Heritability estimates for efficiency were not as high as most reported values but estimates for yield were also low; estimates for feed intake were, however, much higher (Tables 5.8, 5.9, and 5.10). Although the number of records analysed was small, and consequently standard errors were high, the results indicate that it is possible to select directly for feed intake and efficiency. The genetic correlations between milk production traits and efficiency were below 0.70, and in fact were similar to those between the milk production traits and feed intake (Tables 5.9 and 5.10). These positive genetic correlations between milk production traits and feed intake and efficiency agree with the correlated responses obtained in Chapter 4. The magnitude of the correlations, however, indicate that the expected correlated responses in efficiency are likely to be smaller than those predicted in systems where cows were fed according to production.

Given the importance of feed efficiency to the overall profitability of dairy production, it may therefore be worthwhile to select directly for either feed intake or efficiency. Conventional progeny testing schemes do not, however, facilitate direct measurement of, and hence selection for, feed intake or efficiency. A more practical suggestion would be to include liveweight or some measure of body size in the selection criteria for genetic improvement of dairy cattle. Estimates of genetic correlations between efficiency and liveweight were very high in this study (Tables 5.9 and 5.10) and as discussed in Chapter 5, were probably inflated. Nevertheless, including liveweight in the selection criteria will improve the accuracy of selection for efficiency compared to selection on yield alone (Table 5.11). Further investigations into these relationships should be carried out given the relative ease of measuring body size traits and their potential for improving efficiency. These investigations should involve more body size measures, particularly those such as stature which are little influenced by temporary changes in cow state.

7.3 Part-whole Relationships

The results from Chapters 4 and 5 have indicated that, under *ad libitum* feeding, selection for increased milk solids production will result in increases in both feed intake and efficiency, but that the correlated response in feed efficiency is not likely to be as high as those predicted in previous studies, where animals were fed according to production. Higher responses may be obtained by selecting directly for intake or efficiency, and heritability estimates (Chapter 5) indicate that this is possible. Direct selection for feed intake and efficiency is feasible in nucleus MOET schemes. Nevertheless, the high cost of recording individual feed intake will place a limit on the number of animals that can be recorded, and thus on the selection intensity that can be achieved. Genetic progress can be increased by using an early part-lactation measure of feed intake and efficiency rather than total lactation measurements. The relationships between these part lactation measures and total lactation measurements are, however, not

known. The study described in Chapter 6 was carried out to address this question.

The results on part-whole relationships indicated that a measure of feed intake and efficiency, taken between 15 to 20 weeks of lactation, will give very good predictions of total lactation intake and efficiency (Tables 6.8 and 6.9). The genetic correlation between 6-week measures and 'total' lactation measurements were lowest for the first period (weeks 3 to 8) suggesting that there will be a conflict between the accuracy of selection and the generation interval when deciding which part lactation record to use, i.e. part records near mid-lactation will give higher accuracies of selection but will result in an increase in the generation interval. In practice, longer periods of recording in early lactation may be used. Based on calculations it appears that measurements taken over a 12 week period in early lactation (weeks 3 to 14) will, however, give little if any advantage, in terms of the accuracy of selection, over a 6-week measurement taken later in lactation (i.e. in the second, third, or fourth periods) (see Discussion Chapter 6). With early part-lactation measurements (up to week 12) being proposed for selection purposes in nucleus MOET schemes, the results obtained here indicate a need for further research to determine the optimum selection strategy for these schemes.

7.4 Conclusions and Future Research

At present, genetic improvement of dairy cattle depends largely on progeny testing schemes. In such schemes it is clearly impractical and unrealistic to select directly for individual feed intake or efficiency. The results from this study indicate that there is a high correlated response in efficiency when selecting for higher yields. Further improvement in efficiency may, however, be obtained by including liveweight and/or body size traits in the selection criteria.

In recent times increasing attention has been given to MOET nucleus schemes, based on sib testing, as an alternative for genetic improvement of dairy cattle, and some such schemes are already in operation. Given that these schemes will provide the

opportunity to select directly for feed intake and efficiency, it may be worthwhile to include these traits directly in some index on which selection will be based. Results from this study also indicate that intake or efficiency need only be recorded for a short period of lactation.

The results on correlated responses to selection on fat plus protein yield are applicable to high input feeding systems, i.e. high input of concentrate feed. In commercial situations feeding systems are usually based on a lower proportion of concentrate. It is therefore important to check whether these correlated responses are also obtained in low input feeding systems. Results with high and low breeding index cows under extensive management system in New Zealand indicate that this is so (Bryant, 1986). At present investigations are underway at the Edinburgh School of Agriculture's Langhill Dairy Farm to address this question. Preliminary results indicate that under both feeding systems, the animals of high genetic merit are more productive and probably more efficient.

Future research, involving larger number of animals, and with information recorded over longer periods, is required to confirm the genetic relationships obtained here, particularly those among production, efficiency, and liveweight traits. Investigations into the optimum selection strategy for nucleus MOET schemes (which will utilise part lactation records for selection purposes) are also required.

In most studies (including this one) efficiency is defined as some ratio of yield to intake. Genetic improvement of efficiency by direct selection on such ratios should be approached cautiously as the responses in the individual components are usually not known. These will vary depending on the coefficient of variation of the component trait. For example, under restricted feeding where the variation in feed intake is likely to be relatively low, milk yield will have a greater influence in determining efficiency. Direct selection on efficiency may then result in a reduced response in feed intake. Also

breeders are more concerned with increasing profit rather than efficiency and it is not always that higher biological efficiency is associated with higher profitability. In practice, it may therefore be better to select for a trait such as margin over cost which will include both biological and economic considerations.

Research into feed intake and efficiency in dairy cattle is obviously expensive. Similarly, the measurement of feed intake in practical breeding schemes is costly and in many cases impractical (though advances in automated system of intake recording, and growing interest in nucleus breeding schemes may lead to more widespread recording of intake in the future). The surplus of dairy products in many developed/developing countries have, however, resulted in a need for breeding goals in dairy cattle breeding to address both inputs and outputs. Further research in this area is therefore urgently required.

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APPENDIX

**PREDICTING FOOD INTAKE IN DAIRY HEIFERS
FROM EARLY LACTATION RECORDS**

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ABSTRACT

Nucleus breeding schemes for dairy cattle give opportunities for selection on characteristics other than milk production, such as food intake or efficiency, and for the application of reproductive technologies such as embryo transfer. The emphasis in such schemes involving embryo transfer will be on early lactation measurements of production and food intake, to minimise generation intervals. The aim of this study was to examine the value of early lactation measurements of food intake and other characteristics in predicting longer term food intake. Intakes of a complete diet, offered *ad libitum*, were available for 101 heifers up to week 38 of lactation, from the Edinburgh School of Agriculture's Langhill herd. Partial correlations between weekly dry matter or metabolisable energy (ME) intakes in early lactation and cumulated intakes to week 38 of lactation, after fitting year and month of calving as fixed effects, and proportion of Holstein blood as a covariate, ranged from 0.27 for week 1, to 0.70 for week 12. Cumulated ME intakes, up to week 38, were regressed on shorter measures of ME intake, together with fat plus protein yield in weeks 1 to 10 of lactation. Other independent variables, such as point estimates of, or changes in, live weight, condition score and backfat depth did not further increase the precision of prediction. The means and standard deviations for milk yield, dry matter intake and ME intake up to week 38 of lactation were 5877 ± 1087 kg, 4070 ± 400 kg and 51579 ± 4614 MJ respectively. For a fixed duration of intake recording, measurements taken later in lactation gave the most precise prediction of 38 week ME intake (eg. residual s.d.s from models including four-week cumulated ME intakes in weeks 1-4, 3-6 and 5-8 of lactation were 2865, 2636 and 2501 MJ respectively, with R^2 values of 0.62, 0.67 and 0.71). Shorter periods of intake recording started in week 5 of lactation gave slightly more precise prediction than longer periods of recording started in weeks 1-4 (eg. residual s.d.s from models including cumulated ME intakes in weeks 1-10, 3-10 and 5-10 were 2391, 2298 and 2277 respectively, with R^2 values of 0.69, 0.75 and 0.76). These results have implications for the cost:benefit of food intake recording in breeding schemes.

KEYWORDS : Dairy cattle, milk production, food intake, selection.

INTRODUCTION

Food currently accounts proportionally for 0.8-0.9 of the variable costs of dairy production in the UK (Milk Marketing Board, 1990). Despite this, current genetic improvement programmes do not use information on food intake of individual animals. This is largely because improvement is by progeny testing, and the numerous daughters of bulls under evaluation are distributed across many herds, making such measurements both expensive and impractical. While there are a number of reports demonstrating that selection for milk production does increase gross food efficiency (Gibson, 1986; Korver, 1988; Persaud, Simm, Parkinson and Hill, 1990), the direct measurement of food intake and efficiency could still lead to more rapid gains in both efficiency and overall economic merit.

The establishment of nucleus breeding schemes with dairy cattle opens up the possibility of more detailed animal measurement procedures, including the recording of individual food intake (Hinks, 1978). By the use of multiple ovulation and embryo transfer (MOET), breeding programmes based on a herd of several hundred cows are predicted to give rates of genetic improvement in milk production which are comparable to those achieved by large scale progeny testing schemes (Woolliams and Smith, 1988; Ruane and Thompson, 1989), while also offering possibilities for greater operational control and more comprehensive assessment. In the UK Genus (formerly the Farm Services Division of the Milk Marketing Board of England and Wales (MMB)) are currently developing the MOET scheme established by Premier Breeders (McGuirk, 1990), within which they will record individual food intakes.

While it is now possible to record food intake automatically (Forbes, Jackson, Johnson, Stockhill and Hoyle, 1986) the facilities are expensive to install and operate. It is clearly beneficial if maximum numbers of animals are recorded through such facilities. This can be achieved by measuring all animals for a short time period, provided that it can be shown that these measurements are highly correlated with whole lactation records. This approach fits in well with the MOET concept, where measurements will be concentrated in early lactation, to minimise generation intervals. While there is good evidence that early lactation milk production records are well-correlated with whole lactation performance (Wilmink, 1987), there is very little information on this point for food intake and efficiency.

The analyses reported here were designed to:

- (i) examine the relationship between food intake in early lactation of heifers, and that over longer periods up to 38 weeks of lactation;
- (ii) examine the additional value of including other early lactation measurements in heifers, such as milk and milk constituent yields, live weight, condition score and ultrasonically measured backfat depth, in addition to early lactation food intake measurements, as predictors of food intake and efficiency over longer periods.

Simple regression analyses were undertaken to calculate phenotypic correlations between traits for inclusion in possible future selection indices. Multiple regression analyses were undertaken to examine, at the phenotypic level, the relative value of various early lactation measurements in predicting longer term food intake and efficiency, and for cases where selection is based on predicted efficiency (or food intake) alone. The size of this data set, for heifers, did not warrant genetic analysis. A subsequent paper reports on genetic relationships between part and whole lactation food intake for a larger number of animals of mixed parities (Persaud and Simm, 1990).

While other authors have examined part-whole lactation food intake or efficiency (Hooven, Miller and Smith, 1972; Gibson, 1987), the data from the Langhill herd used in this study are particularly suited to this purpose because of the high genetic merit of the animals involved (the herd currently has the highest average heifer Cow Genetic Index (CGI) in the UK) and the fact that the cows were offered a high quality complete diet *ad libitum*.

MATERIAL AND METHODS

Since 1973 a long-term dairy cattle breeding experiment has been in progress at the Edinburgh School of Agriculture's Langhill dairy farm (Simm and Neilson, 1986). The original aim of the work was to show that bull transmitting abilities, estimated from dairy progeny testing schemes, were a reliable guide to daughter performance. This was initially done within a single herd of high average genetic merit, the selection line, until 1976 when a control line was also established. Older cows in the herd were allocated to the control line, and bred at random using semen from a panel of 50 bulls which entered MMB or Scottish Milk Marketing Board (SMMB) progeny tests in 1976. The selection herd has numbered about 160 cows, whilst the control herd was built up to about 30 cows by 1985. The proven pedigree Holstein-Friesian bulls used in the experiment have been selected on their Improved Contemporary Comparison (ICC) for kg fat plus kg protein. While bulls used in the early years were predominantly British Friesian, over the past 10 years an increasing number of Canadian Holstein bulls have been used. These were selected on the basis of their progeny test results for kg fat plus kg protein either in Canada or the UK. Since 1978 both selection and control cows at Langhill have been fed, during the housed period, on a high quality complete diet, based on silage, draff and concentrates, offered ad libitum.

Animals and Management

Proportionally, about 0.9 of the herd at Langhill calves between late August and January. During the winter feeding period cows are loose-housed in a cubicle shed, in 4 groups according to date of calving. From 1979 onwards individual feeding gates (Calan-Broadbent electronic gates) were used to record intakes in 40 to 86 of the earlier calving cows per year.

From 1983 onwards the cows were fed through the individual feeding gates indoors until July so that food intake was recorded for at least 38 weeks for most cows. This study is based on data from 101 heifers calving between late August and early December in 1983-1987. Six to eight weeks prior to calving, the heifers were trained to use the individual feeding gates. They were reintroduced to the yards with gates within a week of calving.

Milk Yield and Fat and Protein Concentrations

Cows were milked twice daily at 05.00 and 15.00 hours. 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 when they were measured weekly. Samples of milk were collected from the Tuesday afternoon and the Wednesday morning milkings. The analyses were done up to 1986 by the Central Testing Laboratory, SMMB and subsequently at the West of Scotland College. Proportionate bulk samples from am and pm samples were analysed at SMMB; analyses at the West of Scotland College were on separate am and pm samples weighted for production.

Food Intake and Food Analysis

The cows were offered a complete diet containing grass silage, wet brewers grains (draff) and a compound balancer meal. Sugar-beet pulp was also included in the ration in some years. The compound balancer meal was formulated on a least-cost basis to contain approximately 13 MJ of ME per kg dry matter, 180 g/kg crude protein (CP; 0.6 estimated degradability), together with minerals and vitamins according to ARC (1980) recommendations. The ratio of silage to concentrate in the mix was varied according to the silage quality so that the complete diet reached target ME concentrations of 11.8-12.0, 11.4-11.6 and 11.0-11.2 MJ/kg DM in early, mid and late lactation respectively. The diet formulation was changed for all animals in a group when the group reached an average of about 100 days of lactation and about 200 days of lactation (with a range of about \pm 30 days for individual cows). Usually concentrate:silage dry matter ratios in the complete diet were around 50:50 for early, 35:65 for mid, and 25:75 for late lactation rations.

The complete diet was dispensed into individual food bins once daily, with an allowance for refusals of 50-100 g/kg above mean daily intake in the previous week. The weight of fresh diet offered and refused was recorded on 4 consecutive days (Monday to Thursday) each week, to the nearest 0.1kg.

Mean daily dry matter intakes for each week of the study were calculated from the dry matter analyses on the food offered and the refusals.

In addition to the complete diet, a fixed amount of concentrate was fed in the parlour to encourage entry of the cows (0.4 or 0.8 kg per milking in different years).

Live Weight and Condition Score

Live weight and condition score were recorded in the 48 hours following calving and weekly thereafter at the same time of day. To reduce variation due to gut fill, 3-week rolling average live weights (mean of the weight in the current week and those in the preceding and succeeding weeks) were calculated for all live weight records, except that at calving.

Ultrasonic Backfat Measurements

From 1984 onwards backfat depth was measured in the lumbar region immediately post-calving, and at 6-week intervals thereafter with a Vetscan real-time 'B' mode ultrasonic scanner.

Missing Data

Food intake data were available for most animals up to week 38 of lactation. A small number of animals had no data available for the first or last week or two of the recording period. This was because the intake recording was not started until at least 4 or 5 animals had calved each year, and some late calving animals were turned out to grass before week 38 of lactation. Also, a small number of animals had missing food intake or milk yield data in other weeks of the recording period, due to temporary removal from the trial due to illness.

The data were also scanned for possibly aberrant values. Plots of weekly dry matter intakes and milk yields were examined for each cow. Milk yield or food intake records which were more than 2 to 3 standard deviations from their expected values, based on values in the preceding and succeeding weeks, were discarded unless they corresponded to weeks when diet quality was unusually low. Some subjective interpretation was used in deciding which threshold to use for discarding records, depending on the pattern of intake or yield for the individual cow. Proportionally about 0.025 of weekly dry matter intake and milk yields were missing, and proportionally a further 0.005 were discarded. Records that were either missing or discarded were predicted as follows:

Prediction of Dry Matter Intake. After examining a number of options, missing dry matter intakes were predicted by fitting a cubic regression:

$$Y = A + B(WK) + C(WK)^2 + D(WK)^3$$

where Y = missing dry matter intake

WK = week number of missing record

A,B,C,D = constants obtained from fitting cubic regressions to all available data for the individual cow.

Prediction of Milk Yield. Missing records between weeks 1-12 were predicted by fitting a quadratic equation, otherwise as above, to the available data for the first 15 weeks of the lactation in which the record was missing.

Records missing in the later part of lactation (ie after week number 12) were predicted by dividing the data from week 12 onwards into 10-week periods (12-22, 20-30, 28-38) and fitting a linear regression to each 10-week period for each part of a lactation where a record was missing.

Prediction of Fat and Protein Concentrations. As fat and protein concentrations varied greatly from week to week for individual animals, missing values were predicted using the overall mean for the individual animal, together with a 'standard' curve of concentration against week of lactation derived from the full data set.

Prediction of Live Weight and Condition Score. Because of the small number of missing records, and the small variation in live weight (after "rolling") and condition score from week to week, missing values were predicted as the mean of the two values in the weeks before and after the missing value.

Derived Variables

Several variables were derived from the basic input and output records, as follows:

Fat and Protein Yields. These were derived as the product of fat or protein concentrations and milk yield in the corresponding week. Fat and protein yields were then accumulated over weeks. In years where fat and protein concentrations were not available each week, cumulated fat and protein yields were scaled up accordingly.

Milk Energy Yield. Milk energy concentration was calculated from the fat and protein concentrations using the equation derived by Tyrrell and Reid (1965) converted to MJ per kg:

$$E = 0.376F + 0.209P + 0.948$$

where E = gross energy concentration of milk (MJ/kg), F = fat concentration (g/kg), and P = protein concentration (g/kg).

Milk energy yields (MKE) were calculated as the product of milk yield and milk energy concentration in the corresponding week, and accumulated and scaled up as described above.

Metabolisable Energy Intake. Metabolisable energy (ME) content of the complete diet was estimated weekly in each year up to 1986, and monthly in 1987. In some years food was not analysed in the later part of the trial, so the mean ME content for the last five weeks in that particular year was used.

In addition to the complete diet, concentrates were fed in the parlour during milking. Up to 1986 these were fed at a rate of 0.8kg (fresh weight) per milking. The parlour concentrate had an average DM content of 870g/kg, an ME of 13 MJ/kg DM, and a CP of 200 g/kg. Thus about 18.1 MJ of ME was obtained from the parlour concentrates each day. In 1987/88 malt culms were fed at a rate of 0.4kg per milking except in calendar weeks 1,2,3 and 12 of the trial when nothing was fed in the parlour. The ME and CP of the malt culms varied from month to month. Average weekly ME intakes for each cow were calculated from the dry matter intakes and energy values of both the complete diet and parlour concentrates.

Gross Energetic Efficiency. In this study gross energetic efficiency (EFF) is defined as the energy in milk (MKE in MJ, derived as above) produced per unit of feed energy consumed (ME in MJ, derived as above). Cumulative efficiency was calculated as the sum of milk energy yield in the relevant period, divided by the sum of ME intake in the same period. .

Statistical Methods

Distributions of Data. Histograms of all variables were examined. All distributions were normal apart from those for backfat depth at calving, and age at calving, which were slightly skew. As both of these effects appeared unimportant in subsequent analyses, transformation was not considered.

Regression analyses. Regression analyses were undertaken using the Genstat 5 computer program (release 1.3; Lawes Agricultural Trust, 1988).

Dependent Variables. The main dependent variables considered in this study were:

- (i) cumulative dry matter intake of the complete diet from weeks 1-38 of lactation (DM 138);
- (ii) cumulative total ME intake (from the complete diet and parlour concentrates) from weeks 1-38 of lactation (ME 138);
- (iii) cumulative gross energetic efficiency from weeks 1-38 of lactation (EFF 138).

Independent Variables. Dry matter and ME intakes were cumulated from weeks 1, 3 or 5 of lactation up to weeks 4, 6, 8, 10 or 12 of lactation. Individual weekly intakes, or intakes cumulated over the periods above, were used in regression analyses to derive partial correlations (see below). Cumulated intakes, together with early lactation measures of milk production, live weight, condition score and backfat (see Table 1) were used in multiple regression analyses. In multiple regression, all combinations of independent variables were examined, except that only a single cumulative dry matter or ME intake and only a single cumulative milk, fat plus protein, or milk energy yield was fitted per model. These variables are referred to hereafter in the abbreviated form shown in Table 1.

Fixed Effects and Covariates. The following fixed effects were examined in regression analyses:

- (i) Year of calving (1983-1987);
- (ii) Month of calving (September, October, November);
- (iii) Genetic line (selection and control).

Four late-August calving heifers were grouped with September calvers, and six early-December calvers were grouped with November calvers. Fifteen of the 101 heifers were control animals.

The following covariates were examined in analyses:

- (iv) Age at calving, in months;
- (v) Sire ICC for kg fat plus protein;
- (vi) Heifer proportion of Holstein blood.

These last two effects were fitted, together or individually, as an alternative to genetic line.

Partial Correlations between Early Lactation ME Intakes and Cumulated ME Intake in Weeks 1 to 38. If

selection is to be on an index including food intake in its own right, rather than directly on efficiency then the correlations between various potential index measurements are of interest. The fixed effects and covariate used in this study may be considered 'artefacts' of this particular data set. Selection in nucleus herds is likely to be amongst heifers calving over a relatively short time period, within one year, and with a relatively homogeneous genetic background. The relevant correlations for use in selection index calculations are therefore the partial correlations amongst variables, after adjusting for significant fixed effects and covariates.

These partial correlations were calculated as:

$$r = \sqrt{1 - (\text{rms}_y / \text{rms}_x)}$$

where r = partial correlation between x and y
 rms_y = residual mean square in x, after fitting fixed effects, covariates and y.
 rms_x = residual mean square in x, after fitting fixed effects and covariates alone.

Significance of Effects in the Models. Regression equations were fitted, with all of the fixed effects and covariates included, (eg. (i), (ii), (iii) and (iv), or (i), (ii), (iv), (v) and (vi)). The significance of all effects fitted was examined and effects were removed in a stepwise manner if the coefficients were not significantly different from zero ($P < 0.05$). Fixed effects and covariates were removed first, in descending order of probability, and then, in multiple regressions, independent variables were removed until all effects left were significant in most models.

TABLE 1 NEAR HERE

RESULTS

Patterns of Food Intake, Milk Yield and Live Weight Change

Figure 1 shows patterns of total ME intake up to 38 weeks of lactation. Mean weekly dry matter intakes showed a very similar pattern. Peak ME intake was reached around week 12-14 of lactation. The reduction in intake between weeks 14 and 16 corresponded to the first reduction in ME concentration of the complete diet. The second reduction in energy concentration of the diet had a less obvious effect on intake.

Figure 2 shows the pattern of milk yield for the heifers. Peak yields were attained at around weeks 7-9 of lactation.

Figures 3 and 4 show patterns of fat and protein yields. There was quite large variation from week to week in both fat and protein yields. This was partly a consequence of fortnightly milk analysis, in all years except 1987 (when milk was analysed weekly). Fortnightly sampling means that adjacent points on the graph represent different cows. However, there was also a large amount of variation between successive milk analyses for individual cows.

Patterns of live weight change are shown in Figure 5. Heifers lost about 10kg live weight, on average, in the first 2 weeks of lactation. They remained at a fairly constant live weight during weeks 2-5, and then gained weight steadily throughout lactation. On average, heifers gained about 90kg live weight over the 38-week recording period.

FIGURES 1 TO 5 HERE

Means and Standard Deviations of the Main Variables

Table 2 shows the means and standard deviations of the main variables. The coefficients of variation (CV) for dry matter and ME intakes were approximately 0.12 in the first few weeks of lactation and declined to around 0.09 over longer periods of recording. The CV of efficiency was around 0.13-0.14.

Although heifers gained live weight over the first 10 weeks of lactation, their condition scores fell over the

same period. This increase of about 10kg of live weight is probably explained by increased gutfill, since mean daily dry matter intakes increased by about 5kg over the same period of lactation.

There was quite a wide variation in sire ICC as a consequence of the two genetic lines, and the increasing genetic merit of selection line sires over the period of this study.

TABLE 2 NEAR HERE

Selection of Statistical Models.

Differences between genetic lines were small and non-significant. Fitting Holstein proportion significantly increased the proportion of variation accounted for in most models predicting DM138 or ME138, but not in EFF138. Fitting sire ICC together with Holstein proportion did not significantly improve the proportion of variation accounted for in dependent variables. Therefore Holstein proportion was fitted alone in all models predicting dry matter or energy intake.

In contrast to other studies, age at calving did not have a significant effect in any models fitted in this study, and was dropped. This may be explained by the relatively small variation in age at calving in this study.

Neither condition score at calving, nor condition score change up to weeks 10 or 12 of lactation, had a significant effect in the models fitted. Similarly, both backfat depth at calving, and change in backfat depth, were non-significant.

Live weight at calving, and live weight change in the first 10 or 12 weeks of lactation, did not significantly improve prediction of dry matter or ME intakes. Live weight at calving was consistently significant in prediction equations for gross efficiency and was retained in all such models. Live weight change did not significantly improve prediction of efficiency up to week 38, and so was dropped from all models.

Thus the reduced models chosen for prediction were:

$$\begin{aligned}
 \text{DM138} &= u + Y + M + H (+ b_1MY_x) + b_2DM_x + e \\
 \text{ME138} &= u + Y + M + H (+ b_1MY_x) + b_2ME_x + e \\
 \text{EFF138} &= u + Y + M (+ b_1MY_x) + b_2LWC + b_3ME_x + e
 \end{aligned}$$

where:	u	=	overall mean
	Y	=	fixed effect of year
	M	=	fixed effect of month of calving
	H	=	covariate for Holstein proportion
	MY	=	cumulative milk yield (or FP or MKE yield) over various periods (dropped from some models).
	DM	=	cumulative dry matter intake over various periods
	ME	=	cumulative ME intake over various periods
	LWC	=	live weight at calving
	x	=	period of intake or milk yield recording
	e	=	error term, assumed random.

Plots of residuals against fitted values appeared randomly distributed, and trial runs with quadratic terms in DM or MY showed no evidence of a curvilinear relationship between dependent and independent variables.

Partial Correlation Coefficients

As results for ME and DM intakes were virtually identical only those for ME intake are presented. Table 3 shows the partial correlations between ME intakes in individual weeks of lactation, and cumulative ME intakes to 38 weeks. Correlations increase quite markedly over the first 6 weeks of lactation, and continue to increase gradually up to week 12 (the last individual week examined).

Table 4 shows partial correlations between cumulative intakes and yields in early lactation and intake to 38 weeks. The main point of interest from this table is that correlations involving cumulative ME intake from week 1 are similar to those based on cumulative ME intakes starting in weeks 3 or 5 of lactation (eg ME16 vs. ME36 and ME56). In other words, intake measurements starting after the first 4 weeks of lactation appear to be as

strongly related to longer periods of intake as measurements starting in week 1, even though the total period recorded is shorter.

TABLES 3 AND 4 NEAR HERE

Relative Precision of Different Models for Predicting Cumulative Intake and Efficiency.

Table 5 shows the means and standard deviations of the dependent variables, together with residual standard deviations after fitting year and month of calving and Holstein proportion (for DM and ME only). These effects account for about 0.37 of the variance in dry matter or ME intake, but none of the variance in efficiency.

Figure 6 shows the residual standard deviations in ME intake up to week 38 of lactation, after fitting year and month as fixed effects and Holstein proportion, together with fat plus protein yield and ME intake in different periods. Figure 7 shows residual standard deviations in efficiency to week 38 after fitting similar models except that Holstein proportion was excluded, and liveweight at calving was included as an independent variable. The graphs show the effect of progressively increasing the period of intake recording from 2-12 weeks duration. The graphs also show the effect of starting intake recording at weeks 1,3 or 5 of lactation for a given duration of recording.

In all models including intake records up to week 12 of lactation, it is assumed that milk or fat plus protein records up to week 12 are also used. However, when intake records up to week 10 or less are used, milk or fat plus protein yield from weeks 1-10 are included in the model. The rationale behind this is that recording up to week 12 may leave insufficient time for selection of donor heifers in MOET schemes. However, even if intake is recorded for less than 10 weeks on cost grounds, milk or fat plus protein yields up to week 10 can be recorded relatively cheaply and will improve the precision of prediction of ME intake or efficiency.

The main points of interest from Figures 6 and 7 are:

- (i) For a fixed duration of intake recording, the precision of predicting ME₁₃₈ increases the later the

starting point for recording. That is, a 4-week period of intake recording commencing at week 5 of lactation is better than a 4-week period starting at week 3, which in turn is better than a 4-week period starting in the first week of lactation. This result is expected, based on the individual weekly correlation coefficients shown in Table 3.

- (ii) Shorter periods of intake recording may give higher precision of predicting ME138 than longer periods, depending on the starting point for recording. For example, a 4-week period of intake recording from week 5 gives a slightly higher precision of predicting ME138 than a 6-week period of intake recording from week 3, or an 8-week period from week 1 (see Figure 6).
- (iii) Of the models compared, the highest precision of predicting ME138 was achieved with an 8-week period of intake recording from week 5 (ME512).
- (iv) In contrast to the results for predicting ME138, the duration of intake recording, and the starting point for recording, had little effect on the precision of predicting EFF138. The apparent improvement from fitting ME112, ME312 or ME512 (see Figure 7) is, in fact, due to the inclusion of FP112 in these models instead of FP110 which was included in all others. The precision achieved from fitting ME112, ME312 or ME512, together with FP110 and LWC, is shown in Figure 7 by the separate points above the 3 joined lines.

TABLES 5 AND 6, FIGURES 6-8 NEAR HERE

Table 6 shows the significance of independent variables in models likely to be chosen for predicting ME138 or EFF138. This table shows that early lactation ME measurements are more important than FP measurements in predicting ME138. Conversely, early lactation FP yields and live weight at calving are more important than ME measurements in predicting EFF138 (although in all models, all effects significantly improve the precision of predicting ME138 or EFF138).

To examine the relative contribution of early lactation ME intakes and FP yields to prediction of ME 138

further, the series of models used to derive the results shown in Figure 6 was rerun after dropping fat plus protein yields. The results are shown in Figure 8.

The proportions of variance accounted for by models with ME as the only independent variable were 0.05-0.10 lower than those in equivalent models including both ME and fat plus protein yields. The drop in precision as a result of omitting FP measurements was greater, the shorter the period of intake measurement included in the model. Otherwise, the results concerning the starting point and duration of intake recording were as for those reported for models including fat plus protein yield, although the advantage to shorter periods of intake recording was slightly lower than that shown in Figure 6.

Summing intakes over the 6 fortnightly periods assumes that each fortnightly intake is equally important in predicting ME138. The simple correlations in Table 4 suggest that this is not so - intakes in early lactation are less strongly correlated with ME138 than those in later lactation. In theory, a model fitting the six fortnightly cumulative intakes as independent variables may give greater precision. In this case the regression coefficients are expected to reflect the increasing contribution of later intake measurements in predicting ME138.

To check this, a model including all six successive 'fortnightly periods' of ME intake was fitted, together with the fixed effects included in previous models. Although there was some evidence that the regression coefficients for later 'fortnightly periods' of intake were significantly higher than those for early 'fortnightly periods' of intake, the residual standard deviation in ME138 was only slightly lower than that from models including the sum of ME intakes from weeks 1 to 12 or the sum of ME intakes over shorter periods.

DISCUSSION

The main aim of the study was to examine the association between short-term food intake measurements made early in lactation, and 38 week totals for intake and efficiency. The partial correlations reported will be useful, along with assumed or published estimates of genetic parameters, in constructing and comparing selection indices for potential use in MOET nucleus breeding schemes. Partial correlations between individual weekly ME intakes and intake up to week 38 were low to moderate in the first few weeks of lactation, but increased progressively up to 0.70 for week 12 of lactation. Cumulating intakes over longer periods between weeks 3 and 12 of lactation resulted in slightly higher correlations with ME intake to week 38.

The multiple regression analyses reported give a more general view, at the phenotypic level, of the relative value of various early lactation measurements in predicting longer term ME intake and efficiency. The results may be of value in schemes where selection is based directly on predicted efficiency or intake, but also in choosing potential index measurements for schemes based on index selection.

In all cases, early lactation measurements of ME intake and milk solids yield significantly improved the precision of prediction of longer term ME intake and efficiency. A number of liveweight, condition score and backfat measurements were also examined to see if their inclusion improved the precision of the prediction equations. However, of these, only live weight at calving significantly improved the precision of prediction (and then for EFF only). The heifers involved in this study had a fairly constant live weight in weeks 2-5 of lactation, on average, and then gained weight up to week 38 of lactation. Also, the loss in condition score in early lactation was small compared to that often reported in older cows. Thus the lack of significance of most measures of cow "state" or "state change" reported here may not apply in the case of animals showing more dramatic state changes or in cases where animals of different parities are being compared. Crawford (1987) illustrated the differences in state change between cows from the Langhill herd in successive lactations.

The main conclusions from this study concern the timing and duration of intake recording. For a fixed duration of intake recording, the later the measurements are taken the higher the precision of predicting ME

intake over 38 weeks. Also, shorter periods of intake recording started in week 5 of lactation may give slightly higher precision of predicting ME138 than longer periods started earlier in lactation. Clearly this has major implications for the cost:benefit of food intake recording.

Gibson (1987) has reported the results of a similar study with both British Friesian and Jersey first and second lactation cows which were involved in a breed comparison and selection experiment (Gibson, 1986). The cows in that study were fed a complete diet to 44 weeks of lactation. While food intakes were similar to those reported here, average yields were only 3457 and 2230 kg for the first lactation and 3805 and 2409 kg for the second lactation (Gibson, 1986). The rather low levels of performance of these animals are probably due to the food offered which, as Gibson (1987) says, is not a typical dairy diet. Both protein and energy concentrations were considerably below those for the complete diet offered here (averages of 137 g CP/kg DM and 9.97 MJ ME/kg DM compared to 160-190 g CP/kg DM and 11.3 to 11.7 MJ ME in the present study). Despite these differences the results are rather similar.

Gibson examined several periods of food conversion efficiency as independent variables based on 2, 4 or 8 weeks cumulated food intake at various starting points throughout lactation. He concluded that, for a given duration of intake recording, measurements taken at mid-, or just after mid-lactation gave the most precise prediction of whole lactation intake. Part lactation records here were restricted to the first 12 weeks of lactation. However, up to this point the trend towards higher precision of predicting 38 week ME intake from later part-lactation records of ME intake were as reported by Gibson. This trend was not apparent in predicting efficiency in the present study because of the greater importance of fat and protein yield, rather than food intake, as an independent variable.

The precision of prediction reported by Gibson (1987) was slightly lower than that achieved here, although efficiency was only measured over 38 weeks in this study, compared with 44 weeks in Gibson's. He reported residual coefficients of variation in total lactation efficiency for Friesians of 0.115 to 0.173 from 1 week's yield divided by 2 weeks' cumulated intake, 0.09 to 0.153 from 4 weeks intake yield divided by 4 weeks' intake and 0.078 to 0.153 from 8 weeks' yield divided by 8 weeks' intake. In each case residual variances were calculated after adjusting for fixed effects such as animal type (breed and origin) and lactation number.

Equivalent figures for residual coefficients of variation in 38 week efficiency from the present study are about 0.07.

These results indicate that the decision on duration of intake recording will depend on the selection criterion chosen for donor heifers. If heifers are selected directly on predicted efficiency, short periods of intake measurement will suffice. If heifers are to be selected on an index including cumulative food or ME intake, as traits in the selection goal, then longer periods of intake measurement would be desirable.

This study was based on phenotypic relationships between part and 'whole' lactation intakes in heifers. The Langhill project will generate sufficient data to provide more reliable estimates of genetic parameters for intake and efficiency, on which little is currently known. In addition, data on intake and efficiency in later lactations is being accumulated. Only when this information is available will it be possible to fully assess the benefits of including direct measurements of intake and efficiency in dairy improvement schemes.

ACKNOWLEDGEMENTS

This study was financed by the Milk Marketing Board of England and Wales. We are grateful to Dr R Thompson for his statistical advice. We are grateful to Dr M Lewis for ration formulations, to Mr L S Hodgson-Jones, Mr J Mills and colleagues for managing the animals. We are also grateful to Avoncroft Cattle Breeders Ltd, Black and White Sires Ltd, the Holstein Friesian Society of Great Britain and Ireland, the MMB, Progressive Holstein Breeders, the SMMB and Semex (UK Sales) Ltd for their support for the Langhill Dairy Cattle Breeding Project.

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TABLE 1

Independent variables used in analyses, in addition to dry matter and ME intakes.

Record	Period of cumulation (weeks of lactation)	Abbreviation
Milk Yield (kg)	1-12	MY112
	1-10	MY110
	3-12	MY312
	3-10	MY310
Fat plus protein yield (kg)	1-12	FP112
	1-10	FP110
	3-12	FP312
	3-10	FP310
Milk energy yield (MJ)	1-12	MKE112
	1-10	MKE110
	3-12	MKE312
	3-10	MKE310
Live weight at calving (kg)	--	LWC
Live weight change (kg)	1-12	LW112
	1-10	LW110
Condition score at calving	--	CSC
Condition score change	1-12	CS112
	1-10	CS110
Backfat at calving (mm)	--	BFC
Backfat change (mm)	1-12	BF112
	1-10	BF110

TABLE 2

Means and standard deviations of the main intake and yield variables for the two data sets.

Number of animals Variable	mean	101	sd
DM14 (kg)	385		45
DM16	605		61
DM18	833		78
DM110	1066		98
DM112	1301		119
DM138	4070		400
ME14 (MJ)	4966		528
ME16	7779		715
ME18	10693		916
ME110	13656		1141
ME112	16637		1391
ME138	51579		4614
MY110 (kg)	1661		323
MY112	2006		389
MY138	5877		1087
EFF138	0.375		0.050
LW calving (kg)	533		41
LW change 110 (kg)	14		33
CS calving	2.72		0.13
CS change 110	-0.08		0.17
Sire ICC fat + protein (kg)	24.7		16.8
Proportion Holstein blood	42.8		18.7

TABLE 3

Partial correlations between ME intake in weeks 1-12 of lactation and cumulative ME intake from weeks 1-38.

ME intake in week	Partial correlation with ME138 [†]
1	0.27
2	0.33
3	0.46
4	0.49
5	0.45
6	0.52
7	0.61
8	0.59
9	0.53
10	0.64
11	0.63
12	0.70

[†] After fitting year, month of calving and proportion Holstein

TABLE 4

Partial correlations amongst early lactation and 38 week milk production and ME intakes

	FP138	FP110	ME138	ME312	ME310	ME38	ME36	ME512	ME510	ME58	LWC
FP138	1.00										
FP110	0.88	1.00									
ME138	0.62	0.54	1.00								
ME312	0.44	0.36	0.76	1.00							
ME310	0.41	0.35	0.72	0.98	1.00						
ME38	0.42	0.40	0.67	0.94	0.97	1.00					
ME36	0.36	0.37	0.61	0.86	0.90	0.96	1.00				
ME512	0.43	0.32	0.76	0.98	0.95	0.87	0.77	1.00			
ME510	0.38	0.29	0.70	0.95	0.97	0.90	0.79	0.97	1.00		
ME58	0.40	0.35	0.65	0.91	0.94	0.95	0.87	0.91	0.95	1.00	
LWC	0.11	0.29	0.33	0.32	0.35	0.35	0.33	0.27	0.29	0.27	1.00

+ After fitting year, month of calving and proportion Holstein

TABLE 5

Means and standard deviations of dependent variables, together with residual standard deviations after fitting year, and month of calving (and proportion Holstein for DM and ME only).

	Mean	sd	rsd	R ²
DM138 (kg)	4070	400	318	37.1
ME138 (MJ)	51579	4614	3658	37.2
EFF138	0.375	0.050	0.050	0.0

TABLE 6

Significance of independent variables in models predicting ME138 and EFF138.

Dependent variable:	ME138	EFF138
Independent variables	t value	
FP112	5.16	-
ME512	10.33	-
FP112	-	17.20
ME512	-	2.99
LWC	-	4.21
FP110	5.42	-
ME510	8.77	-
FP110	-	15.04
ME510	-	2.19
LWC	-	3.83
FP110	4.77	-
ME310	8.59	-
FP110	-	15.08
ME310	-	2.39
LWC	-	3.62
FP110	4.21	-
ME38	6.92	-
FP110	-	14.88
ME38	-	2.31
LWC	-	3.67

Figure 1: Mean daily ME intake by week of lactation.

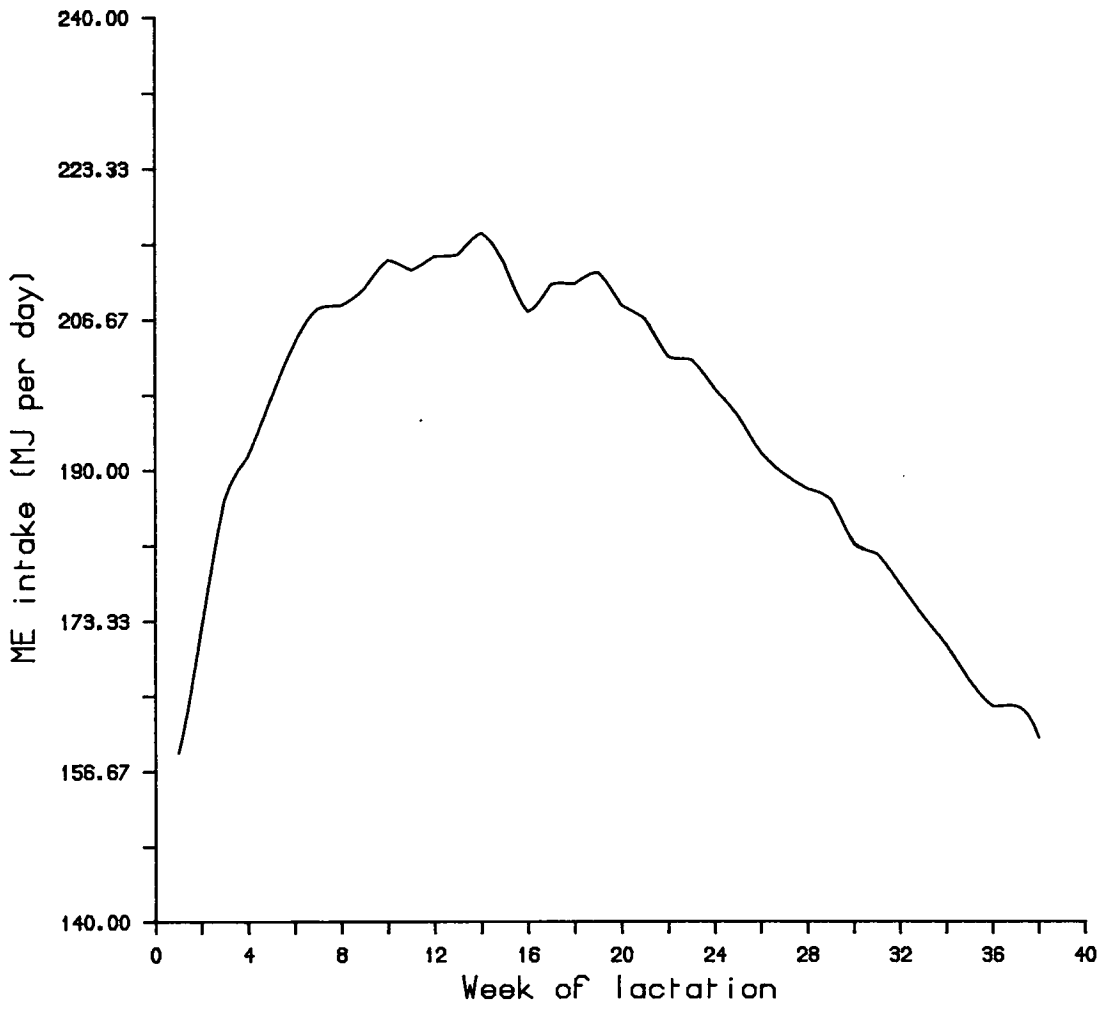


Figure 2: Pattern of milk yield by week of lactation.

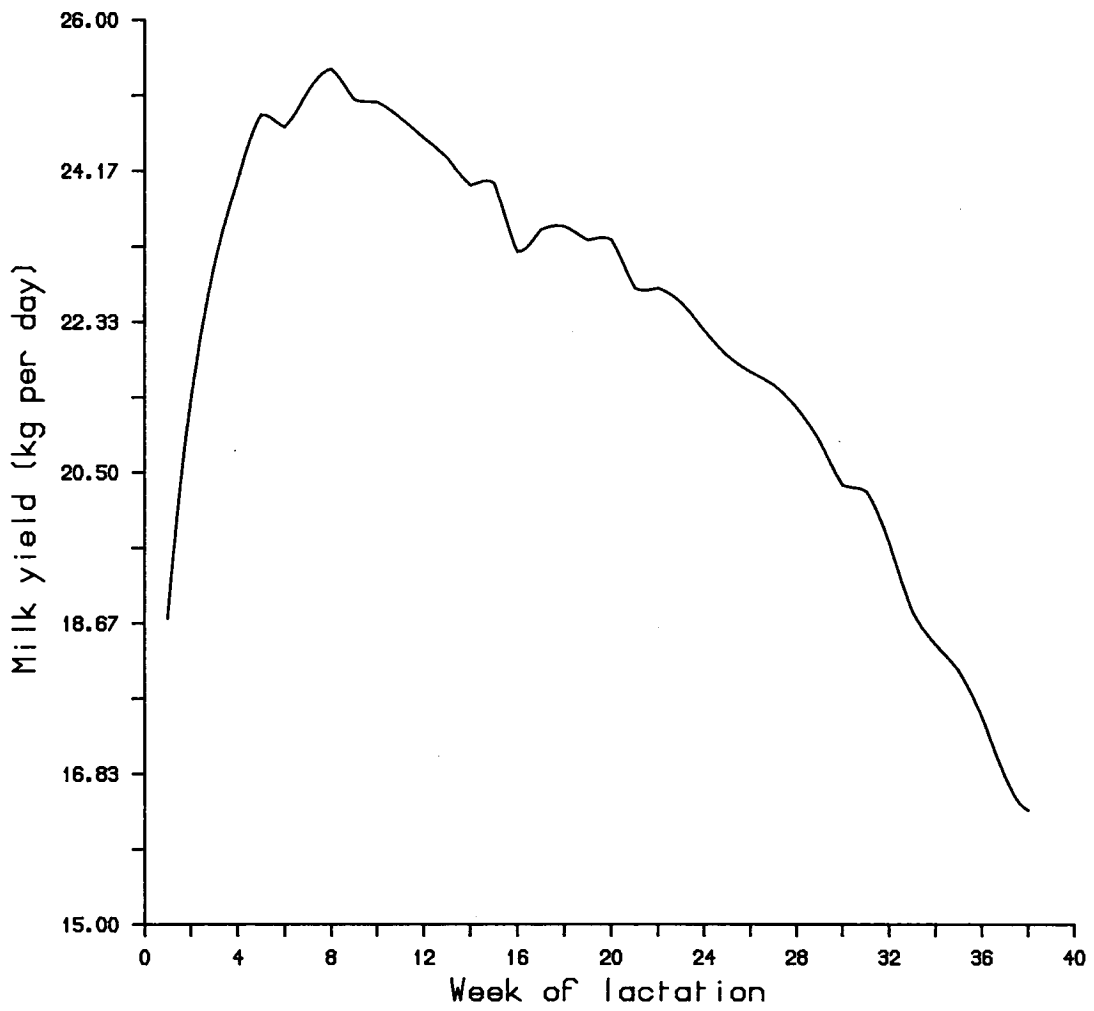


Figure 3: Mean daily fat yield by week of lactation.

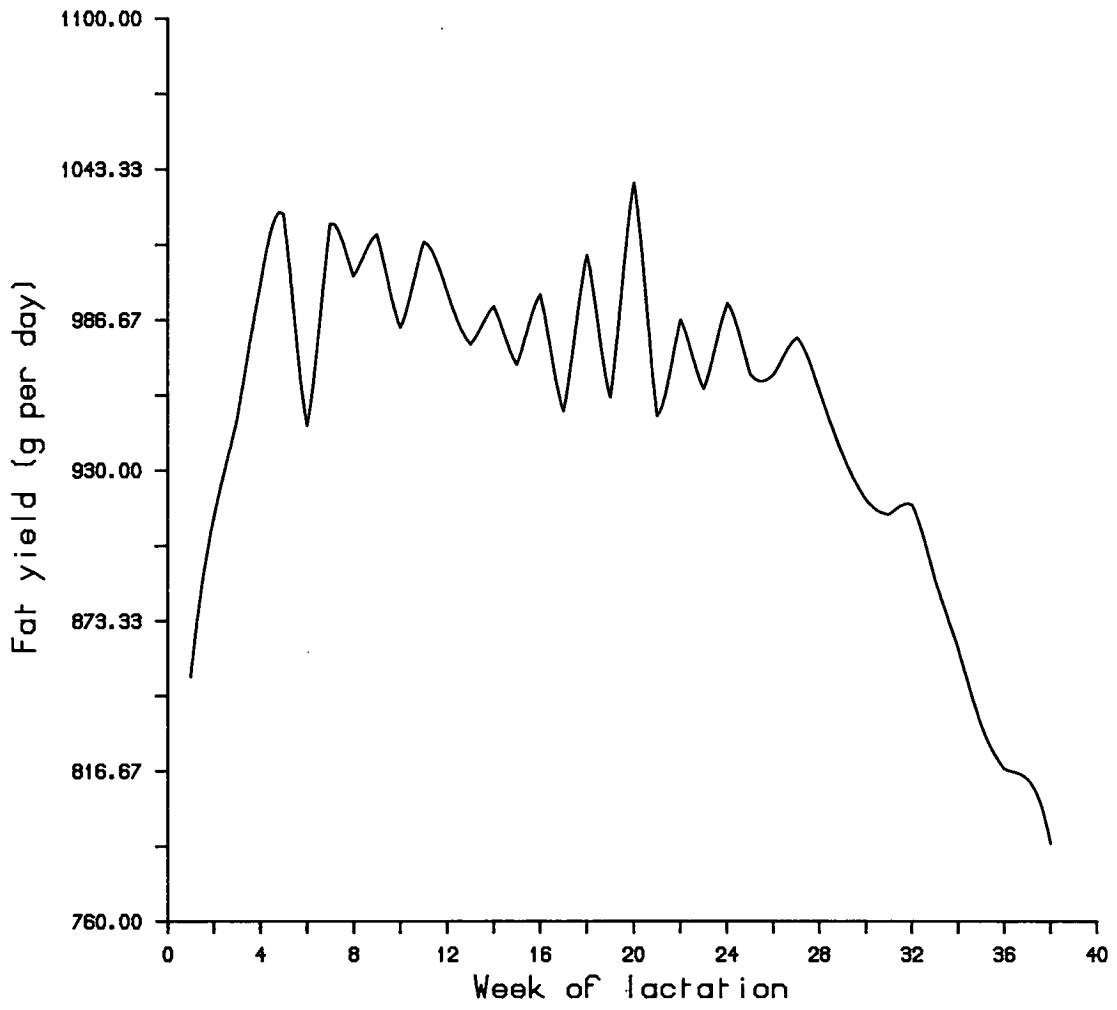


Figure 4: Mean daily protein yield by week of lactation.

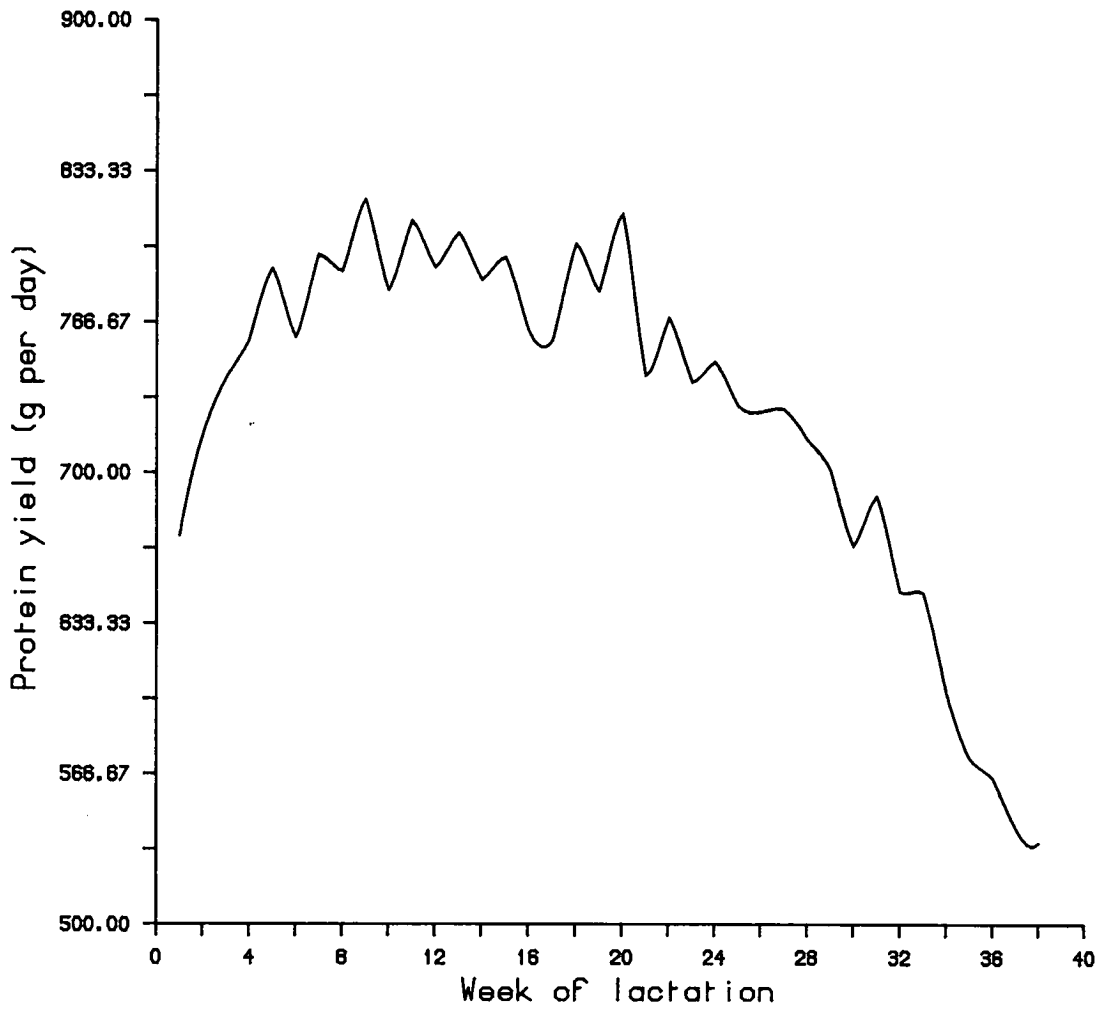


Figure 5: Mean live weight by week of lactation.

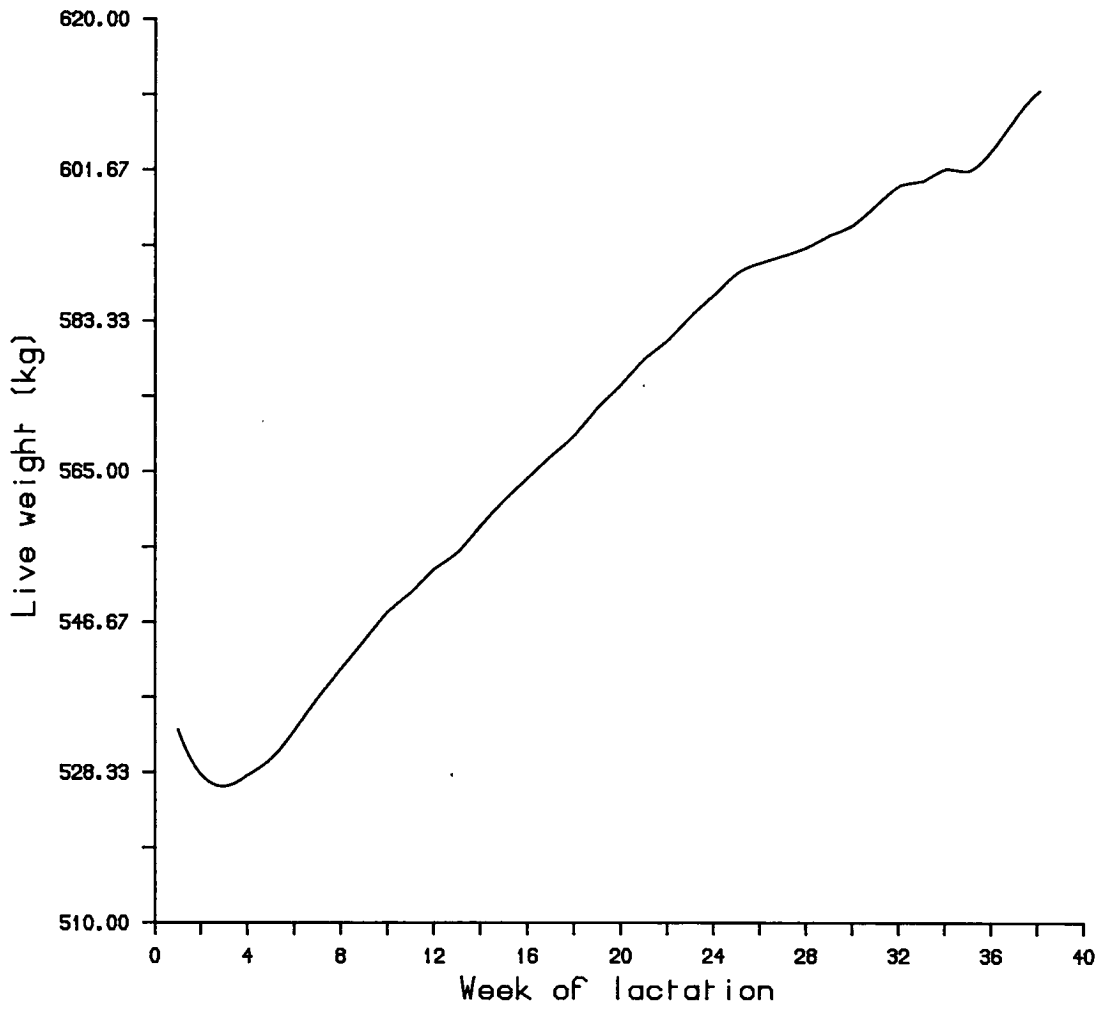


Figure 6: Residual standard deviation in cumulated ME intake to week 38, after fitting year, month, Holstein proportion, FP112 or FP110 and ME intake over different periods.

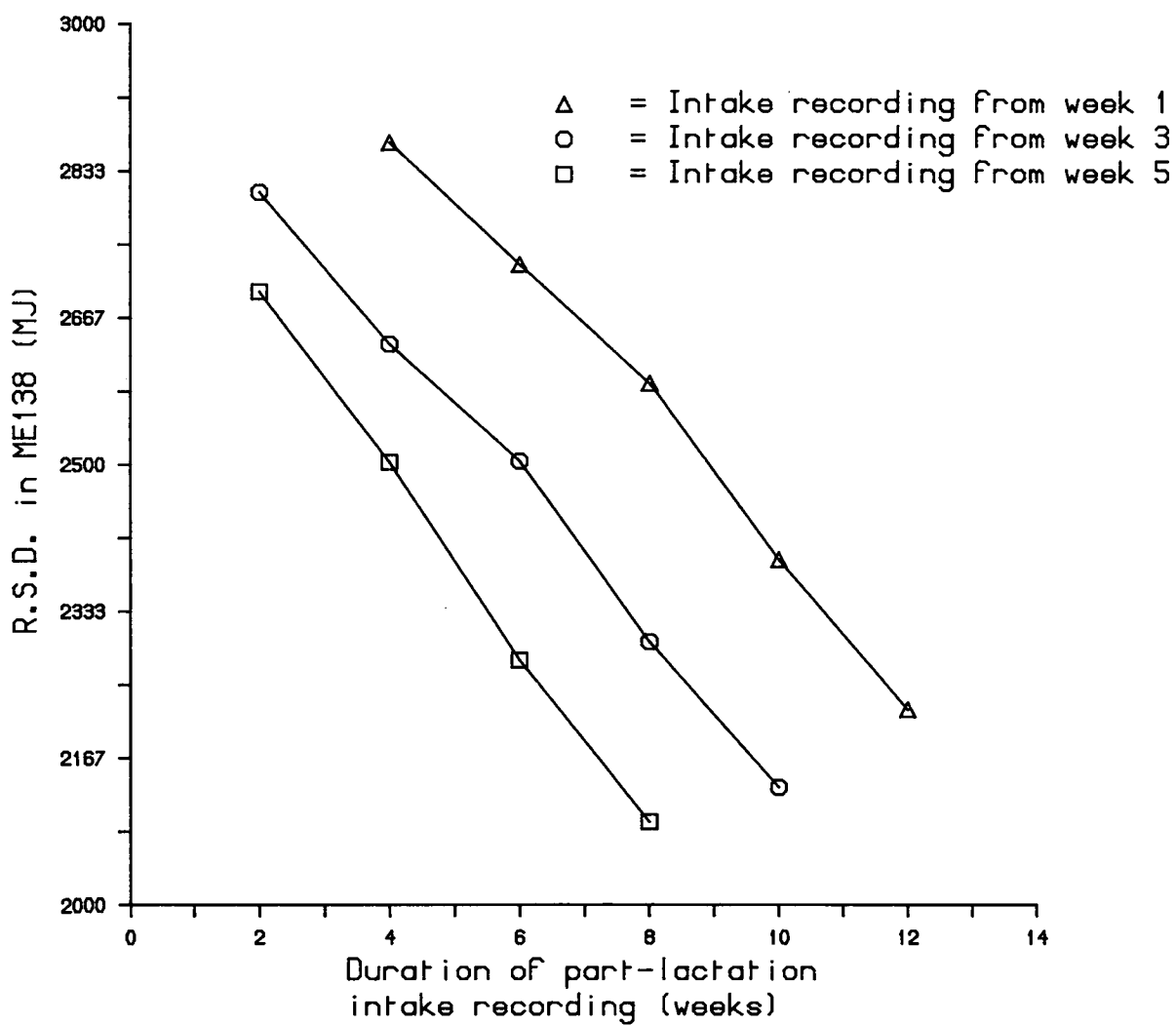


Figure 7: Residual standard deviation in cumulated efficiency to week 38, after fitting year, month, FP112, or FP110, LWC and ME intake over different periods. (The larger solid symbols represent RSDs for models with FP110 and ME512, ME312 or ME112)

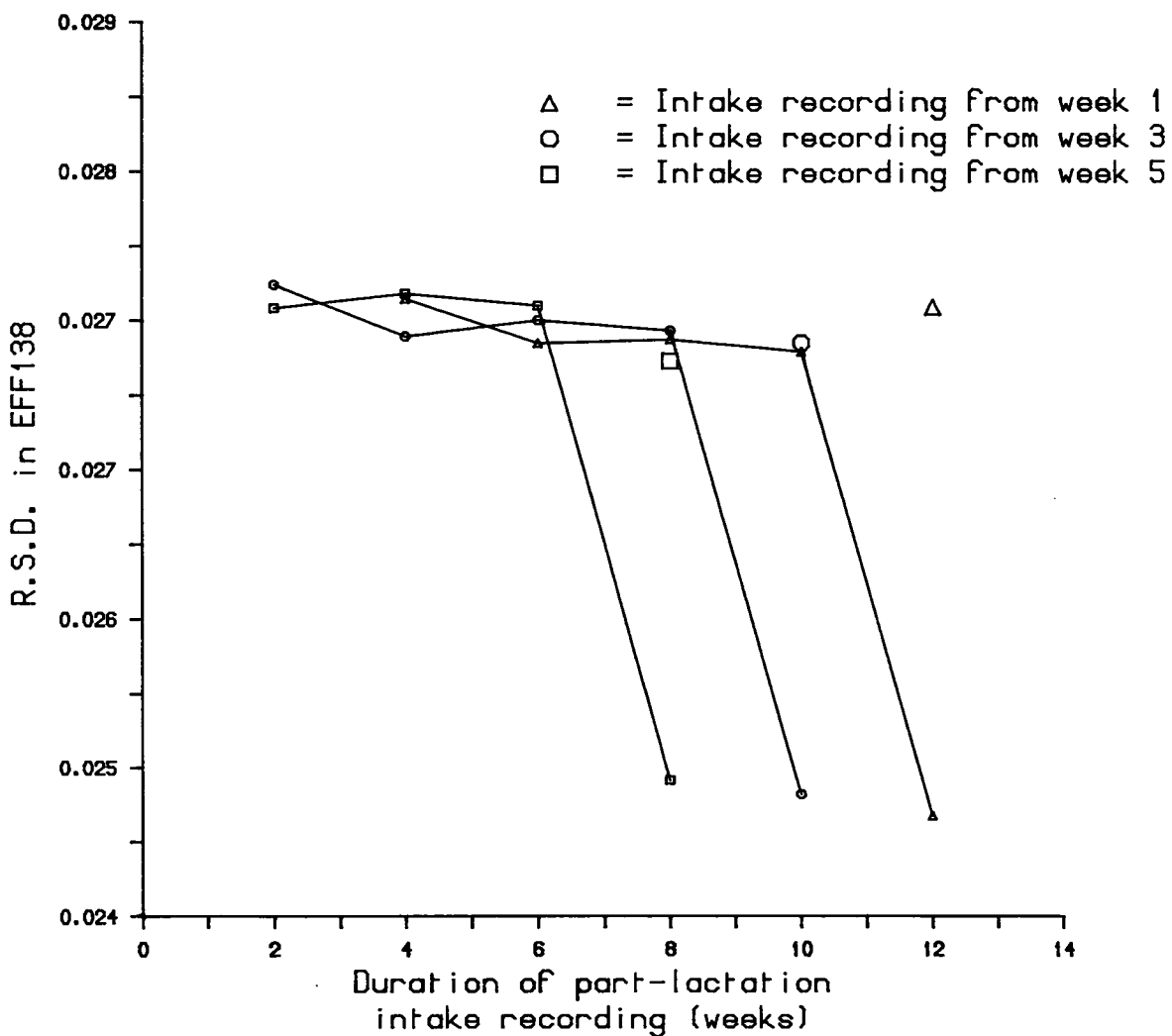


Figure 8: Residual standard deviation in cumulated ME intake to week 38, after fitting year, month, Holstein proportion and EI over different periods.

