GENETIC VARIATION IN THE EFFICIENCY OF FEED UTILISATION BY ANIMALS

A thesis submitted in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

by

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May 1996

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Abstract

Genetic variation in efficiency of feed utilisation by animals and the potential for selection to improve efficiency was examined. The work began with the analysis of feed intake and growth data from cattle, which indicated that genetic variation exists in post-weaning efficiency of growth. However, as the feed requirements of the breeding herd form a large proportion of the total feed used in beef production it is important to understand the implications of selection for post-weaning efficiency on the efficiency of mature animals. Analyses of post-weaning data showed that feed intake and efficiency were moderately repeatable over a short period, but were less repeatable over longer periods. This suggested that there was unlikely to be a strong phenotypic relationship between efficiency post-weaning and at maturity, although it was possible that a genetic relationship existed.

Experiments were conducted with mice as a model for cattle to examine the relationship between post-weaning efficiency and mature efficiency. It was found that the phenotypic relationship between post-weaning efficiency and mature maintenance efficiency was weak. However, estimation of genetic parameters in mice showed that post-weaning efficiency was genetically related to maintenance efficiency. Selection based on post-weaning efficiency is likely to lead to a favourable correlated response in maintenance efficiency of mature animals. The correlations indicated that the improvements in efficiency would be achieved by a decrease in feed intake both post-weaning and at maturity, with no change in post-weaning growth, mature weight or post-weaning body composition, although mature animals may be slightly leaner.

The optimum length of test for measurement of feed intake and efficiency in cattle was also examined. It was found that a 5 week test is sufficient to measure feed intake. However, measurement of efficiency requires 10 weeks, due to limitations in measuring growth rate.

The thesis concludes with a consideration of how post-weaning feed intake information can be used in genetic improvement programs. Series of simulations were performed which demonstrated that feed intake data may add valuable information to selection decisions under a wide range of situations.

Declaration

I hereby declare that this work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

Jason Archer

Acknowledgments

First and foremost I would like to acknowledge the support and assistance given to me by my supervisors, Dr Wayne Pitchford and Dr Peter Parnell. Wayne's advice with many aspects of the project and his encouragement and belief in myself and the project were invaluable. A PhD supervisor must be so much more than a capable scientist, and I thank Wayne for his help both as a supervisor and as a friend. Peter's advice and assistance were of immense value also. Although distances meant that communication was not always easy, Peter had an input into many aspects of the project and his influence on the project was very significant. I thank Peter for both his expertise and his friendship.

I would also like to thank Dr Paul Arthur and Dr Raul Ponzoni for significant contributions to aspects of the project. Paul enabled me to access the data in Chapter 4 for use in my thesis and his comments on the chapter were appreciated. Raul's help with the work presented in Chapter 7 was invaluable, both with technical advice and helping me come to grips with selection index theory. Raul's comments on other aspects of the project were also greatly appreciated.

I must especially thank Toby Hughes for the many hours we both spent working in "the mouse house", and for assistance in caring for animals and collecting data at times when I was unable to. Toby's sense of humour went a long way towards preserving sanity during times when the work was tedious. Thanks also to Jim Zupp for his help in maintaining the small animal facility. David Rutley and Enoch Aduli have my thanks for the companionship of fellow post-grads working in the same lab, and for the many good times we had in "Wayne's World". Thanks also to all the staff and students in the Department of Animal Science who made life as a post-grad a rewarding experience, and for their help in many details.

I am grateful for the financial assistance provided by the J.S. Davies Bequest Fund.

Finally, I would like to thank my wife, Steph, for the many sacrifices she made as a girlfriend, fiancee and then wife of a post-graduate student.

Chapter 1. Introduction

As competition for the sale of agricultural produce in the international market place increases, the marketing of agricultural products is becoming increasingly difficult. In an economy where agricultural exports constitute a significant proportion of the nation's income, this is likely to have an impact on the wealth of the nation unless changes are made to increase the competitiveness of agricultural products in the global market place. Two approaches are commonly used by many industries to address these issues. One approach is to improve the quality or marketability of the product in order to obtain higher prices and to retain or increase market share. The other approach is to improve the efficiency of the industry in order increase the level of production without increasing inputs, or alternatively to reduce inputs without a decrease in production.

The beef industry in Australia is now in a situation where world markets dictate that change must occur if the industry is to survive. Currently a great deal of effort and research is being directed at improving quality of beef by more consistently meeting market specifications. However it is the intention of this thesis to examine opportunities to improve the efficiency of beef production.

One of the major inputs to any animal production system is the cost of feed. This has been clearly recognised in the intensive animal production industries such as the pig and chicken industries where the feed costs are more easily quantified and account for a large proportion (often 70 -80 %) of total production costs. These industries have made large improvements in feed utilisation efficiency over the last 20 - 30 years. The realisation of the high cost of feed to the beef industry is growing and there is an awareness of the need to improve the efficiency of feed utilisation in the beef industry if beef is to remain competitive with other meat products.

There appears to be a high level of variation in feed utilisation efficiency in the beef industry. In a comparison made with lines of Angus cattle selected for and against weaning weight at Trangie, New South Wales, it was found that there was substantial variation in the efficiency of the cow/calf unit when expressed as weight of calf output per unit feed input for both dam and calf, with some cows producing twice as much calf output per unit feed input as others within the same line (P. Parnell, personal communication). In addition the differences between selection lines were small compared to the variation within the lines, suggesting that selection for growth produced very little change in biological efficiency. In another study conducted in the United States of America it was also found that the production efficiency of cow/calf units varied considerably (Shuey *et al.* 1993), although the variation was not as great as that found with in the Australian study.

If the beef industry is to improve the efficiency with which feed is converted to meat it will be important to identify the factors associated with efficiency which make one cow/calf unit twice as efficient as another. Once identified, these factors may be manipulated to make improvements. The factors may be both environmental and genetic in origin, and possible improvements may be made through management and breeding decisions.

Thompson and Barlow (1986) modelled the biological efficiency of meat production in cattle and sheep, including feed inputs and production outputs in their equations. Their model suggested that an increase in mature weight would give only a very slight improvement in biological efficiency, a prediction in line with the results from the Angus selection lines at Trangie. Two approaches for improving efficiency were identified. The first of these was to decrease the maintenance cost of the mature animal. The second approach was to change the shape of the growth curve. The approach which this thesis will examine is the possibility of genetic improvements in efficiency of feed utilisation through selection to decrease feed costs of animals without changing growth.

Chapter 2. Literature Review

2.1 Maintenance efficiency

2.1.1 Defining maintenance

Maintenance has been defined by various authors in many different ways, to suit a variety of purposes. However most definitions of maintenance have encompassed the basic concept summarised by Ferrell and Jenkins (1985) who defined maintenance as "the feed energy required for zero body energy change (energy stasis) or feed energy required for zero body weight change (weight stasis)". This definition could be further improved however by restricting the definition of maintenance to animals in a non-productive state, so that maintenance is defined as the feed energy intake required by an animal in a stable, non-productive state (i.e. a non-pregnant, non-lactating animal in which there is no change in body weight or body energy). Additional stringency to the definition could also be added by specifying that the animal is maintained in a thermo-neutral environment and in the absence of external stresses.

Maintenance efficiency refers to the relationship between the feed required for maintenance and the body weight maintained at this level of feeding. Maintenance efficiency may be expressed as the ratio between maintenance requirement and body weight maintained. However, much of the literature expresses maintenance efficiency on the basis of body weight raised to some power, normally 0.73 or 0.75, in order to remove the inherent change in maintenance efficiency which occurs with an increase in size when examined on a between species basis (Brody, 1945). This practice of scaling by metabolic body weight assumes that the same relationship which Brody observed across species (on a "mouse to elephant" scale) also holds true when examined on an intra-species basis. The validity of this assumption has been questioned by several researchers (e.g. Thonney *et al.* 1976).

As maintenance is defined as a state in which there are no changes in body weight occurring, maintenance efficiency should theoretically be measured in animals which have achieved this state. It is unwise to extrapolate the processes occurring in an animal in body weight stasis to make inferences about animals in which body weight is changing, as this may lead to erroneous conclusions. Koong *et al.* (1985) cautioned that the division of feed requirements of a growing animal into that required for maintenance and that required for production is an artificial division, as energy metabolism is a function of complex interactions between many physiological processes. Partitioning of energy usage into that used for maintenance and that used for productive purposes has been useful for studying energy metabolism and for developing predictive equations for feeding animals. However, as pointed out by Stephens (1991), maintenance requirement of animals in which productive processes such as growth, pregnancy or lactation are occurring is essentially conceptual. Hence, very rarely in animal production are animals in a state of true maintenance, as generally all animals are contributing in some way towards production, and even mature animals are in a productive state, either in pregnancy or lactation. However, the concept of a maintenance requirement may still have some value, as a reduction in the amount of energy required to keep an animal in a state of "true maintenance" *may* lead to an improvement in the overall efficiency of the animal when in a productive state. This assumption has been the basis of recommendations that the maintenance efficiency of animals could be altered to improve production system efficiency (eg Thompson and Barlow 1986). However while this assumption seems likely to be true, some evidence against this has been presented by Shuey *et al.* (1993).

2.1.2 The importance of maintenance

The proportion of feed used by the breeding herd varies greatly between species and between production systems. Webster (1989) compared the production of poultry broilers, pork, sheep and beef sucklers (shown in Table 2.1), and broke down the production systems into components in order to identify strategies for improving the efficiency of meat production. The comparison demonstrates the large differences in the relative costs of feeding the breeding herd compared to the slaughter generation over different production systems. Two strategies can be identified for improving efficiency of meat production, both of which act by reducing the cost of maintaining the breeding population. These are to increase the reproductive rate, so that more progeny per adult animals are produced, or to increase the slaughter weight relative to the maternal weight, or more importantly, relative to the maternal feed requirements.

Table 2.1 An estimate of the relative amounts of metabolisable energy required for maintenance of the parent population and growth of the slaughter generation in four different production systems (from Webster 1989).

	Poultry broilers	Pig, pork	Sheep	Beef sucklers
Weight of dam (kg)	3.0	180	75	450
Weight of product (carcass, kg)	1.5	50	18	250
Weight of carcass: dam	0.50	0.28	0.24	0.55
Progeny per year	240	22	1.5	0.9
Weight carcass per year: dam weight	120	6.2	0.36	0.50
Proportion of ME* per annum:				
to dam	0.04	0.20	0.70	0.52
to progeny	0.96	0.80	0.30	0.48

* Metabolisable Energy

In species with high reproductive rates, such as pigs and poultry, the cost of maintaining the breeding herd is low, and so it is sensible to direct most attention towards the efficiency and quality of carcasses produced by the slaughter generation. However, in species with low reproductive rates, such as sheep and cattle, more attention should be given to improvements in the breeding herd. The most obvious of these is to improve reproductive rate of the breeding herd, as this will have a very large effect on the efficiency of the production system. However the heritability of reproductive traits is generally low and biological limits to reproductive rate exist in these species, making genetic improvements to reproductive rate difficult to achieve by selection. Hence the alternative approach of decreasing maintenance costs of the breeding herd in proportion to the weight of carcass produced is worth pursuing. The simplest and quickest way to achieve these gains is to cross large, lean terminal sires with small maternal type females. However, it is also of interest to make improvements within breeds by selection to decrease the maintenance costs of females.

The estimate of proportion of feed consumed by cows for beef production by Webster (1989) lies at the lower end of the range of published estimates. Ferrell and Jenkins (1985) estimated that of the total feed used by a breeding cow, 70 to 75 % was used for maintenance. This translates to 50 % of the total feed energy required for beef production (Ferrell and Jenkins 1984a). Hotovy *et al.* (1991) quoted figures around 70 % of feed used for maintenance, depending on the proportion of animals in each category. Thompson and Barlow (1986) modelled feed use in beef production systems and found that dams consumed 89 % of the total feed used for the enterprise. Whatever the real cost is, and this will vary between production systems and environments, it is certain that the breeding herd consumes a very significant proportion of the total feed used in a beef enterprise.

2.1.3 Estimating maintenance requirements

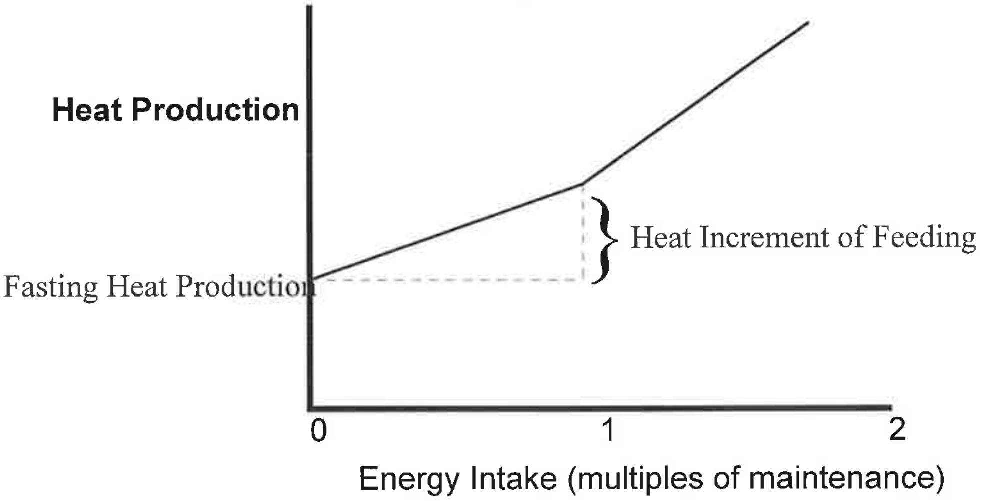
There are a number of methods available for estimation of the maintenance requirement of individual animals and groups of animals. The estimate obtained from any two methods may differ as each method is a reflection of slightly different attributes of the energy balance of animals and animals may not be in an identical physiological state. For example, some methods require the animal to be in a fasting state, while others require animals to be fed at levels below, at and above maintenance levels.

2.1.3.1 Fasting heat production

A common method for estimating maintenance requirements is to measure the amount of energy expended by an animal in a fasting, post-absorptive state in order to obtain an indication of the energy required to maintain essential body processes. This measurement is termed the "fasting heat production" and is made by measuring the energy output from an animal in the form of heat production after a period of fasting (usually about three to four days for sheep or cattle) when the absorption of nutrients occurring in the gut is negligible. This measure is normally assumed to represent the minimal level of metabolism of the animal, and hence is often referred to in the literature as the "basal metabolic rate". Maintenance requirements can be estimated as the equivalent amount of metabolisable energy as the animal expends in the fasting state.

As the fasting heat production represents the energy expenditure of an animal in a post-absorptive state, the energetic cost of the processes of feeding, digestion and absorption of feed is not accounted for. A fasting animal has a negative energy retention, and as maintenance has been defined as the feed required for zero energy retention, the energetic costs of obtaining sufficient energy to attain a state of zero energy retention should be included in the maintenance requirement. The difference between the energy required to achieve zero energy retention and the fasting heat production is termed the "heat increment of feeding". The relationship between energy intake and heat production is represented diagrammatically in Figure 2.1.

Figure 2.1 Relationship between heat production and energy intake (adapted from McDonald *et al.* 1988).



2.1.3.2 Regression of energy retention on feed intake

Fasting heat production involves measurements made on animals which are not being fed. In this respect it differs from the approach where energy retention is regressed on the feed intake of animals fed at levels around maintenance. This approach uses the definition of maintenance, so that the estimate of maintenance obtained is the feed intake at which there is zero energy retention. Animals are fed at levels slightly below and above an estimated maintenance requirement to produce a range of positive and negative energy retentions, from which a relationship between energy retention and feed intake in a range where energy retention is close to zero can be obtained, and the intercept on the feed intake axis where energy retention equals zero is calculated from the relationship obtained.

This approach has the difficulty that energy retention is very difficult to measure due to the lack of a method for accurately estimating body composition on live animals. For this reason maintenance is often measured as feed intake required for zero weight change, and so using this definition changes in liveweight are regressed on feed intake to determine the feed intake at which liveweight does not change. This method assumes that at zero liveweight change there is no change in body energy. This assumption is not necessarily correct as body composition may be changing although there is no change in liveweight, and hence energy retention may be non-zero.

An additional limitation to this method is that several data points at different levels of feeding are required and so in practical terms this approach is restricted to measuring maintenance on a group or class of animals. Although it is possible to measure maintenance efficiency on individuals by regressing feed intake on energy retention (e.g. Solis *et al.* 1988), measurements made on an individual animal at different feeding levels must be confounded with time. Hence, while this method is suitable for breed comparisons and similar studies, it is not very appropriate or practical for examining individual variation in maintenance requirements.

2.1.3.3 Long-term feeding at constant levels

Another approach to estimating maintenance efficiency is to maintain animals at a constant feeding level for prolonged periods until an equilibrium weight is achieved (i.e. the animal has zero energy retention). Maintenance efficiency can then be derived from the feed intake and the equilibrium weight achieved. This method of estimation can be used on immature animals where feed intake is restricted to a level below the *ad libitum* intake, as the animal will attain an equilibrium weight which is less than that attained on *ad libitum* intake. When animals are fed *ad libitum* the equilibrium weight attained is referred to as the mature weight, and the level of feed intake is referred to as the mature feed intake.

This approach to measuring maintenance efficiency was used by Taylor *et al.* (1981) who restricted female Ayrshire twin cattle to six different constant feeding levels until an equilibrium weight was achieved. Taylor *et al.* (1981) found that when an animal was moved to a new feeding level after a prolonged period on a fixed feeding level, a new equilibrium weight was achieved and the within-animal repeatability of maintenance efficiency measured at different levels of feeding was 0.7. They also found that there was no systematic change in equilibrium maintenance efficiency with stage of maturity over a range from 25% to 100% mature, and maintenance efficiency was also independent of age, except for small increases at ages greater than 8 to 9 years. This evidence suggests that the equilibrium maintenance efficiency of an animal is constant over a wide range of body weight, and it would seem that maintenance efficiency is an inherent property of an individual which may be determined by genetic effects or by permanent environmental effects in early life.

A practical limitation to this approach is the length of time required to achieve a state of equilibrium in immature animals when feed intake is restricted below *ad libitum*. Taylor *et al.* (1981) found that a period of 2 years was required for cattle to reach an equilibrium body weight. Hence this approach for measuring maintenance efficiency is restricted to measurements taken for experimental purposes only.

2.1.4 Factors affecting maintenance efficiency

2.1.4.1 Body composition

The proportions of fat and lean in the body is known to affect maintenance efficiency when expressed as a function of bodyweight. Many studies have shown that maintenance requirements per unit body weight are lower in fat animals than in lean animals (e.g. Klosterman *et al.* 1968; Thompson *et al.* 1983; Russel and Wright 1983; Pullar and Webster 1977; DiCostanzo *et al.* 1990). The underlying cause of this observation is generally thought to be due to the difference in metabolic activity between protein and adipose tissue, as protein is energetically much more expensive to maintain than fat (with the exception of brown adipose tissue).

The difference in maintenance requirements between fat and lean animals has led a number of researchers to suggest that maintenance requirement is more accurately predicted on the basis of protein mass than on total body mass. Pullar and Webster (1977) using lean and congenitally obese Zucker rats which are extremely different in fat deposition found that the difference in maintenance requirement between the two genotypes when expressed on a body weight basis was greatly reduced when expressed per gram of protein. Webster (1981) compared published estimates and found that when expressed per kg body protein$^{0.75}$ the difference in maintenance requirement of fat and lean adult sheep was removed. However, the differences between classes of cattle (yearling Friesian vs Hereford x Friesian) and age of sheep (yearling vs 'old') remained when expressed per kg body protein$^{0.75}$, indicating that effects other than the fat/lean ratio were causing the differences in maintenance requirements between these animals. These results agree with those of Koong *et al.* (1985) who found that the rate of heat production by animals would be better predicted by inclusion of body protein mass and rate of protein accretion rather than total body mass and rate of weight gain.

While many studies have found that fat animals had lower maintenance requirements than lean animals, other studies have found that fat animals had higher maintenance requirements (e.g. Graham 1969). Ferrell and Jenkins (1984b) found that when mature Angus, Hereford and Simmental cows were fed at different rates prior to measurement of maintenance efficiency, the fatter animals had higher maintenance requirements. This result agrees with other studies where differences in body composition were confounded with effects of previous nutrition on maintenance requirements (see section 2.1.4.2). Ferrell and Jenkins (1984b) proposed that conflicting results on the effect of fat : lean ratio on maintenance requirements may be due to the influence of previous level of nutrition in those studies which found that fatter animals produced by high levels of feeding had higher maintenance requirements than leaner animals on lower feed intakes. Hence in these studies the higher maintenance requirements were a result of the previous nutritional regime rather than the body composition of the animals.

2.1.4.2 Previous nutrition

The level of nutrition at which an animal has been fed prior to measurement has an effect on the fasting heat production. Koong *et al.* (1982) fed pigs at three different levels so that the final weight gain was identical across the three groups but the weight was achieved via different pathways; one group was fed to gain 19 kg and then lose 5 kg, another to gain 7 kg over both periods and another to lose 5 kg and gain 19 kg. At the end of these treatments the fasting heat production of the pigs were measured and the animals slaughtered and the weights of the internal organs measured. They found that animals on the higher plane of nutrition during the second period had higher fasting heat production and heavier internal organ weights than those on low nutrition. This study suggests that nutritional status has an effect on fasting heat production (and presumably maintenance requirement) independent of differences in body weight, and that fasting heat production is correlated to the weights of the metabolically active visceral organs.

Koong *et al.* (1985) repeated this work with rats and sheep, using an experimental design which allowed comparison of animals of different weights growing at the same or different rates, and animals of the same weight and age which had achieved the weight via different growth patterns. The results of these experiments agreed with those obtained using pigs, and demonstrated significant effects of previous nutrition on fasting heat production and maintenance requirements. These experiments also showed a high correlation of visceral organ weight (particularly liver and gut weights) with fasting heat production.

The work of Koong *et al.* (1982, 1985) used growing animals to examine the effects of previous nutrition on fasting heat production. Extrapolation of these results to maintenance requirements of mature animals is difficult as fasting heat production of a growing animal may not be an appropriate reflection of the energy used for maintenance in the mature animal. However, the work of Ledger and Sayers (1977) suggests that the conclusions of Koong *et al.* also apply to adult cattle during periods of maintenance. In groups of *Bos indicus* and *Bos taurus* x *Bos indicus* steers kept at constant liveweight for periods of up to 24 weeks it was found that the daily feed requirement for maintenance of constant liveweight decreased for a period of about 12 weeks as the animals adapted to the restricted feed regime. They also found that the body composition of the steers changed during the period in which feed intake decreased, with the relative weight of digestive tract and internal organs decreasing. Frisch and Vercoe (1977) also showed fasting metabolism varied according to prior levels of nutrition and weight gain in cattle, and showed differences between breeds in their ability to adapt fasting metabolism to previous nutritional regime. The work of Ledger and Sayers (1977) and that of Koong *et al.* (1982, 1985) indicates that animals have an ability to adjust maintenance requirements according to prior nutrition, and that the internal organs may be associated with the changes in the efficiency of maintenance. It is possible that breed variation in the ability to adapt to different nutritional levels observed by Frisch and Vercoe (1977) is due to differences between breeds in the extent to which the relative proportions of visceral organs can change. While it is known that breed differences in proportions of visceral organs do exist in cattle (Ferrell and Jenkins 1984c), the extent to which nutritional regime changes these proportions in different breeds has not been fully investigated.

The evidence cited above showing that previous nutrition can affect fasting heat production and maintenance requirements raises the question as to what extent may the previous level of nutrition affect the measurement of feed intake and efficiency in animals, and how long a period of standardisation is necessary before these effects can be ignored? It would seem to be important to include some period of adjustment at a constant feeding level before measurement of efficiency. The question of possible confounding maternal effects when measuring efficiency soon after weaning is also one which may need addressing. If the previous milk supply from the dam had an effect on efficiency, then selection on a measure of efficiency which did not include an adjustment for maternal effects may place selection pressure on maternal ability.

2.1.4.3 Physiological state

If the narrow definition of maintenance suggested in section 2.1.1 is accepted, then there is no variation in physiological state under which maintenance requirements are measured. However, many studies (e.g. Montano-Bermudez *et al.* 1990; Shuey *et al.* 1993) have reported measures of "maintenance requirements" of animals which are outside of the conditions defined for maintenance. Alterations to physiological state can refer to effects of previous nutritional regime (as covered in section 2.1.4.2), animals which are growing, animals in gestation and lactating animals. The influence of external stresses (e.g. temperature stresses) may also act to alter the physiological state of the animal, and so may have an effect on maintenance (e.g. Close 1978). Measures of maintenance requirement on animals in a physiological state which falls outside the narrow definition given in section 2.1.1 can be difficult to interpret, as many such measures rely on the partitioning of nutrients between that utilised for production and that utilised for maintenance.

An example of the complicating factors introduced in animals in a different physiological state can be seen in the effect of lactation on estimated maintenance requirements. The energy requirement for maintenance of a lactating animal appears to be considerably higher than that of a non-lactating animal. This has been demonstrated by Hutton (1962) in dairy cattle, and agrees with other results of Neville and McCullough (1969) and Neville (1974) using Hereford cows. The increased maintenance requirement of lactating animals has also been demonstrated in rats by Canas *et al.* (1982), who showed that the increase in maintenance was associated with an increase in the relative weights and metabolic activity of some visceral organs. Hence it seems that the maintenance requirement of an animal is not fixed across a wide range of physiological states, but is better regarded as a moving target. Consequently, comparisons of maintenance should be made between animals within a narrowly defined physiological status.

2.1.4.4 Genetic effects

Evidence for a genetic component which determines maintenance efficiency comes from comparisons made across species (e.g. Brody 1945), across breeds within species (e.g. Taylor *et al.* 1986), within breeds (e.g. Carstens *et al.* 1989) and also evidence from lines selected divergently for maintenance requirements (Stephens 1991). However, when considered in the context of the potential for genetic improvement of existing animal production systems, comparisons made within a species are more relevant than comparisons between species, and so the discussion here will be limited to within species comparisons. These comparisons can be categorised as those within and between breeds.

Genetic variation between breeds

There is a substantial body of evidence which shows that differences in maintenance efficiency between breeds of cattle exist, and that these differences are correlated with differences in "productive potential" of breeds. Ferrell and Jenkins (1984a) compared the maintenance requirements of four breed types of cattle, chosen to represent moderate mature size - moderate milk production potential (Angus - Hereford crosses), large mature size - moderate milk production potential (Charolais crossed with Hereford or Angus), small mature size - high milk production potential (Jersey crossed with Hereford or Angus) and large mature size - high milk production potential (Simmental crossed with Hereford or Angus). Maintenance requirements were estimated by feeding at three different levels and regressing intake on body weight change to determine the feed intake required to achieve body weight stasis and expressed as kcal.kg$^{-0.75}$.day^{-1}. No difference between breed size was found in maintenance requirements adjusted for metabolic body weight (kg$^{0.75}$), but breeds with a higher milk production potential (i.e. Jersey and Simmental crosses) had higher maintenance requirements than breeds with moderate milk production potential.

Solis *et al.* (1988) performed a study similar to that of Ferrell and Jenkins (1984a), using non-pregnant, non-lactating mature cows of five breeds (Angus, Brahman, Hereford, Holstein and Jersey) and their crosses. Each cow was fed for four periods at four levels, with body composition measures made at the beginning and end of each period. Maintenance efficiency was calculated for body weight stasis and energy stasis by regression of energy intake on weight gain or energy retention and adjusted for metabolic body weight. For both measures of maintenance it was found that the Jerseys and Holsteins had significantly higher maintenance requirements than the beef breeds. The energy requirement for changes in body weight also differed between breeds, which was attributed to the different composition of the gain between breeds, as fat is energetically more expensive to deposit on a weight basis than protein.

Another similar trial examining maintenance requirements was performed by Montano-Bermudez *et al.* (1990) using crosses of beef and dual-purpose breeds of approximately the same mature size (Hereford, Red Poll and Milking Shorthorn) with Angus to produce a range of genetic potential for milk production, albeit a smaller range than that used by Solis *et al.* (1988) and Ferrell and Jenkins (1984a) who used high producing dairy breeds (Friesian and Jersey) and lower producing beef breeds (e.g. Brahman). Maintenance requirements were also estimated from feed intake and body weight changes, although a slightly different approach was used as these cows were pregnant or lactating and adjustments were made for these factors. The results of this experiment must be interpreted with caution, as the animals were not in a non-productive state, and hence the concept of maintenance efficiency of these animals is an artificial one (as discussed in section 2.1.4.3). In addition, some of the methods used to calculate maintenance requirements in this experiment are not appropriate for making comparisons between breeds, as adjusting for energy requirements of lactating or gestating cows by using published k_l or k_g values can create spurious genetic differences if there is error in the values used (Taylor *et al.* 1986). Despite these concerns, it was found that maintenance requirements expressed per metabolic body weight were higher in breeds with higher genetic potential for milk production.

Milk production is not the only indicator of the "production potential" of cattle, and other studies have shown differences between breeds of cattle. For example, Frisch and Vercoe (1984) found that on a low quality maintenance ration, Hereford x Shorthorn bulls (15 months old) required approximately 20% more feed to maintain the same body weight as Brahman bulls, which was also reflected in differences in fasting metabolism, although the differences in fasting metabolism were not as great as those in feed intake. When the comparison was made feeding a high quality ration, there was still a 20% difference in feed intake between the Brahmans and Hereford x Shorthorn crosses, but the Hereford x Shorthorn cross bulls had 20% higher growth rates, as they were able to express their higher growth potential. This suggests that the higher growth potential of the Hereford x Shorthorn was associated with lower maintenance efficiency.

While the studies cited above indicate that breed differences in maintenance efficiency exist, not all studies have shown this. For example, Russel and Wright (1983) did not find any difference in maintenance efficiency between Hereford x Friesians and White Shorthorn x Galloway cows, although they made adjustments for body condition which may have removed the genotype effect. Other studies making comparisons between dairy breeds or between beef breeds have also failed to find differences in maintenance efficiency (eg Klosterman *et al.* 1968), possibly because the differences between breeds within a type are very small or non-existent.

Taylor *et al.* (1986) examined in detail the relationship between maintenance efficiency and productive potential. They measured maintenance efficiency by long-term feeding of animals at constant intakes until an equilibrium body weight was achieved, and also found that breeds with higher milk production potential were less efficient at maintaining bodyweight than breeds with lower milk production. Taylor *et al.* took the findings further and examined the literature on the maintenance requirements of various breeds of cattle. All literature estimates used in the comparison were adjusted by metabolic body weight. Breed types were classified as Zebu, Zebu x Beef, Beef, Beef x Dairy and Dairy to produce a gradient of genetic potential for productivity from low to high. Estimates of maintenance efficiency taken from experiments where maintenance requirements were estimated on fed animals (i.e. by regression of energy retention on intake or by long-term feeding to an equilibrium body weight) gave a significant regression of maintenance requirement on productive potential. However, estimates of maintenance efficiency taken from experiments where maintenance requirements were estimated on fasted animals (i.e. by measurement of fasting heat production) did not give a significant regression of maintenance requirement on productive potential. This led Taylor *et al.* (1986) to suggest that basal metabolism is the same at all levels of production from zebu to dairy, and that genetic differences in maintenance efficiency are due to differences in the heat increment of feeding (i.e. in the efficiency with which feed is used for maintenance). This hypothesis has not been tested under controlled conditions, but is of great interest as it represents one of the few attempts made to break maintenance efficiency down into component traits, and support or rejection of the hypothesis would provide some clues as to the biological basis of differences in maintenance efficiency and productivity.

Genetic variation within breeds

The existence of differences in maintenance efficiency between breeds indicates that there is some genetic variation for the trait within the species. However, if we are interested in improving maintenance efficiency by selection within breeds, the amount of genetic variation existing for maintenance efficiency within a breed is the factor of most interest. There are two studies in the literature which suggest that genetic variation in maintenance efficiency within cattle breeds exists. The low number of such studies is probably due in part to the difficulties and expense of measuring maintenance efficiency on a sufficient number of animals to give an indication of the genetic variation present within a breed. The two studies both used twins to enable information on genetic variation to be extracted from records on a limited number of animals. The first of these studies was that of Taylor *et al.* (1981), who fed twin Ayrshire females at a constant level until they reached an equilibrium body weight to estimate maintenance efficiency. They found a genetic coefficient of variation of 6.4%, indicating that genetic variation in maintenance efficiency existed within the Ayrshire breed. Carstens *et al.* (1989) measured fasting heat production and heat production at maintenance on monozygotic twin pairs from Barzona x Hereford and Angus x Hereford at 9 months and 20 months of age. They found that there was significant variation in maintenance requirements between twin pairs and estimated heritabilities of 0.71 ± 0.17 and 0.49 ± 0.22 at 9 and 20 months respectively.

In other species it has also been shown that genetic variation in maintenance efficiency exists. Stephens *et al.* (1988) working with mice found that the heritability of maintenance efficiency was 0.35 ± 0.18, with a genetic coefficient of variation of 2.3 %. However, when variation in body fat was removed the heritability was reduced to 0.24 ± 0.18, indicating that some of the genetic variation in maintenance efficiency was related to body composition. Stephens (1991) selected lines of mice on maintenance efficiency and produced a selection response, confirming that variation in maintenance efficiency exists in mice.

2.1.4.5 Visceral organs

As has been discussed in the previous sections, a wide range of factors can interact to determine the efficiency of the process of maintenance of body function. However, there appears to be a common underlying thread running through these factors, that is the proportion of body weight made up by the more metabolically active tissues. It is well documented that the visceral organs including the gut, liver and heart have high metabolic rates and contribute a disproportionate amount to the total energy expenditure of the body (eg Webster 1981; McBride and Kelly 1990). The higher metabolic activity of lean tissue compared to fat means that energy expenditure is more closely related to lean mass than total mass. The total energy expenditure of the body may be described at least in concept as the summation of the weight of each organ multiplied by its metabolic activity per unit mass. Hence changes in the mass of these metabolically active tissues can have a large influence on total energy consumption even when metabolic activity per unit mass remains constant, and where animals differ in the proportion of metabolically active tissues a simple adjustment for body weight does not explain all variation in energy requirements or expenditure.

It is possible that most of the factors which have been observed to influence maintenance requirements or energy expenditure could be explained, in part if not in entirety, by differences in body composition encompassing both the fat : lean ratio (as discussed in section 2.1.4.1) and the proportion of visceral organs in the body. The influence of the previous level of nutrition on maintenance requirements has been shown to be associated with differences in proportion of visceral organs in the studies of Koong *et al.* (1982, 1985) and Ledger and Sayers (1977) using different approaches to the same issue. Variation in maintenance requirements of animals in different physiological states might also be explained by changes in the relative mass of metabolically active tissues. Canas *et al.* (1982) demonstrated increases in the mass of internal organs in rats during lactation. Similar increases have been observed in cows during lactation and pregnancy (Smith and Baldwin 1974) and sheep during lactation (Fell *et al.* 1972).

Variation in total energy expenditure may also be a result of changes in the metabolic activity of tissues per unit mass, as well as changes in the mass of each tissue. Burrin *et al.* (1990) found that different levels of feeding did not alter the *in vitro* oxygen consumption of liver in sheep, although the total liver oxygen consumption was increased due to an increase in the mass of the liver. However, changes in physiological state have been shown by others (McBride and Kelly 1990; Canas *et al.* 1982) to produce increases in the metabolic activity per unit mass of tissues. Hence it is likely that changes in mass of metabolically active organs cannot totally account for differences in energetic requirements under all circumstances, as energy expenditure can also be influenced by changes in metabolic activity per unit mass.

Genetic variation in maintenance efficiency is also likely to be partly a function of the visceral organ mass. It has been shown that differences between breeds in the relative proportion of visceral organs exist, and that breeds with higher productive potential tend to have higher proportions of visceral organs (Jenkins *et al.* 1986). This offers an explanation for the differences in maintenance efficiency which exist between breeds of different productive potential, and suggests an alternative way of considering the contribution of visceral organs to production.

Visceral organs may be considered as the machinery whereby the energy for production is obtained and processed to a useable form for the tissues where production principally occurs (e.g. muscle for growth of lean tissue, mammary gland for milk production, etc.). The machinery itself has a high overhead cost, and hence is used most efficiently when running at maximum capacity. This agrees with the thoughts of Taylor *et al.* (1986) who suggested that maximum efficiency is only obtained when an animal is producing at the limit of its genetic productive potential, and hence it is important to match the genotype to the environment in order to maximise efficiency. A genotype with high productive potential requires a large mass of the metabolically active organs in order to obtain and process sufficient energy to supply the productive processes, and so this genotype must also have a higher maintenance requirement due to the increase in metabolically active tissue. Genotypes with lower productive potential require less visceral organ mass to support their level of production and have lower maintenance requirements, with the trade off that when nutrient supply is not limiting they are unable to increase nutrient uptake and production to the same level as the genotype with higher visceral organ mass. Hence the antagonistic relationship between production potential and maintenance efficiency.

The antagonistic relationship between production potential and maintenance efficiency may be of little consequence in a constant environment as genotypes can be matched to the production environment to maximise efficiency. However, in extensive animal production systems a constant environment is the exception rather than the rule, as animals have to contend with wide seasonal fluctuations in availability of nutrition. An extreme example of the fluctuations in environment which livestock must contend with may be seen in cattle production in northern Australia where nutrition ranges from high availability of feed of variable quality during the wet season to very poor quality and low availability during the dry season. Here animal production is based on short periods of high production (or high weight gain), interrupted by extended periods of maintenance or sub-maintenance. Other production systems in other localities may have less extreme fluctuations but the principle remains that the rate of production is limited by environmental constraints and is not constant. Hence most extensive production systems require an animal to perform two roles which are conflicting. An animal is required to perform at a maximum level of production while nutrition is not limiting, and then to maintain itself efficiently during periods of limiting nutrition. As previously shown in this section, these requirements are antagonistic as one requires a genotype with a high proportion of metabolically active organs (for high production), while the other requires a genotype with a lower proportion of metabolically active organs (for efficient maintenance). Where then does the ideal genotype for production lie?

The conflict between the two requirements of an animal suggest that the dynamic nature of the proportion of visceral organs is of vital importance to animal production. The ideal genotype is likely to be the one which is able to both maintain itself efficiently during nutritional restriction and produce at a maximum rate when nutrition is not limiting. Hence it may well be that the most appropriate genotype is the one with the greatest ability to increase or decrease the amount of metabolically active tissue it must carry. To the authors knowledge there is no literature identifying genetic variation in the ability of animals to increase or decrease the proportion of visceral organs. However, Frisch and Vercoe (1977) showed that differences between genotypes existed in the response in fasting heat production to varying levels of nutrition. This sort of study may be the one which is most useful for identifying the most appropriate genotype for any production system. A possible strategy may be to evaluate a number of genotypes across a wide range of nutritional levels and choose the most appropriate genotype according to the range in nutrition normally encountered in the particular production system under consideration. The value of such a system is not able to be predicted without further research into this area.

2.2 Efficiency of growth

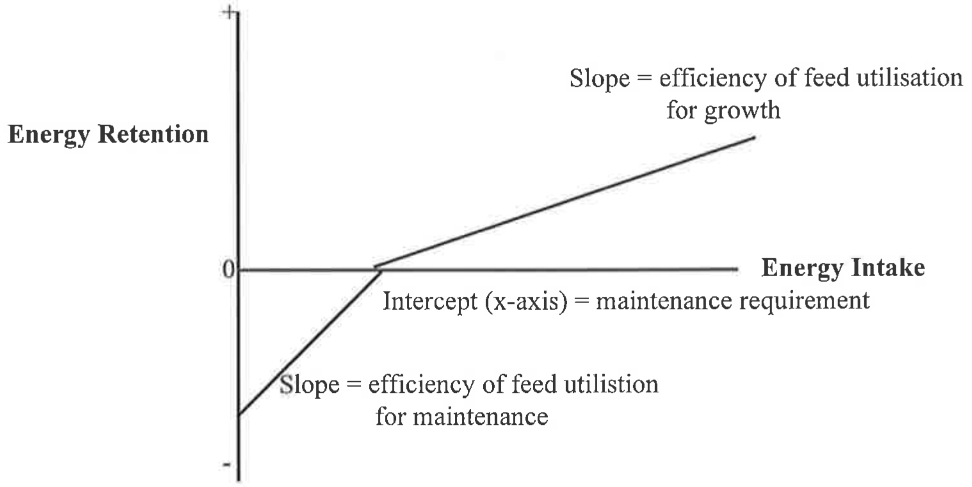
2.2.1 Definition and problems associated with the efficiency of growth

The efficiency of growth is a concept which has arisen from attempts by nutritionists to predict the feed requirements of growing animals. These feed prediction models (e.g. ARC 1980) have been formed by partitioning feed requirements into that used by the animal for maintenance and that used for growth. Other adjustment factors have also been added to the models to improve the accuracy of prediction. In order to provide functional predictive equations able to be used for animals over a wide range of liveweights and growing at different rates, constants have been developed which describe the amount of feed required to maintain or gain a unit of liveweight. Under these feeding systems, these constants represent the efficiency of maintenance and growth. This system has merit in forming predictive equations for feeding standards. However, it has the danger in that it tends to constrain one's thinking into assuming that a constant efficiency of growth exists and can be quantified.

It is well recognised (ARC 1980) that the relationship between energy retention and feed intake is curvilinear, following the law of diminishing returns. As the efficiency of growth is essentially the slope of the curve when there is a positive energy retention, this means that the efficiency of growth changes according to the level of feeding. Feed prediction models approximate this curvilinear relationship using two linear relationships for positive and negative energy retention (Figure 2.2). However, one should be mindful of the assumptions made when forming these approximations.

The inappropriateness of partitioning energy requirements into that for maintenance and growth in growing animals is seen in the experiments of Koong *et al.* (1982, 1985) where the fasting heat production of pigs, rats and sheep varied with growth rate. This shows that assigning a fixed maintenance cost to a growing animal at a particular weight does not accurately represent the energetic balance of the animal. Hence it is not possible to simply partition feed intake into that for growth and maintenance on growing animals. For the purpose of predicting feed requirements this can be ignored, as the extra maintenance requirement of growing animals can be considered as a necessary part of the cost of growth as discussed by Turner and Taylor (1983). However, for other purposes such as examining variation in efficiency of growth, this extra maintenance requirement should not be included in the cost of growth as it may confound the results.

Figure 2.2 Energy retention vs energy intake. The relationship is represented here as two linear functions above and below maintenance as this portrays the nutritional model commonly used (ARC 1980). In reality this function is curvilinear.



Logic suggests that efficiency of growth in terms of feed required above maintenance per unit weight gain should also change with stage of maturity. As animals mature, the composition of weight gain changes from young animals depositing mostly lean tissue (protein) to older animals which move into a fattening phase and deposit more fat (Searle *et al.* 1988). Pullar and Webster (1977) found that the metabolisable energy input required to deposit one gram of protein or fat in rats is almost identical (approximately 53 kJ/g). However, the water content of fat and lean tissue differ, and so when measured on the basis of energy required to deposit liveweight, adipose tissue is energetically more expensive to deposit than lean (calculated on the basis of figures given by Webster (1980) the energy required to deposit one gram of tissue is 11 and 52 kJ/g for lean and fat respectively). Hence, if efficiency of growth is calculated on a liveweight basis rather than on the basis of energy retention, the efficiency of growth will be higher in young animals depositing mostly lean tissue than in older animals which are depositing proportionately more fat. In this way growth efficiency can also become confounded with the effects of stage of maturity since, at the same liveweight, an animal with a larger mature weight is less mature and hence is depositing proportionately less fat than an animal with smaller mature size.

The above factors indicate that the efficiency of growth is affected by a number of factors, and that it is not possible to separate energy used for growth from that used for maintenance simply by allocating maintenance requirement on the basis of bodyweight. Additionally, when considered from a biological viewpoint this approach is flawed as, in reality, nutrients are not partitioned between maintenance and growth in the animal and growth is the summation of the rates of synthesis and breakdown of the chemical components of the body. Therefore it is not sensible to make comparisons on the efficiency of growth without reference to the other factors which can affect efficiency of growth. Much of the problem arises from the lack of a suitable and convenient method for measuring body composition of live animals, which restricts comparisons to the basis of liveweight rather than to energy retention which is biologically more appropriate.

The model of energy requirements and growth based on requirements for maintenance and for growth has some obvious flaws which the discussion above has highlighted. A model conceptually and biologically more appropriate would involve separate descriptions of the rates of synthesis and degradation of protein, fat and other components. Such mechanistic models have been developed (e.g. Di Marco and Baldwin 1989; Oltjen *et al.* 1986). While these models may provide a more satisfactory description of the energy balance of the animal, the type of data required restricts the practical application of such a model with current technology, and so it would seem that for many purposes the simple model of maintenance and growth must remain. However, when using such a simple model with obvious deficiencies it is wise to remain conscious of the limitations or constraints associated with the model.

Improved models of feed intake and growth could be of great benefit, both to practical agriculture and to research. From the researchers point of view, a better model can be used to show where deficiencies in our current knowledge exist and to define new research priorities. From a practical point of view such a model may be able to explain much of the variation in responses seen in many supplementary feeding trials and enable the prediction of circumstances under which phenomena such as compensatory gain occur. Additionally, an improved model may be able to be developed to such an extent that, given the starting material and the desired carcass specifications, it is possible to design an optimum feeding regime to produce a carcass of the desired composition most efficiently, on either a feed energy or an economic basis. With the inclusion of a genetic component in the model it may be possible to model entire production systems for optimum efficiency.

2.2.2 Genetic variation in efficiency of growth

There is little information on genetic variation in the energetic efficiency of growth in the literature. This is probably due to the difficulties associated with partitioning energy intake into that used for maintenance and growth. This means that the measurement of growth efficiency often involves making assumptions about the energy required for maintenance and the efficiency of growth is dependant upon these assumptions. Hence comparisons among growth efficiency of individuals is complicated and the variation in growth efficiency is difficult to quantify.

The majority of attempts to examine variation in the efficiency of growth have used the approach of feeding animals at a number of different feeding levels around maintenance, and regressing energy retention or weight change on energy intake. The slope of the regression line obtained represents the energetic requirement for growth (in units of energy intake per body energy gain or weight gain), and the intercept of the energy intake axis represents the maintenance requirement as energy retention is zero (see Figure 2.2). Whilst it is known that the relationship between energy retention and feed intake is curvilinear (ARC 1980), by choosing a sufficiently narrow range of feed intakes around maintenance linearity can be assumed. However, the regression coefficient obtained with intakes around maintenance should not be extrapolated to intakes significantly higher or lower than maintenance.

The method described above has been used to examine differences between breeds or lines of cattle in efficiency of growth. Herd *et al.* (1990) compared two lines of Angus cattle selected for high and low growth rates at Trangie, New South Wales. A significant difference between maintenance efficiency of the two lines was found, but there was no difference between the slopes for the two genotypes, suggesting that there was no difference between the lines in growth efficiency. Solis *et al.* (1988) found significant differences in growth efficiency when measured as weight change per unit energy intake, between Jersey, Hereford, Angus, Holstein and Brahman (in order from lowest to highest) cows. Russel and Wright (1983) regressed relative liveweight change on relative feed intake of Hereford x Friesian and White Shorthorn x Galloway cows, and adjusted for condition score. No significant breed differences were found. Jenkins and Ferrell (1983) compared cows from crosses of Charolais, Jersey and Simmental with Hereford and Angus cows, and Hereford x Angus and reported that there was no significant breed difference in growth efficiency, although breed type approached significance.

All the studies quoted above used regressions on weight change and not energy retention. This means that there are problems in interpreting the results in terms of the efficiency of growth, as there may be effects of different composition of gain which are involved in these comparisons. These effects may obscure real differences in efficiency if they do exist, or they may show differences between breeds as significant which are simply due to breed differences in composition of gain. Hence it is very difficult to conclude whether breed differences in growth efficiency independent of the composition of gain exist.

The literature referred to above compared growth efficiency between different groups of animals, and the regression lines were fitted to data points from a number of animals fed at different levels. However, this approach does not allow the comparison of individual animals within a group. DiCostanzo *et al.* (1990) examined variation in efficiency of growth of individual animals within a herd using regression of energy intake on an energy retention at two feeding levels per animal, thereby removing effects of the composition of gain. They found a coefficient of variation in efficiency of energy retention of 30%, and compared this to the 19% variation between breeds found by Solis *et al.* (1988), concluding that large differences in energetic efficiency of growth may exist. The problem with this approach is that when comparing regression slope coefficients from regressions fitted to only two points per individual it is impossible to separate experimental error from real differences in growth efficiency between individuals. Therefore little can be concluded from this approach with only two feeding levels for each individual.

2.3 Measurement of efficiency

A number of methods for measuring and expressing efficiency exist. The method used to express efficiency is very important when considering efficiency, as how efficiency is expressed often determines the outcome of comparisons (e.g. Gibson 1986). There is no measure of efficiency which can be universally recommended for all situations, as different measures reflect different biological and mathematical aspects of efficiency, and are appropriate for some situations but not for others, depending on the comparisons being made. As this thesis is concerned with making gains in efficiency of feed utilisation by selection, measurement of efficiency will be discussed in this context.

In order to make comparisons of the efficiency with which feed is utilised between animals, an appropriate measure of feed efficiency is required. The ideal measure of feed utilisation efficiency should identify individuals with the greatest efficiency over a production lifecycle. Efficiency over a production lifecycle could be defined as the ratio of the total feed required to produce the saleable production output(s), including the cost of obtaining and maintaining a breeding nucleus from which the production is based, to the total production output. This will vary according to how the production system is defined.

Lifecycle production efficiency is a complex biological trait which is the summation of many other traits of importance and is not able to be easily measured on individuals. Hence it is useful to break lifecycle production efficiency down into component traits. This is essentially the approach taken by Thompson and Barlow (1986) and others who have recommended that improvement of maintenance efficiency is a potential means whereby the efficiency of production can be improved in species with low reproductive rates, such as beef cattle (see section 2.1.2). If improvements in production efficiency are to be made by improving maintenance efficiency, an appropriate measure of efficiency is required as a selection criteria to improve maintenance efficiency. Hence this section will review current methods for expressing efficiency in the context of potential selection criteria upon which selection to improve lifecycle production efficiency and more specifically maintenance efficiency will be based.

2.3.1 Considerations in formulating selection criteria for efficiency

Choosing a criteria for selection to improve maintenance efficiency has special considerations associated with it. These considerations arise from two aspects of efficiency. The first is that feed intake is a very expensive trait to measure, both in terms of money and time required for the animal to be on test. The second is that maintenance efficiency is not expressed until maturity, and so any direct measurement on maintenance efficiency cannot be performed early in life. The choice of a selection criteria must take these factors into account, and from an applied point of view, must also consider the likelihood of adoption by producers.

The cost of measuring feed intake with current technology means that the information should be collected carefully on the appropriate animals which are likely to contribute the maximum amount of genetic information. Hence it is likely that selection on feed utilisation efficiency will be based on performance testing of elite individuals at a central testing station. A possible selection criteria may be on a test of elite animals for maintenance efficiency at maturity. This approach would extend the generation interval, hence reducing the rate of response to selection in other traits included in the breeding objective, and so is unlikely to be adopted by animal breeders. Hence direct selection on maintenance efficiency is not a viable option. In order to reduce the generation interval it would be more desirable to test young animals for efficiency using a post-weaning test, and use post-weaning efficiency as a selection criteria to indirectly select for maintenance efficiency.

The correlated response in the desired trait by indirect selection on a secondary trait is given by Falconer (1981) as:

$$CR_Y = i_X h_X r_g \sigma_{g_Y} \qquad 2.1$$

where:

CR_Y = correlated response in trait Y to selection on trait X;
i_X = intensity of selection on trait X;
h_X = square root of the heritability of trait X;
r_g = additive genetic correlation between traits X and Y;
σ_{g_Y} = additive genetic standard deviation in trait Y.

Assuming that additive genetic variation for the desired trait exists, the essential features of a second trait to be used as an indirect selection criteria are that it is heritable and is genetically correlated with the desired trait. Hence, for indirect selection to improve maintenance efficiency a measure of efficiency is required which can be measured on young animals, is heritable and is genetically correlated with maintenance efficiency. The different measures of efficiency discussed in this section will be evaluated in light of these requirements.

2.3.2 Gross Efficiency

The most widely used measure of efficiency in the literature is that of gross efficiency or its inverse, feed conversion ratio. Gross efficiency is defined as the ratio between feed inputs and production outputs. For meat production systems where the outputs can be measured as the weight gain of animals, gross efficiency becomes the ratio between feed intake and weight gain. Hence gross efficiency is normally expressed as the gain : feed ratio (or as feed : gain, i.e. feed conversion ratio) over a defined period of growth. The period of growth over which gross efficiency is measured may be defined on a time constant basis (growth and feed measured between two set points in time), a weight constant basis (feed required for growth from weight *a* to weight *b*) or a maturity constant basis (feed and weight gain measured from stage of maturity *a* to *b*, where maturity may be defined as weight as a proportion of mature weight).

It is well documented that gross efficiency is both phenotypically and genetically correlated with growth rate. Brelin and Brannang (1982) summarised four studies on cattle which reported a genetic correlation between growth rate and feed conversion ratio defined on a weight constant basis ranging from -0.61 to -0.95. Heritability estimates for feed conversion ratio from these studies ranged from 0.36 ± 0.07 to 0.45 ± 0.05. Brelin and Brannang (1982) estimated genetic and phenotypic correlations between feed conversion ratio and daily weight gain to be -0.93 ± 0.56 and -0.55 respectively, with feed conversion ratio having a heritability of 0.35 ± 0.24 in a group of Swedish Red and White cattle of mixed sex.

Gross efficiency is also highly correlated with production in dairy cows. Buttazzoni and Mao (1989) cite a number of studies showing high positive phenotypic correlations and very high genetic correlations between the gross efficiency of milk production and milk yield. Korver (1988) reviewed the literature on gross efficiency of dairy production and concluded that gross efficiency mostly reflects the greater dilution of the maintenance requirement in high producing cows. The high genetic correlations between gross efficiency and production have led several investigators to suggest that selection for production (growth rate, milk production, etc) in livestock will produce a correlated increase in gross efficiency (eg Korver 1988; Mrode *et al.* 1990), and hence there is little justification for measuring feed intake in order to improve gross efficiency.

While selection for gross efficiency, whether by direct or indirect selection, may improve the efficiency of the animals actually producing the saleable product, it will not necessarily improve the efficiency of the entire production system. To use beef production as an example, genotypes with high growth rates and hence high gross efficiency while growing tend to also have high mature weights and hence higher feed requirements at maturity. Gross efficiency of growing animals is largely a function of maturity patterns (Salmon *et al.* 1990) and if an increase in feed requirements at maturity offsets the gains in growth efficiency there may be no change in biological efficiency. There is a multitude of literature discussing the impact of increases in mature size on biological efficiency, with the general conclusion being that an increase in mature size will have little effect on efficiency, at least in maternal breeds (eg Holmes 1973; Andersen 1978; Dickerson 1978; Fitzhugh 1978; Barlow 1984).

As discussed in section 2.1.2, the impact of an increase in feed required to maintain adults on the overall efficiency of an entire production system will depend on the system itself and the species. For species with high reproductive rates, an increase in gross efficiency may provide an increase in the efficiency of the entire system as the increase in maintenance requirement for the breeding herd is relatively small. However, in production systems where the maintenance costs of the breeding herd are high relative to production output, such as in beef production, an increase in the maintenance requirement of adult animals may offset the gains which are made by increasing the gross efficiency of growing animals.

Gross efficiency is a relevant measure of efficiency for situations where only growing animals are fed, such as in a feed-lot. It is also useful for nutritional comparisons where uniform genotypes are used. However, gross efficiency is inadequate for making comparisons between the efficiency of genotypes in the context of an entire production system where reproductive rates are low and the maintenance cost of the breeding herd is significant,.

2.3.3 Net Efficiency

Net efficiency, or partial efficiency of growth, is essentially the ratio of feed intake in excess of maintenance requirement to weight gain. This concept has been used extensively by nutritionists when formulating equations to predict feed requirements. However, as discussed in section 2.2.1, the division of feed requirements of growing animals into requirements for maintenance and for gain is an artificial division and is not necessarily appropriate for consideration of the efficiency complex. In addition, measurement of net efficiency on individual animals requires complex metabolic studies and therefore net efficiency is not suitable for use in selection programs to make genetic improvements to the efficiency of a production system.

An alternative method for estimating net efficiency using data collected under normal field conditions was suggested by Walter and Mao (1989). This essentially involved fitting regressions which allow the estimation of net efficiency from the regression coefficients, and gave reasonable agreement with estimates from more complex metabolic studies. However Veerkamp and Emmans (1995) reviewed this method and concluded that "although this method of identifying genetic variation in partial efficiency and genetic covariances between the partial efficiencies is appealing ... it is not clear that the technique is a valid one".

2.3.4 Residual Feed Intake

2.3.4.1 Defining residual feed intake

The concept of "residual feed intake" was first used by Koch *et al.* (1963) who examined a number of statistical adjustments which could be used to provide a measure of feed efficiency which recognised that differences in both weight maintained and weight gain affect feed requirements. Koch *et al.* (1963) suggested that feed intake data could be adjusted for body weight and weight gain, effectively partitioning feed intake into two components: 1) that used for maintenance and weight gain; and 2) a residual portion. The residual portion of feed intake is then an indicator of the efficiency of an individual, with a negative residual feed intake indicating an individual which has consumed less feed to achieve a given level of production than would be expected from the population average.

This concept can be extended further and residual feed intake can simply be defined as the difference between the actual feed intake observed and the feed intake predicted from a model. The model can be formulated to include adjustments for any factors which may affect feed intake, such as weight maintained, changes in bodyweight and other production traits. Because residual feed intake is essentially the error term in the statistical model used to predict feed intake, the phenotypic correlation of residual feed intake with any factor included in the model is zero, and hence residual feed intake as a measure of feed efficiency is phenotypically independent of the level of production. In this way residual feed intake differs from gross efficiency which tends to be highly correlated with the level of production.

Some authors (e.g. Brelin and Brannang 1982; Korver 1988) have suggested that residual feed intake represents inherent variation in the basic processes of efficiency, such as efficiency of nutrient absorption, the rate of basal metabolism and the energetic efficiencies of the processes of growth and maintenance. If this is the case then there may be a strong relationship between residual feed intake of growing animals and other aspects of efficiency (e.g. efficiency of maintenance at maturity), as residual feed intake would represent variation in the intrinsic efficiency of individuals. For this reason residual feed intake has been identified as the measure of efficiency most likely to be suitable for improving maintenance and production efficiency.

2.3.4.2 Components of residual feed intake

Residual feed intake reflects variation in feed intake which is not explained by a model, and so the results obtained will depend upon the model which is used. The source of this variation is of interest, as any additional factors which explain some of the residual variation may improve our understanding of the efficiency complex. The unexplained variation may arise from a number of different sources. These sources include measurement errors and random deviations from the model as well as individual variation in the coefficients of the model and other variation not explained by the model. Hence it is unlikely that all of the residual variation observed is due to differences between individuals in their efficiency of utilising feed. However the question of interest when variation in feed utilisation efficiency is being examined is how much of the residual variation reflects real differences in efficiency between individuals, and what is the cause of these differences?

In genetic terminology residual feed intake may be considered to consist of genetic effects, environmental effects and random error. The potential of residual feed intake as a measure on which selection for efficiency can be based will be determined by the heritability of residual feed intake and its genetic correlation with maintenance or production efficiency. As residual feed intake is dependant on the model of feed intake used in the calculation, it follows that the heritability of residual feed intake must also be dependant on the model used. However, a search of the literature reveals that most authors estimating the heritability of residual feed intake have used a similar model to calculate residual feed intake which essentially adjusts for body weight (or metabolic body weight) maintained and any identifiable energy sink associated with production, such as changes in body weight, level of milk production or egg production, during the period in which feed intake was measured, and so it is possible to make meaningful comparisons between different studies.

2.3.4.3 Genetic variation in residual feed intake

The literature contains reports which suggest that genetic variation in residual feed intake of poultry, pigs and cattle exists, and the results for these species are summarised below. There has been little work on genetic variation in residual feed intake in other livestock species.

Poultry

In a review of energy metabolism in poultry, Luiting (1987) found that between 30 and 90% of the variation in metabolisable energy intake by laying hens could be explained by variation in metabolic weight, egg production and weight gain. Inclusion of interactions, quadratic terms, estimates of metabolic weight other than $(\text{body weight})^{0.75}$, age at first egg and separation of changes in body weight into positive and negative components generally did not increase the amount of variation in feed intake accounted for by the model. Estimates of heritability of residual feed intake in poultry include 0.22 ± 0.08 to 0.64 ± 0.15 (Hagger and Abplanalp 1978), 0.25 ± 0.04 to 0.33 ± 0.05 (Wing and Nordskog 1982), 0.07 ± 0.25 to 0.51 ± 0.29 in Rhode Island Reds and 0.22 ± 0.14 to 0.52 ± 0.17 in White Leghorns (Bentsen 1983) and 0.42 to 0.62 (Luiting 1991). From these estimates it would appear that there is genetic variation in residual feed intake of poultry, and that it is moderately heritable.

Several studies have examined changes in the heritability of residual feed intake over time in poultry, including those of Hagger and Abplanalp (1978), Bentsen (1983) and Luiting (1991). These studies revealed a trend for the heritability of residual feed intake to be high early during the laying period and decreasing later to stabilise at around 0.2 to 0.4. Luiting (1991) examined this trend in greater detail by separating the components of additive genetic variance and environmental variance and examining the trend of these over time. The amount of additive variance seemed to show little trend with time whereas the amount of environmental variance increased with increasing age of the hens, indicating that the trend seen in the heritability of residual feed intake was due to the increase in environmental variance. Luiting (1991) also found that the genetic correlations of residual feed intake between measurements were moderate (between 0.6 and 0.8) in young birds (up to 32 weeks of age) and were high (close to unity) in mature birds. Bentsen (1983) and Luiting (1991) both concluded that the genetic sources causing variation in residual feed intake during the early period of laying differed from those giving rise to the variation observed in later periods.

Pigs

There is little information in the literature concerning residual feed intake measured on pigs although the information present suggests that there genetic variation in residual feed intake of pigs exists. Foster *et al.* (1983) estimated residual feed intake on three breeds, Landrace, Large White and Welsh, and obtained a pooled estimate of heritability of 0.30 ± 0.08. Mrode and Kennedy (1993) estimated residual feed intake of littermate pairs of Landrace, Yorkshire and Duroc pigs. They reported differences between breeds, with Landrace having higher residual feed intakes (i.e. less efficient) than Yorkshire and Durocs. The three models used to calculate residual feed intake in their study accounted for 48 to 56 % of the phenotypic variation in feed intake, and resulted in estimates of heritability from 0.30 ± 0.06 to 0.38 ± 0.05. Residual feed intake showed a positive genetic correlation with average daily gain and backfat thickness, although the magnitude of the correlation varied considerably according to the model used.

Roehe *et al.* (1994) examined residual feed intake on boars from 100 to 170 days of age, with feed intake recorded every second week throughout the test period. The heritability of residual feed intake fluctuated between different measurement weeks, and ranged from 0.14 ± 0.07 to 0.46 ± 0.11. In contrast to Luiting's results with poultry, Roehe *et al.* found that the fluctuations in heritability of residual feed intake of pigs were due to fluctuations in both the additive genetic variance and in environmental variance. Heritability of residual feed intake was equal to or greater than that of gross efficiency in all periods examined.

Cattle

The literature reporting the measurement of residual feed intake in cattle is sparse and is taken from a limited number of studies, most of which were published during the past 10 years although the concept has been used in poultry and pigs for longer than this. The exception to this is the study of Koch *et al.* (1963), when the concept of residual feed intake was initially suggested. Koch *et al.* reported a heritability estimate of 0.28 ±0.11 on bull and heifer calves of British beef breeds. This estimate is similar to most other estimates on the heritability of residual feed intake in growing cattle. Other estimates of heritability of residual feed intake of growing cattle are 0.27 ± 0.23 (Brelin and Brannang 1982), 0.25 and 0.22 ± 0.11 (Korver *et al.* 1988, 1991), 0.08 ± 0.05 to 0.36 ± 0.17 (depending on age, feeding regime and the model used in calculation of residual feed intake; Jensen *et al.* 1992) and 0.14 ± 0.12 (Fan *et al.* 1995). The studies of Brelin and Brannang (1982) and Jensen *et al.* (1992) included measures of body composition in the model used in the calculation of residual feed intake. Estimates of residual feed intake in lactating cattle which involve corrections made for milk production include 0.19 ± 0.12 (van Arendonk *et al.* 1991), 0.02 (Ngwerume and Mao 1992) and 0.00 or 0.04 (Svendsen *et al.* 1993).

The estimates cited above show that residual feed intake in growing cattle has a component of additive genetic variation and so it is likely that some response in patterns of feeding and growth would occur if selection for residual feed intake was to be practised. Whether any genetic variation exists in lactating dairy cattle is still open to debate. If residual feed intake is to be used as a criteria for indirect selection to improve maintenance or production efficiency, the genetic correlation between residual feed intake of growing animals and maintenance or production efficiency of mature animals is also important. The literature contains only one estimate of this nature, between residual feed intake of growing dairy heifers and residual feed intake of lactating dairy heifers where the genetic correlation was 0.58 (Nieuwhof *et al.* 1992). This estimate suggests that residual feed intake is a promising selection criteria for improvement of efficiency. However more estimates of a similar nature are required for beef cattle on roughage diets in order to determine the potential use of residual feed intake in a different cattle population and under a different production system. The estimate of Nieuwhof *et al.* (1992) does not give any clues as to the basis of the variation in production efficiency and whether the correlated response is due to improvement in maintenance efficiency. While improvement of production efficiency is the ultimate objective, it is of interest to understand how the relationships between feed intake, growth and production will be altered.

2.3.4.4 Genetic vs phenotypic residual feed intake

Although residual feed intake is phenotypically independent of the traits used as adjustments in the model, Kennedy *et al.* (1993) pointed out that where residual feed intake is calculated by adjusting for phenotypic production traits, the genetic correlation between residual feed intake and the production traits will not necessarily be zero, and hence there may be some correlated response in these traits. This has been shown in practice in the studies of Jensen *et al.* (1992) and Mrode and Kennedy (1993) where residual feed intake was not phenotypically correlated with traits included in the model used to calculate residual feed intake, but was genetically correlated with these traits. This has implications on the assessment of genetic variation in residual feed intake, as the heritability of residual feed intake calculated from a phenotypic regression may largely reflect genetic variation in the component traits rather than genetic variation in the relationship between feed intake and production. All of the studies quoted above where heritability of residual feed intake was estimated used residual feed intake calculated from a phenotypic regression.

Kennedy *et al.* (1993) suggested that to obtain a measure of efficiency which is genetically independent of production, residual feed intake could be calculated from genotypic regression of feed intake on production traits, rather than phenotypic regression. This would ensure that the genetic correlation of residual feed intake with the production traits is zero and hence the only response to selection on residual feed intake would be a decrease in feed intake, with no correlated response in the production traits. In general, the heritability of residual feed intake estimated from genotypic regression is lower than that estimated from phenotypic regression as it only reflects genetic variation in the relationship between feed intake and production.

Only two studies have evaluated the heritability of residual feed intake calculated from genotypic regression. Kennedy *et al.* (1993) utilised an example from the data of Moore *et al.* (1992), where residual feed intake was calculated using genotypic regression adjusting for fat-corrected milk yield and body weight. The heritability of residual feed intake calculated using this method was 0.01, compared to an estimate of 0.14 obtained using residual feed intake calculated from phenotypic regression. This suggests that there is no genetic variation in the relationship between feed intake and production in dairy cows. Veerkamp *et al.* (1995) also estimated the heritability of residual feed intake of dairy cows calculated by genotypic regression, with the result (0.05) being similar to that of Kennedy *et al.* However Veerkamp *et al.* (1995) showed that when residual feed intake is estimated by genotypic regression from parameters obtained from relatively small data sets, the heritability is biased downwards. Hence these results are not conclusive evidence that genetic variation in the relationship between feed intake and production does not exist in dairy cows. Further estimates of this nature are required from larger data sets and in different populations (eg beef cattle).

It is important to note that residual feed intake does not add any genetic information to that known from the component traits. This was pointed out by Kennedy *et al.* (1993), who showed that single trait selection on residual feed intake (calculated from phenotypic regression) is equivalent to multiple trait index selection on feed intake and the production traits. Residual feed intake calculated from genetic regression is equivalent to a restricted selection index calculated to produce no change in the production traits. Kennedy *et al.* (1993) showed that the genetic parameters of residual feed intake (and hence the value of including feed intake information in selection decisions) are dependant on the heritabilities of feed intake and the component production traits, and the genetic and environmental correlations between them. In particular, if the genetic correlation between feed intake and the production traits is high there is likely to be little genetic variation in residual feed intake independent of production traits, and hence there would be little value in measuring feed intake.

Kennedy *et al.* (1993) suggested that selection for efficiency would be best achieved using a conventional selection index with relative values determined from an appropriate profit function. This approach would ensure that the index is optimal for improving the efficiency of an entire production system as all feed inputs and production outputs of the system can be included. However, as pointed out by Veerkamp *et al.* (1995), residual feed intake is still of interest as it allows comparison of efficiency between individuals.

2.3.4.5 Correlated responses to selection on residual feed intake

The value of selection to improve efficiency will be determined not only by the amount of response in efficiency which is achieved, but also by other correlated responses to selection. A knowledge of the correlated responses to selection is important in any selection program as the correlated responses may be of great significance in determining the value of selection in economic terms.

There is very little information on the genetic correlations of residual feed intake with other traits and the likely consequences of selection on residual feed intake in the literature. Published estimates of genetic correlations with residual feed intake include those of Korver *et al.* (1991), Van Arendonk *et al.* (1991) and Nieuwhof *et al.* (1992) on growth, feed intake and milk production traits and those of Jensen *et al.* (1992) on growth, feed intake and carcass traits. Hence speculation as to possible correlated responses to selection on residual feed intake is frequently based on indirect evidence rather than on published estimates of genetic correlations.

Intuitively one might expect some correlated response to selection on residual feed intake in body composition traits, as body composition has a large effect on efficiency (see section 2.1.4.1). However, the magnitude and direction of the response is difficult to predict, as lean animals are energetically more efficient to grow, but are less efficient to maintain. Hence the response may depend very much on the stage of maturity of the animal when residual feed intake is measured, as stage of maturity determines body composition and the relative partitioning of energy between maintenance and growth. Jensen *et al.* (1992) compared residual feed intake calculated from models with or without adjustments for carcass composition and found that the models were closely correlated, suggesting that similar results with residual feed intake would be obtained regardless of whether carcass composition was included in the model or not. The genetic correlations estimated in this study had large standard errors, and almost all estimates were within one standard error from zero, and so it is difficult to make firm predictions about correlated responses from these estimates. In general the study showed that there was a negative correlation between residual feed intake and fatness, so that genetically fatter animals were more efficient, suggesting that selection for residual feed intake would lead to increased deposition of fat. This may not be a desirable response on marketing grounds. On an important practical note, many meat quality traits are affected by body composition, and so it is possible that these traits may also be genetically correlated with residual feed intake. Knowledge of these genetic correlations before selection programs are implemented is important, as no selection for biological efficiency will be economically beneficial if meat quality is compromised.

Van Arendonk *et al.* (1991) examined the genetic correlation of residual feed intake with milk production of dairy heifers after a phenotypic adjustment for fat and protein corrected milk production had been included in the model for residual feed intake. They found a genetic correlation of 0.02 and -0.13 between residual feed intake and fat and protein corrected milk production at 105 and 305 days of lactation respectively. This result suggests that selection for residual feed intake would produce little correlated response in milk production. The comparisons of Ferrell and Jenkins (1984a), Taylor *et al.* (1986), Solis *et al.* (1988) and Montano-Bermudez *et al.* (1990) across breeds showed that efficiency of maintenance is associated with differences in milk production, and so one might expect that selection for efficiency may have some affect on milk production. The conflict between this expectation and the results of Van Arendonk *et al.* (1991) may be due to the much greater variation across breeds than between the cattle in van Arendonk's study. Alternatively, residual feed intake of lactating heifers measured in the study of Van Arendonk *et al.* (1991) may not be related to maintenance efficiency in non-producing animals.

The inter-breed comparisons cited above relate maintenance efficiency to variation in productive potential, of which milk production is just one aspect. Hence it is also possible that improvements made in the efficiency of maintenance may result in correlated responses in other traits which determine productivity. One such trait which has a large effect on the overall efficiency of an entire production system is reproduction. Improvements in maintenance efficiency may influence reproductive traits such as age at puberty, gestation length, post-partum anoestrus interval and other associated traits. Again the direction and magnitude of the correlated response is difficult to predict. For instance, as Bos Indicus cattle have higher maintenance efficiency (Frisch and Vercoe, 1984) but poorer reproductive rates than British breeds in the absence of environmental stresses (Pitchford *et al.* 1993), one might predict that selection for improved maintenance efficiency may reduce the ability of the female to return to calf. Alternatively it might be argued that an animal with higher maintenance efficiency may have more surplus energy available after the cost of maintenance is removed, and therefore more energy is available for reproduction. The outcome will be dependant on the genetic and environmental influences on each trait, which are largely unknown for efficiency. More definitive experiments are still required to examine the relationships between maintenance efficiency and such traits, and the likely correlated responses in these traits to selection for efficiency.

The other trait of interest when selecting on residual feed intake is the correlated response in feed intake itself. Three studies report genetic correlations between intake and residual feed intake. Korver *et al.* (1991) estimated a high genetic correlation between residual feed intake and energy intake of 0.97 on growing dairy heifers. Jensen *et al.* (1992) found a genetic correlation between daily energy intake and residual feed intake of 0.60 ± 0.12 on bull calves of dairy breeds. Van Arendonk *et al.* (1991) using lactating dairy heifers found an genetic correlation between residual feed intake and energy intake of 0.89. These studies all suggest that selection for improved efficiency (i.e. lower residual feed intake) will produce a correlated genetic reduction in feed intake.

2.4 SUMMARY

Improvement of feed utilisation efficiency is an important avenue for increasing profitability of animal production systems in Australia, as has been demonstrated in the last 20 years in the intensive monogastric industries. Improvement of feed efficiency has not received as much emphasis in the extensive, ruminant based industries, largely because of difficulties in quantifying the cost of feed and measuring feed consumption, but also because so much emphasis has been placed on improving productive output per animal. However, more economically relevant is productive output per hectare, and improvements in this may be made by improving feed utilisation of individual animals.

It seems fairly certain that genetic variation in the efficiency of feed utilisation for maintenance exists in cattle. There is less certainty as to the amount of genetic variation in growth efficiency in cattle. Improving maintenance efficiency appears to be the best strategy for improving the overall feed efficiency of an entire production system in species with low reproductive rates, such as cattle. This assumes that maintenance efficiency of non-producing animals is correlated with the efficiency of a producing animal, an assumption which seems likely but should be tested.

If selection for maintenance or production efficiency is to be implemented, there are a number of issues which must be resolved. The first of these is the choice of a selection criterion upon which selection can be based. Due to the practical difficulties involved in measuring feed intake with current technology, this question is of real concern as only a limited number of elite animals will be able to be measured, and it is unlikely that maintenance efficiency will be selected on directly. Hence an appropriate selection criteria will probably involve indirect selection of animals on a measure which can be taken on young animals in a post-weaning test. This assumes that there is a relationship between post-weaning feed intake and efficiency and efficiency of maintenance or production at maturity.

Although residual feed intake is equivalent to a biological selection index and may not be the optimal index for selection for efficiency, it is an appropriate measure of efficiency for making comparisons between animals. Hence residual feed intake can be used to investigate genetic variation in feed intake and efficiency. Currently there are gaps in the knowledge required to implement selection for efficiency. These gaps include issues such as the optimum stage of maturity at which to measure efficiency, the optimum length of test for feed intake and efficiency, the repeatability of efficiency and the relationship between post-weaning efficiency and efficiency of maintenance and production at maturity.

Another issue of concern is the consequences of selection for efficiency. It has been shown that some of the variation in maintenance efficiency between breeds is associated with differences in productive potential and body composition. Hence it is possible that selection for maintenance efficiency within a breed may produce correlated responses in other traits, such as reproductive traits and body composition traits affecting meat quality and meat yield. It is important to have some knowledge of the likely outcomes of selection for efficiency before the transfer of the technology to industry.

An overall limitation to the process of improving the efficiency of feed utilisation is the deficiency of knowledge about the basic biology controlling efficiency. Quantification of the energetic costs of deposition and turn over of protein and fat is difficult as in reality, growth of animals is a result of a large number of physiological interactions. Perhaps one of the biggest limitations in the field is the lack of suitable methods for measurement of body composition of live animals, as this means that energy retention is difficult to quantify and is often approximated by live weight changes, an approximation which is not always accurate or even appropriate. Improvements in the understanding of the processes involved in growth and efficiency may assist in the design of strategies to improve the efficiency of feed utilisation in animal production.

Chapter 3. Variation in feed intake and efficiency of Angus bulls.

3.1 Introduction

In Chapter 2 literature was cited which suggested that a possible avenue to improve the production system efficiency of species with low reproductive rates was to improve the efficiency with which mature animals use feed for maintenance (e.g. Thompson and Barlow 1986; Webster 1989). A number of studies were reviewed which showed that genetic variation exists in maintenance efficiency of cattle. It was concluded that it may be possible to use selection to make genetic gains in maintenance efficiency.

In order to select for maintenance efficiency a selection criteria is required which can be measured on young animals and will give rise to a correlated response in the efficiency of mature animals. Residual feed intake has been identified as a potential measure useful for investigation of variation in efficiency. Residual feed intake has been shown to be moderately heritable in young cattle in a number of studies (see section 2.3.4.3) but there are still a number of gaps in the knowledge of genetic and phenotypic parameters associated with feed intake and residual feed intake.

Possibly the most important information required are the phenotypic and genetic relationships between efficiency of young, growing cattle and maintenance and production efficiency of mature cows. Currently there are no data sets from which these parameters can be estimated for beef cattle, although a current research initiative at Trangie Agricultural Research Centre is developing a data set from which the relevant parameters for Australian British breed cattle will be able to be estimated. Other missing information concerning efficiency of growing cattle includes the repeatability and changes which may occur over a relatively short period. This information is of interest and can be estimated from data sets which are currently available. There has been no published reports of the repeatability of residual feed intake, with the exception of the results of Jensen *et al.* (1992) where the feeding regime differed across periods and so the correlation between periods was confounded with feeding regime.

This chapter reports the analysis of an existing data set to examine questions concerning the repeatability of feed intake and residual feed intake over relatively short periods. The data also gave the opportunity to make some comparisons between residual feed intake and feed conversion ratio as two alternative measures of feed efficiency.

3.2 Materials and methods

3.2.1 Description of data

The data used in this chapter consisted of post-weaning feed intake and weight data collected on young bulls from the Angus herd at Trangie Agricultural Research Centre (NSW Agriculture) from 1964 to 1973. Bulls were born during the autumn of each year and were raised together until weaning. After weaning the bulls were put into small bare yards which contained water troughs which the bulls had access to at all times except during feeding times. Twice a day, in the morning and afternoon, the bulls were locked in individual stalls for two hours and offered feed ad libitum during this time. The weight of feed offered and the refusals were recorded at each feeding time. The liveweight of each bull was recorded fortnightly during the test period in all years except 1964 when liveweight was recorded monthly.

The composition of the ration offered remained constant across years and consisted of fixed proportions of maize (10 %), oats (23 %), barley (7 %), bran (5 %), linseed meal (3 %), meat meal (2 %), lucerne chaff (13 %) and cereal chaff (37 %). The average energy concentration of the ration was 9.4 MJ/kg dry matter, with 12 % crude protein. While the composition of the ration was constant, the quality of the ration varied across years due to variations in the feed value of the ration constituents.

Data was available on a total of 377 bulls from 1964 to 1973, with the exception of 1969 when no data was available. The bulls were by 58 sires, of which 30 sires also had feed intake records. Thirteen of the sires were used in more than one year, providing some links across years, although not all years were linked. Details on the number of bulls tested in each year and sire usage are given in Table 3.1. The average number of progeny per sire used was 6.5.

Table 3.1 Summary of the structure of the data from Angus bulls.

Year	Number of bulls tested	Number of sires represented	Number of days of feed intake data
1964	35	8	140
1965	39	8 (+ 1)[a]	161
1966	19	3 (+ 3)	169
1967	29	4 (+ 2)	170
1968	51	4 (+ 5)	153
1970	55	8	154
1971	46	7 (+ 2)	126
1972	53	11	140
1973	50	5	91
Total	377	58	

[a] Numbers in the brackets represent sires already used in previous years.

3.2.2 Derivation of traits

The feed intake data was divided into five periods for analysis. The divisions consisted of a pre-test period and four test periods of 4 weeks each. In 1971 and 1973 there was insufficient data for four test periods and so only 12 and 8 weeks of data were analysed respectively. The length of the pre-test period varied between years but consisted of at least 4 weeks of feeding. This data was removed from the analysis as the bulls were adjusting to the feeding regime during this time and the data contained irregularities. Each trait was calculated for each of the four test periods, defined as weeks 1-4, 5-8, 9-12 and 13-16. The traits were also calculated for three combination periods consisting of weeks 1-8, 9-16, and 1-16. The exception to this was average daily gain which was calculated over the four test periods using a regression approach as outlined below.

Weight data for each animal over the total test period (excluding the pre-test period) was modelled by regression against age using PROC REG (SAS 1989) with the model shown below used.

$$W_i = a + b.(AGE_i) + e_i \qquad 3.1$$

Where:

W_i = Weight of the bull at time i;
a, b = regression estimates for the intercept and slope of the regression;
AGE_i = age of the bull at time i;
e_i = error in weight at time i.

This approach was adopted in order to minimise the influence of measurement errors on the weight data which was to be used in the model of feed intake. The estimates obtained from the regression were then used to describe the growth of each individual during each four week feeding period. Average daily gain during the period was equal to the slope of the regression (b). As the regression was calculated using all available data the slope represented the daily gain averaged across all periods, and therefore the same estimate was used in calculations involving each of the four periods. This approach has recently been shown to increase the accuracy of measurement of residual feed intake where feed intake is measured over short periods and insufficient weight data is available to provide an accurate description of growth during this period in which feed intake is measured (D. Robinson, personal communication). The mid-weight of the animal for each period was calculated as the weight of the animal at the mid-point of the feeding period by using the regression estimates and substituting the age of the bull halfway through the feeding period into equation 3.1. Metabolic mid-weight was the mid-weight of the bull raised to the power of 0.73.

Feed intake data was modelled by multiple linear regression (Proc GLM, SAS 1989) in order to calculate the residual feed intake of each animal. The model fitted is given below.

$$F_{ij} = \mu + Y_j + \beta_1(A_i - \overline{A}_.) + \beta_2(M_i - \overline{M}_.) + \beta_3(G_i - \overline{G}_.) + Y_j * \beta_{2_j}(M_i - \overline{M}_.) + Y_j * \beta_{3_j}(G_i - \overline{G}_.) + e_{ij}$$

Where:

F_{ij} = daily feed intake for bull i during the feeding period;
μ = mean daily feed intake;
Y_j = year of test (1964 - 68, 1970 - 73);
$\beta_{1,2,3}$ = partial regression coefficient of feed intake on age, metabolic mid - weight and average daily gain respectively;
A_i = age of bull i at start of test;
G_i = average daily gain of bull i during the whole test period;
M_i = metabolic mid - weight of bull i during the feeding period;
e_{ij} = residual error in daily feed intake

The model was fitted to data from periods 1-4, 5-8, 9-12, 13-16, 1-8, 9-16 and 1-16. Residual feed intake was calculated as the residual error in daily feed intake remaining after the model had been fitted to the data.

Feed conversion ratio for each period was calculated as the average daily feed intake for the period divided by the average daily gain over the entire test period.

3.2.3 Analyses

Phenotypic analysis

The traits used in the phenotypic analysis of the data included daily feed intake, residual feed intake, feed conversion ratio, metabolic mid-weight and average daily weight gain. Partial correlations were calculated between periods within traits and between traits calculated over the four test periods after adjusting the data for year and age of the bulls at the start of the period. The correlations were formed using the repeated measures option of Proc GLM (SAS 1989). Repeatability over the four 28-day periods was calculated for actual feed intake and residual feed intake from the formula given below (see Appendix B for derivation of formula).

$$R = \frac{MS_B - MS_W}{MS_B + (n-1)\,MS_W}$$

where:

R = repeatability of the trait;
MS_B = Mean squares between subject;
MS_W = Mean squares within subjects;
n = number of repeated measurements.

Genetic Analysis

The genetic analysis of the data was restricted to univariate analysis of actual feed intake, residual feed intake and feed conversion ratio. The genetic correlations between the traits were unable to be reliably estimated due to an insufficient number of records in the data. For most traits there were 377 records available, with the exception of traits which involved period 3 or 4 which had missing data for 1971 and 1973. For analysis of the period including the four test periods all available data for bulls in 1971 and 1973 was used. A further 938 animals were included in the analysis from base pedigree information. All genetic analyses were performed using DFREML v2.1 (Meyer 1993). The same model (model 1) was fitted to all traits and is given below.

$$y_{ij} = \mu + Y_i + b_1 AGE_{ij} + a_j + e_{ij}$$

where:

y_{ij} = the trait measured in year i on bull j;
μ = overall mean of all observations;
Y_i = fixed effect of year (i = 1964..1968, 1970..1973);
AGE_{ij} = age of bull j at the start of the test period;
b_1 = partial regression coefficient of AGE;
a_j = random effect of the additive genetic merit of bull j;
e_{ij} = error component of the model.

Phenotypic coefficients of variation for various traits were calculated from the genetic analysis after the effects of year and age were removed. Because the mean residual feed intake is zero (by definition), the coefficient of variation for residual feed intake was calculated by dividing the standard deviation in residual feed intake with the mean feed intake.

3.3 Results

Mean age at weaning, age and weight at the start of the test period, daily weight gain and daily feed intake are shown for each year in Table 3.2. The weight at the start of period one and the average daily gain are calculated from the regressions which were fitted to the weight data over the entire test period. Visual examination of plots of the fitted line and the raw weight data showed that the regression described the growth of the bulls over the test period adequately as growth during the test period appeared to be linear. The only exception to this was for bulls in 1971 where the bulls appeared to have low growth rates for the first 28-day period, after which growth rates improved. The reason for the low initial growth rates in 1971 is not known, but the average daily feed intake of the bulls was also considerably lower in this year. These aberrations may be due to the quality of the ration in 1971, as a mouse plague that year meant that there was considerable feed spoilage (R. Barlow, personal communication). The data from 1971 was retained in the analysis, as it contained records of bulls which were used as sires in subsequent years and so contributed valuable genetic information. However, as data from 1971 and 1973 did not contain four feeding periods this data was not used in the calculation of correlations.

A summary of the analysis of variance table for the linear model of feed intake is presented in Table 3.3. The model accounted for a large amount of the variation in feed intake in all periods examined, ranging from 86.1 to 95.2 % of the variation. The effects of year and age at the start of the test accounted for a large amount of the variation in the type I (SAS 1989) sums of squares (results not shown), but were of less importance in type III sums of squares, suggesting that most of the differences in feed intake between years was able to be explained by differences in bodyweight. The interactions of year with metabolic midweight and weight gain were included to allow for differences in the quality of the ration offered between years and were significant in most periods. Metabolic midweight accounted for a greater amount of variation in feed intake than average daily gain in all periods, suggesting that variation in weight maintained had a larger influence on feed intake than variation in growth rate.

Table 3.2 Means (± s.d.) for age at weaning, age and weight at start of test period, average daily gain and average daily feed intake during the test.

Year	Age at Weaning (days)	Age at start of test (days)	Weight at start of test (kg)	Average daily gain (kg)	Average daily feed intake (kg)
1964	227 ± 30	255 ± 30	293 ± 29	1.14 ± 0.12	8.94 ± 0.94
1965	174 ± 21	223 ± 21	232 ± 28	1.17 ± 0.11	8.31 ± 0.71
1966	194 ± 18	251 ± 18	286 ± 27	1.20 ± 0.13	8.91 ± 0.92
1967	176 ± 22	234 ± 22	272 ± 31	1.21 ± 0.12	7.69 ± 0.86
1968	206 ± 29	247 ± 29	214 ± 23	1.05 ± 0.11	7.96 ± 0.65
1970	218 ± 18	260 ± 18	269 ± 28	1.00 ± 0.12	8.95 ± 0.89
1971	218 ± 19	260 ± 19	219 ± 25	0.82 ± 0.17	4.43 ± 0.59
1972	227 ± 14	255 ± 14	228 ± 22	1.08 ± 0.12	7.42 ± 0.69
1973	223 ± 16	258 ± 16	266 ± 30	0.94 ± 0.17	7.21 ± 0.93
Overall	210 ± 28	250 ± 24	249 ± 38	1.05 ± 0.18	7.65 ± 1.57

Table 3.3 Percentage sums of squares (type III) accounted for by terms included in the model of feed intake[a].

	1-4	5-8	9-12	13-16	1-8	9-16	1-16
Year	0.5 *	0.2	0.3*	0.8*	0.3	0.6*	0.6**
Age	0.0	0.0	0.0	1.3***	0.0	0.6***	0.2*
midwt$^{0.73}$	9.0 ***	8.3***	4.7***	9.8***	8.9***	13.7***	17.5***
ADG	0.3 ***	0.7***	0.4***	0.5**	0.5***	0.7***	0.8***
Year*midwt$^{0.73}$	0.7 ***	0.5*	0.6***	0.7*	0.5**	0.3	0.2
Year*ADG	0.4 *	0.4	0.3*	0.7*	0.3*	0.7*	0.3
Residual	8.1	9.9	4.8	13.9	7.0	12.2	9.2

* P<0.05; ** P<.01; *** P<.001;

[a] Degrees of freedom for terms including Year were 8 in periods 1-4, 5-8, and 1-8, 7 in period 9-12 and 6 in periods 13-16, 9-16 and 1-16. Residual degrees of freedom were 349 in periods 1-4, 5-8, and 1-8, 301 in period 9-12 and 259 in periods 13-16, 9-16 and 1-16.

Partial correlations between periods for feed intake and residual feed intake are given in Table 3.4. The partial correlations for feed conversion ratio are not presented as they were similar to those for feed intake, due to the fact that feed conversion ratio for each period was calculated using the same value for weight gain and so the variation between periods was solely due to variation in feed intake. Partial correlations between periods were generally higher for feed intake than for residual feed intake. For both feed intake and residual feed intake, correlations between adjacent 28-day periods were higher than correlations between periods separated by a longer period of time. This progressive decrease as the interval between periods increased indicated that the changes in feed intake and residual feed intake between periods were systematic and not just a consequence of random variation and experimental error. The correlation between feed intake over 28 days and feed intake over the total period was around 0.9, indicating that feed intake was still relatively consistent between periods despite these systematic changes occurring. Correlations between residual feed intake measured over 28 days and over the total period were between 0.6 and 0.8, suggesting that residual feed intake was less consistent between periods than was feed intake. The repeatabilities calculated for feed intake and residual feed intake support this conclusion; the repeatability was 0.77 for feed intake and 0.35 for residual feed intake.

Partial correlations between traits calculated using the total test period are given in Table 3.5. The correlations of residual feed intake with average daily gain and metabolic mid-weight were zero as expected as these terms were included in the model used to calculate residual feed intake. The correlation between residual feed intake and feed conversion ratio was 0.38, indicating that the two measures of feed efficiency are not equivalent and reflect different variation. Feed conversion ratio was not correlated with feed intake, but was correlated with average daily gain, indicating that the growth performance of the bull played a large part in determining feed conversion ratio.

The results from the genetic analysis of the feed intake, residual feed intake and feed conversion ratio are given in Table 3.6. The phenotypic coefficient of variation for feed intake and residual feed intake was consistent between periods, being 9 to 10 % for feed intake and 5 to 6 % for residual feed intake. The phenotypic coefficient of variation in feed conversion ratio was more variable between periods, ranging from 9 to 15 %. Heritability of feed intake was low (0.07 to 0.18), while heritability of residual feed intake varied considerably between periods and converged to zero in periods 9-12, 13-16 and 9-16, although values of up to 0.26 were obtained from other periods. The results for periods 9-12, 13-16 and 9-16 may have been due to the fact that fewer records were available for these periods, although estimates for feed intake and feed conversion ratio were obtained. All heritability estimates had moderate standard errors due to the limited number of records available for analysis. Feed conversion ratio was moderately heritable, with heritabilities of around 0.3 for most periods.

Table 3.4 Partial correlations between periods for feed intake, residual feed intake and feed conversion ratio.

Period	1-4	5-8	9-12	13-16	1-8	9-16
Feed intake						
5-8	0.82					
9-12	0.74	0.85				
13-16	0.65	0.76	0.85			
1-8	0.95	0.96	0.84	0.74		
9-16	0.72	0.83	0.96	0.97	0.82	
1-16	0.87	0.93	0.94	0.90	0.95	0.96
Residual feed intake						
5-8	0.51					
9-12	0.26	0.54				
13-16	0.07	0.27	0.54			
1-8	0.87	0.87	0.46	0.20		
9-16	0.18	0.45	0.85	0.90	0.36	
1-16	0.62	0.79	0.79	0.68	0.81	0.83

Table 3.5 Partial correlations between feed intake (FI), average daily gain (ADG), metabolic mid-weight (MMIDWT), residual feed intake (RFI) and feed conversion ratio (FCR) calculated over period 1-16.

	FI	ADG	MMIDWT	RFI
ADG	0.53			
MMIDWT	0.83	0.47		
RFI	0.50	0.00	0.00	
FCR	0.02	-0.69	0.14	0.38

Table 3.6 Genetic parameters from univariate analysis for feed intake, residual feed intake and feed conversion ratio.

	Period						
	1-4	5-8	9-12	13-16	1-8	9-12	1-16
Feed intake							
additive genetic variance	0.096	0.044	0.051	0.134	0.069	0.981	0.066
error variance	0.426	0.557	0.476	0.621	0.436	0.512	0.437
phenotypic c.v.	10.4	10.3	9.0	9.7	9.8	8.9	9.3
heritability	0.18	0.07	0.10	0.18	0.14	0.16	0.13
s.e.	0.09	0.07	0.08	0.10	0.08	0.10	0.08
Residual feed intake							
additive genetic variance	0.049	0.017	0.000	0.000	0.035	0.000	0.018
error variance	0.136	0.194	0.149	0.242	0.115	0.151	0.108
phenotypic c.v.	6.2	6.1	4.8	5.5	5.3	4.4	4.6
heritability	0.26	0.08	0.00	0.00	0.24	0.00	0.14
s.e.	0.12	0.09	-	-	0.12	-	0.11
Feed conversion ratio							
additive genetic variance	0.323	0.322	0.095	0.151	0.335	0.143	0.293
error variance	0.638	0.620	0.462	0.456	0.563	0.368	0.563
phenotypic c.v.	14.6	13.3	9.9	9.4	13.5	8.9	12.5
heritability	0.34	0.34	0.17	0.25	0.37	0.28	0.34
s.e.	0.16	0.15	0.15	0.16	0.16	0.16	0.16

3.4 Discussion

Caution should be exercised when interpreting the results from this analysis due to the feeding regime the bulls were on during the collection of the data. The bulls only had access to feed for two periods of two hours each per day, and so feed intake here is not truly *ad libitum*. Hence the high repeatability of feed intake in this data set may be due to the capacity of the animal to take in sufficient feed during the four hours when it had access to feed. This would not be a factor in animals which had constant access to feed, as the animals without the capacity to take in large amounts of feed in a short period may be able to compensate by eating at a slower rate but for a longer time. The effect of the feeding regime on feed intake is not yet known.

The estimates of repeatability obtained from this data set suggest that while feed intake measured over a 28 day period is relatively repeatable, residual feed intake is less repeatable. The estimates of repeatability for residual feed intake of cattle have no counterparts in the literature with which they can be compared, and so the relevance of this data set to cattle fed *ad libitum* is difficult to assess. The low repeatability of residual feed intake may be due to 28 days being an insufficient period of time for accurate measurement of feed intake and growth performance. Hence a longer test period may be justified. The question of the length of time over which feed intake should be measured in order to obtain a repeatable measure of efficiency is of interest, as expense in measuring feed intake and the inconvenience in management of animals in a central test station means that a short test is preferable. It is difficult to know how best to assess the optimum length of the test period as any measurement of feed intake in growing animals is confounded with age and changes in stage of maturity of the animals. In practice, the best measurement of feed intake or residual feed intake will be the measurement which produces the highest correlated response in desirable traits, such as maintenance efficiency.

The decrease in correlations between 28-day periods with an increase in interval between the periods is of concern as it suggests that the changes in the ranking of animals for residual feed intake which occurred within the 112 day test period were systematic rather than solely due to random error. A similar decrease was also observed in laying hens by Bentsen (1983) and Luiting (1991). The decrease in correlations may be due to temporary environmental effects on feed intake and residual feed intake which cause higher correlations between close periods.

Alternatively the decrease may be due to the action of different genes on feed intake during different periods, as the cattle were growing and maturing during the test. This hypothesis could be tested if sufficient data was available to reliably estimate genetic correlations between feed intake measured in different four week periods. Genetic correlations significantly less than unity would indicate that feed intake was controlled by different genes at different stages of maturity. Alternatively if genetic correlations for feed intake between periods were not significantly different from one, this would support the hypothesis that the decrease in phenotypic correlations observed is due to the action of temporary environmental effects. Unfortunately there was insufficient data available in this study to estimate the heritability of feed intake or genetic correlations of feed intake with other periods.

The decrease in correlations between periods as animals grow older raises the question as to the ability of residual feed intake to predict the maintenance efficiency of an animal when it is mature, either at a phenotypic or genetic level. If changes in ranking for residual feed intake occur over a short period it is probable that there will be greater changes occurring between growing and mature animals and this is likely to have an impact on the use of residual feed intake as a selection criteria upon which indirect selection for maintenance efficiency can be based. Changes in ranking of bulls during growth may be a function of different maturity patterns of individuals with relative changes in body composition influencing efficiency of bulls. Alternatively the changes may reflect changing emphasis in nutrient partitioning and different physiological processes as the animal's metabolism shifts away from accretion of protein and fat and the balance between synthesis and degradation of protein and fat changes. This may mean that the age or stage of maturity at which residual feed intake is measured may be important in determining the response to selection, as residual feed intake measured at different ages may reflect different genetic variation.

The only published study where residual feed intake has been measured at two different stages of maturity is that of Nieuwhof *et al.* (1992), who found that the phenotypic relationship between residual feed intake of growing and lactating dairy heifers was low ($r_p = 0.07$), but the genetic correlation was moderate ($r_g = 0.58$). The results of the present study suggest that in beef cattle there is unlikely to be a strong phenotypic relationship between efficiency post-weaning and at maturity. However, there may still be a genetic relationship between post-weaning and mature efficiency (as suggested by the results of Nieuwhof *et al.* 1992), and therefore further work on the effect of age on residual feed intake appears to be warranted.

The heritability estimates for feed intake in this study were lower than most published estimates. Heritability estimates for feed intake of growing cattle include 0.36 ± 0.24 (Brelin and Brannang 1982), 0.57 ± 0.11 (Korver *et al.* 1991), 0.45 ± 0.17 (MacNeil *et al.* 1991) and 0.25 ± 0.13 (Fan *et al.* 1995). The respective coefficients of variation in feed intake found in these studies were 6.9 %, 9.7 %, 9.7% and 10.1 % to 12.4 %. In this study the heritability for feed intake calculated across the total test period was 0.13 ± 0.08 and the coefficient of variation was 9.3 %. It is difficult to assign any reason for the low heritability found in this data set compared to other estimates. It may be tempting to attribute the low estimate to the feeding regime of the bulls in this data set, as the restriction in feeding time may have removed important variation in feed intake. However, the coefficient of variation in feed intake found in this study is comparable to that reported from other studies, and so there is no evidence suggesting that the feeding regime altered the phenotypic variation in feed intake.

Similarly the heritability of residual feed intake found here was lower than most of those found in the literature. Estimates for heritability of residual feed intake of growing cattle include 0.28 ± 0.11 (Koch *et al.* 1963), 0.27 ± 0.23 (Brelin and Brannang 1982), 0.22 ± 0.11 (Korver *et al.* 1991) and 0.14 ± 0.12 (Fan *et al.* (1995), with coefficients of variation of 4.3 %, 7.7 % and 6.7 % to 11.9 % reported from the latter three studies. This compares with a heritability estimate of 0.14 ± 0.11 and a coefficient of variation of 4.6 % calculated over the total test period in this study.

The heritability of feed conversion ratio was considerably higher than that of residual feed intake in all periods examined. The heritability estimates from this data set (0.20 to 0.35) were similar to those from the literature, as summarised by Brelin and Brannang (1982). Initially this may suggest that feed conversion ratio would be a more appropriate measure of efficiency upon which selection could be based, as a higher rate of genetic gain is likely. However the literature shows that the genetic correlation between feed conversion ratio and growth traits is high (see section 2.3.2), and so selection based on feed conversion ratio is similar to selecting for growth traits alone. This is demonstrated by the study of Mrode *et al.* (1990) who found that selection for lean growth rate to 400 days produced a greater correlated response in feed conversion ratio than was achieved by direct selection on feed conversion ratio. The phenotypic correlations estimated here indicate that feed conversion ratio calculated in the present study was largely influenced by growth rate, whereas residual feed intake is phenotypically independent of growth rate and bodyweight.

Use of feed conversion ratio is problematic from a theoretical point of view also as it is a trait defined as a ratio of two other traits. Simm *et al.* (1987) showed that use of a product trait such as feed conversion ratio does not always lead to appropriate selection decisions. Gunsett (1984) discussed the use of ratio traits and concluded that, when selecting for a trait defined as a ratio, a linear selection index containing the numerator and denominator traits is a more appropriate method of selection. Kennedy *et al.* (1993) showed that residual feed intake is essentially a linear selection index for feed intake and the component traits. Hence residual feed intake, being linear, may be a more desirable method for combining feed intake and growth information for selection decisions than feed conversion ratio.

3.5 Summary

This chapter presents the analysis of feed intake and growth data from Angus bulls fed at Trangie Agricultural Research Centre from 1964 to 1973 in order to investigate aspects of efficiency. Feed intake was highly repeatable, but the repeatability of residual feed intake was considerably lower. The effect of the feeding regime of the bulls on the repeatability and heritability estimates is unknown. Also unknown is the minimum length of feed intake test required in order to produce accurate estimates of feed intake and residual feed intake for use in selection programs.

The results indicated that there may be systematic changes in the ranking of bulls for residual feed intake over a period of 16 weeks. This suggested that changes in residual feed intake may also occur over a longer period as animals grow and mature. If this is the case, then the age or stage of maturity at which residual feed intake is measured may influence the resultant response in maintenance efficiency. This would occur if residual feed intake measured at different ages was determined by a different set of genes (i.e. if the genetic correlation between ages was low), and should be considered when developing appropriate selection strategies for improving maintenance efficiency. Therefore further investigation into the changes in feed intake and residual feed intake which occur as animals mature is needed. Data collected over 16 weeks in cattle is not sufficient to answer questions about such changes.

Chapter 4. Genetic variation and optimal length of test for feed intake, growth rate and efficiency of British breed cattle.

4.1 Introduction

In Chapter 3 results from the analysis of feed intake data collected on Angus bulls from Trangie were reported. These results raised some interesting questions, but interpretation of the results was complicated by the fact that the bulls were on a "restricted *ad libitum*" feeding regime. The effect of this on the repeatability of feed intake and efficiency traits was uncertain. It was suggested that it may be appropriate to repeat the analysis on another data set in order to determine whether similar results were obtained using data collected on animals on a true *ad libitum* feeding regime. This chapter presents a similar analysis performed on another data set for comparison with the results obtained in Chapter 3.

The analysis presented in Chapter 3 showed that while feed intake was repeatable, the repeatability of residual feed intake was only low to moderate when tested over a 28 day period. It was suggested that this was due to the short period over which residual feed intake was calculated and that a longer test may reduce measurement error, resulting in a more repeatable measure of efficiency. This raises the question of what is the optimal length of test for accurate measurement of growth, feed intake and efficiency? The literature contains reports of optimal length of test for measurement of growth rate in central test stations (eg Liu and Makarechian 1993a), but there is a lack of information on the optimal length of test for measurement of feed intake and efficiency. This issue is of considerable practical importance as measurement of feed intake at centralised test stations is expensive and also may be inconvenient for management of animals. Any reduction in the length of feed intake test required would present considerable savings and make the measurement of feed intake both more attractive and affordable for commercial testing of cattle. It has also been suggested that a shorter test would alleviate problems such as excessive fatness and unsound feet and legs (Kemp 1990).

In order to determine the optimal length of test, criteria are required by which the optimal test can be assessed. Various criteria have been used to determine optimal length of test for growth rate in the literature, including phenotypic correlations between performance in a standard test and that measured in shorter tests and the heritability of the trait in the test period compared to that in a standard period. Liu and Makarechian (1993a) also suggested that the test should be chosen to minimise the impact of herd of origin effects on the results.

If test results are to be used in selection programs, the overall aim is to have a test which will produce the maximum response in the breeding objective for the minimum cost. Hence, in theory, the most appropriate way to assess the length of test required is to estimate all phenotypic and genetic parameters required to calculate an appropriate selection index and the response in the breeding objective to selection can be calculated. A similar concept was used to assess optimum test length for post-weaning gain by Swiger and Hazel (1961). If this procedure is performed for each test length it would be possible to compare the cost of measurement of feed intake verses the extra economic gain in the breeding objective in some sort of cost-benefit analysis to determine which test length produces optimal results. However where the breeding objective includes many traits the data required for this type of analysis becomes prohibitive and other criteria must be sought.

If it is assumed that the maximum test length provides the best possible measure of the trait of interest, then an alternative criteria for assessment of optimum test length is the shortest test which maximises the correlated response in the trait measured over the longest test length. The correlated response in trait Y (the maximum length test) from selection on trait X (the shortened test) is given by Falconer (1981) as:

$$CR_Y = i_X h_X r_g \sigma_{g_Y} \tag{4.1}$$

where:

CR_Y = correlated response in trait Y to selection on trait X;
i_X = intensity of selection on trait X;
h_X = square root of the heritability of trait X;
r_g = additive genetic correlation between traits X and Y;
σ_{g_Y} = additive genetic standard deviation in trait Y.

The correlated response in trait Y to selection on trait X can be expressed relative to the direct response to selection on trait Y (R_Y) to compare the efficiency of indirect selection with direct selection.

$$\begin{aligned}\frac{CR_Y}{R_Y} &= \frac{i_X h_X r_g \sigma_{g_Y}}{i_Y h_Y \sigma_{g_Y}} \\ &= r_g . \frac{i_X}{i_Y} . \frac{h_X}{h_Y}\end{aligned} \tag{4.2}$$

If the intensity of selection on the shortened test is the same as the intensity of selection on the full test, the efficiency of selection based on the shortened test is a function of the heritability of the shortened test and the genetic correlation of the shortened test with the long test. Hence these parameters appear to be the most appropriate by which to assess the optimal length of performance test in centralised test stations. Many previous studies assessing optimum test length for growth rate have used phenotypic correlations between the shortened test and the maximum test as a criteria. While the phenotypic correlations used as criteria in other studies are a useful indication of the ability of the shortened test to predict results from the full test, the argument developed above shows that the genetic correlation is more relevant in the context of selection.

The data used in Chapter 3 was not suitable for assessing the optimum length of test as insufficient data was available to estimate genetic correlations. In addition, as previously discussed, the feeding regime of the bulls may complicate the interpretation of the results. Feed intake and weight data for cattle on an *ad* libitum feeding regime were available from the Meat Research Corporation funded DAN.75 project currently being conducted at Trangie Agricultural Research Centre by NSW Agriculture. This data presented the opportunity to make a comparison of the results of Chapter 3 with results from animals on an *ad libitum* feeding regime, as well as providing a suitable data set for determining the optimum length of an efficiency test. This chapter presents analyses of the DAN.75 data in order to address the issues outlined above.

4.2 Materials and methods

4.2.1 Description of data

The data used consisted of feed intake and weight data from Angus bulls and heifers and Hereford, Poll Hereford and Shorthorn heifers, and was collected from the first four groups of animals tested for post-weaning efficiency as part of the DAN.75 project at Trangie. The data was collected from March 1994 to March 1996, with each group of animals spending approximately five months on the test. A pre-test period of at least 21 days was allowed for the animals to adapt to the automated feeding system and diet. This was followed by a 119 day (17 week) test.

Animals

The first and third groups of animals tested consisted of bulls and heifers from the Angus herd kept at the Trangie Agricultural Research Centre and were born in the Spring of 1993 and 1994. The herd at Trangie had been closed since 1963 and the bulls from Chapter 3 were also taken from this herd. Between 1974 and 1992 the herd was broken into three lines and selected for high and low weight gain from birth to yearling, with a randomly bred control line being maintained. Further details regarding the history of the herd during the selection phase were given by Parnell *et al.* (1994). After the evaluation of the selection lines was completed the low growth rate line was dispersed, while the high growth rate and control lines were kept to form the basis of the cow herd from which the animals used in the DAN.75 project are derived. In 1993 a number of Angus bulls were purchased from leading industry herds which were representative of the current direction of the Angus breed in Australia. These bulls were joined to cows in the Trangie herd to produce the animals on which the feed intake and efficiency data were collected.

The second and fourth groups of animals tested consisted of heifers from industry herds. These herds were all autumn calving herds and were part of the Breedplan Validation project, and so had pedigree information and some linked sires. The breeds tested included Angus, Hereford, Poll Hereford and Shorthorn. After weaning, the animals were transported to Trangie and tested for efficiency after a short period was allowed to adjust to the environment at Trangie. The efficiency test for these animals started in October 1994 and 1995 and finished in March 1995 and 1996.

Efficiency test

The efficiency test was conducted using an automated feeding system which allowed measurement of the individual intakes of each animal. The animals were held in bare pens with constant access to water. The feed was delivered in automated hoppers and was weighed before and after each meal, with the feed intake data being logged directly to a computer. The animals were weighed weekly while on the efficiency test.

The ration fed to the animals was a roughage based ration (70% hay, 30% grain) which had been pelleted for use with the feeders. The energy concentration of the pellets was measured regularly during the test and the average energy concentration during each test ranged from 10.2 to 10.5 MJ/Kg. Crude protein level was 12.5%. In addition to the pelleted ration, 0.5 kg/head of straw was placed in the pens daily in order to provide a roughage source to maintain rumen function. The individual intake of straw was not measured, but each animal was assumed to have consumed 0.5 kg/day. As the energy concentration of the straw was only 6.8 MJ/kg, the total energy intake of straw was small compared to the energy intake of the pelleted ration.

During the tests a number of animals were removed from the test due to sickness or death (mainly due to bloat). All animals which did not complete the test or had data missing for some other reason were excluded from the analysis.

4.2.2 Derivation of traits

Average daily gain

In order to utilise the maximum amount of information from the weight data and to minimise the effect of measurement errors, the growth of individual animals over each test period was modelled by regression of liveweight against days on test. In Chapter 3 the data analysed consisted of weights taken fortnightly (monthly in some years) and showed a considerable amount of variation between measurements, possibly due to variation in gut fill at the time of weighing. This meant that in order to describe the growth of the bull with any accuracy it was necessary to perform a regression using all the available data over the whole test and use this equation to describe growth over a smaller period of time. However, in contrast to the bull data in Chapter 3, the current data set included weekly measurements of liveweight and there appeared to be little deviation from a continuous growth pattern. This meant that when the data was considered in smaller periods, a separate regression using weight data only collected during the period under consideration could be fitted reliably and was an accurate description of growth performance during the period. Hence it was possible to test more hypotheses using this data than was possible with the data from bulls analysed in Chapter 3, as each trait could be calculated independently for each period rather than using a common regression equation to describe growth. The regression equation fitted to the weight data is shown below (equation 4.3), and an example of the regression fitted to data is shown in Figure 4.1.

$$Y_i = \alpha + \beta x_i + e_i \qquad (4.3)$$

where : Y_i = weight of the animal at observation i;
α = regression intercept;
β = regression coefficient of weight on days;
x_i = number of days since start of period at observation i;
e_i = residual error in weight at observation i;

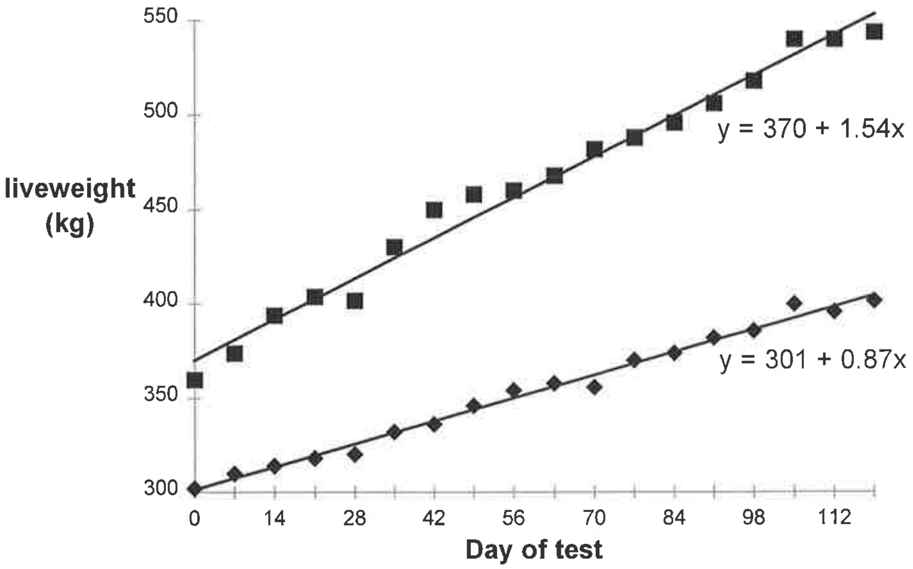
The coefficients of the regression equation (4.1) were used to calculate average daily gain, start weight, end weight, mid-weight and metabolic mid-weight for each period. The calculations were:

average daily gain = β
start weight = α
end weight = $\alpha + \beta$*(length of period in days)
mid-weight = (start weight + end weight)/2
metabolic mid-weight = $(\text{mid-weight})^{0.73}$

Daily feed intake

The feed intake data consisted of weekly feed intakes for 17 weeks in kg of ration consumed. Before analysis the additional intake of 3.4 MJ/day of straw (being 0.5 kg/day at 6.8 MJ/kg) was added to the weekly energy intake data and then the total intake was adjusted to a constant energy concentration of 10 MJ/kg to provide an intake in kg feed/week. This adjusted intake was used in subsequent analyses. For each period the total feed intake during the period was calculated and divided by the number of days in the period to give daily feed intake. Daily feed intake was used in the calculation of feed traits so that periods of different length were expressed in the same units to facilitate comparisons between periods.

Figure 4.1 Liveweight and fitted regressions for an Angus bull (closed squares) and heifer (closed diamonds) from the first test.



Residual feed intake

Residual feed intake was calculated using a generalised linear model of daily feed intake. A separate model was fitted for each test and for each sex within a test using the general linear models facility (Proc GLM) of SAS (1989). Previous analyses with this data set had fitted a separate model to bulls and heifers in order to produce results which can be compared with nutritional feeding standards which are given separately for each sex. An alternative method would be to include all data in one analysis and to fit test and sex as fixed effects in the model, along with the interactions with the covariables in the model so that effectively a separate regression line is fitted for each sex and test class. The results obtained from each method should be similar, although slight differences are likely. It was decided to adopt the approach using separate models for sexes and tests in order to keep in line with the previous analysis of this data. The final model fitted for each period is given below (equation 4.4). Residual feed intake was calculated as the residual error term in the model.

$$Y_i = \mu + \beta_1(ADG_i - \overline{ADG_.}) + \beta_2(MMWT_i - \overline{MMWT_.}) + e_i \qquad (4.4)$$

where :

Y_i = daily feed intake of animal i;

μ = overall mean for daily feed intake;

β_1, β_2 = partial regression coefficients of feed intake on ADG and MMWT respectively;

ADG_i = average daily gain of animal i;

$MMWT_i$ = metabolic mid-weight of animal i;

e_i = residual error in feed intake (i.e. residual feed intake) of animal i;

Periods for calculation of traits

Each trait was calculated over a number of different periods. The periods were chosen to facilitate two analyses, one to provide a comparison with results from Chapter 3, and the second to examine the length of test required.

In order to provide a comparison with the results in Chapter 3, traits were calculated over 4 week periods in the same way as in Chapter 3. Each trait was calculated over weeks 1 to 4, 5 to 8, 9 to 12 and 13 to 16. In addition, data from longer periods was examined by calculating traits over weeks 1 to 8, 9 to 16 and 1 to 16. Hence the periods used are equivalent to the periods in Chapter 3.

To assess the optimal length of test the traits were calculated for different lengths of tests. All tests started at week 1 and the length of the test was altered by including more data in weekly increments. Length of the test periods ranged from 1 week through to the full 17 week test.

4.2.3 Analyses

Repeatability analysis

The repeatability of daily feed intake, residual feed intake and feed conversion ratio measured over 4 weeks was calculated after fitting a model which included terms for the class variables test, sex, breed and herd nested within breed, with age of the animal at the start of the period fitted as a covariate and the interaction of age with all the class variables. The repeated measures option of the generalised linear models procedure (SAS 1989) was used to calculate the between subject (MS_B) and within subject (MS_W) mean squares after the effects in the model had been removed. This was then used to calculate the repeatability (R) over four measurements (n = no. of measurements) using the formula given in Equation 4.5 (see Appendix B for derivation of equation).

$$R = \frac{MS_B - MS_W}{MS_B + (n-1)MS_W} \tag{4.5}$$

Genetic analyses

Genetic analyses were performed using the DFREML programs (version 2.1.14) written by Meyer (1993) and operated through a front-end package (Swan 1995). A total of 760 records representing 78 sires were available, with a total of 971 animals included in the analysis from base pedigree information. The model fitted included test group, sex, breed and herd of origin as fixed effects, age at the start of the test as a covariable and a random term for the additive genetic merit of the animal. Hereford and Poll Hereford breeds were pooled and treated as one breed. Heritabilities were calculated from univariate analyses. Phenotypic, environmental and genetic correlations between traits were calculated from pairwise multivariate analyses.

4.3 Results

4.3.1 Summary of animal performance

Least squares means for relevant performance traits calculated over the full 17 week test are presented for each test-sex-breed subclass in Table 4.1. The cattle from the Trangie Angus herd in tests 1 and 3 were older and heavier than the heifers from industry herds in tests 2 and 4 at the start of the test period, and had higher daily feed intakes. The bulls in tests 1 and 3 were heavier than the heifers and had considerably higher average daily gain and feed intake, which was in line with expectation. The data did not lend itself to making appropriate comparisons between breeds, as the sampling of sires within breeds was not designed for breed comparisons. In addition, breed is confounded with herd of origin effects and thus environmental differences between herds may influence comparisons between breeds.

4.3.2 Analyses of traits calculated over 4 week periods

The heritability of average daily gain, daily feed intake and residual feed intake calculated over 4 week periods is given in Table 4.2. The heritability of average daily gain measured over four weeks was low, and in weeks 13 to 16 the estimate of heritability converged to zero. When average daily gain was measured over a longer period the heritability was variable, ranging from low to moderate. The heritability of feed intake was moderate to high, and was fairly consistent between periods. The heritability of residual feed intake was also moderate to high, but tended to be slightly lower than that of feed intake in most periods.

The phenotypic and genetic correlations between periods for average daily gain, daily feed intake and residual feed intake are given in Table 4.3. Phenotypic correlations between average daily gain measured over 4 weeks were very low, which was also reflected by the low repeatability of 0.02. However, despite the low repeatability and heritability of average daily gain, the genetic correlations between periods were considerably higher than the phenotypic correlations.

Table 4.1 Least squares means (± s.e.) for daily feed intake, residual feed intake, average daily gain, liveweight at the start of the test and age at the start of the test.

Test	Sex	Breed	No.	Daily feed intake (kg)	Residual feed intake (kg)	Average daily gain (kg)	Start weight (kg)	Start age (days)
1	bull	Angus	97	12.59 ± 0.11	0.00 ± 0.06	1.31 ± 0.01	359 ± 3	292 ± 2
1	heifer	Angus	96	11.50 ± 0.11	0.00 ± 0.06	1.01 ± 0.01	311 ± 3	289 ± 2
2	heifer	Angus	65	10.35 ± 0.13	0.12 ± 0.07	1.15 ± 0.02	245 ± 4	252 ± 2
2	heifer	Hereford	64	9.26 ± 0.13	-0.18 ± 0.07	1.24 ± 0.02	201 ± 4	230 ± 2
2	heifer	Shorthorn	62	10.70 ± 0.14	0.08 ± 0.07	1.22 ± 0.02	252 ± 4	254 ± 2
3	bull	Angus	88	12.20 ± 0.11	0.00 ± 0.06	1.42 ± 0.01	334 ± 3	271 ± 2
3	heifer	Angus	99	11.30 ± 0.11	-0.01 ± 0.06	1.12 ± 0.01	299 ± 3	271 ± 2
4	heifer	Angus	62	10.21 ± 0.14	0.05 ± 0.07	1.13 ± 0.02	254 ± 4	246 ± 2
4	heifer	Hereford	83	9.79 ± 0.12	-0.09 ± 0.06	1.21 ± 0.02	228 ± 4	247 ± 2
4	heifer	Shorthorn	46	10.64 ± 0.16	0.09 ± 0.08	1.14 ± 0.02	271 ± 5	253 ± 3
Overall mean				11.00 ± 1.07	0.00 ± 0.56	1.20 ± 0.14	283 ± 32	264 ± 20

Table 4.2 Heritability of average daily gain, feed intake and residual feed intake calculated over four week periods.

Period	Average daily gain	Feed intake	Residual feed intake
1-4	0.13 ± 0.08	0.62 ± 0.12	0.53 ± 0.13
5-8	0.19 ± 0.10	0.56 ± 0.12	0.38 ± 0.11
9-12	0.09 ± 0.08	0.57 ± 0.12	0.46 ± 0.12
13-16	-	0.42 ± 0.12	0.29 ± 0.12
1-8	0.38 ± 0.11	0.61 ± 0.12	0.56 ± 0.13
9-16	0.03 ± 0.07	0.53 ± 0.12	0.43 ± 0.14
1-16	0.26 ± 0.10	0.60 ± 0.12	0.62 ± 0.15

Table 4.3 Phenotypic and genetic correlations between periods for average daily gain, daily feed intake and residual feed intake (phenotypic correlations above the diagonal, genetic correlations below the diagonal).

	1-4	5-8	9-12	13-16	1-8	9-16	1-16
Average daily gain							
1-4		-0.04	0.05	0.16	0.50	0.19	0.33
5-8	0.93		-0.10	0.12	0.65	0.10	0.56
9-12	0.20	0.48		-0.05	0.06	0.61	0.48
13-16	1.00	1.00	0.99		0.21	0.64	0.41
1-8	1.00	1.00	0.45	1.00		0.28	0.76
9-16	0.61	1.00	1.00	1.00	1.00		0.73
1-16	0.95	1.00	0.63	1.00	1.00	1.00	
Feed intake							
1-4		0.82	0.69	0.58	0.95	0.66	0.86
5-8	0.90		0.84	0.73	0.95	0.81	0.94
9-12	0.80	0.99		0.86	0.80	0.96	0.94
13-16	0.86	0.97	1.00		0.68	0.97	0.88
1-8	0.98	0.97	0.92	0.93		0.77	0.94
9-16	0.83	0.98	1.00	1.00	0.92		0.94
1-16	0.82	1.00	0.98	0.98	0.98	0.98	
Residual feed intake							
1-4		0.60	0.44	0.34	0.89	0.42	0.72
5-8	0.90		0.64	0.51	0.84	0.61	0.81
9-12	0.66	1.00		0.69	0.57	0.89	0.80
13-16	0.70	0.94	0.94		0.45	0.88	0.72
1-8	0.99	0.94	0.83	0.83		0.56	0.87
9-16	0.72	1.00	0.99	0.99	0.89		0.86
1-16	0.91	1.00	0.92	0.93	0.98	0.97	

Phenotypic correlations between periods for feed intake were very similar to those calculated for the bulls in Chapter 3, and were moderate to high, although correlations between periods separated by a longer intervening period of time were lower than correlations between adjacent periods. The repeatability of feed intake was high at 0.75. The correlation of each 4 week period with the 16 week period were high, ranging from 0.88 to 0.94, suggesting that feed intake over 4 weeks was phenotypically a good predictor of feed intake over a longer period. Genetic correlations between feed intake measured over 4 weeks were higher than the phenotypic correlations, and did not show the same tendency to decrease as the intervening period increased, although there was some variation in the estimates probably due to sampling variance.

Phenotypic correlations between periods for residual feed intake measured over 4 weeks were lower than the corresponding correlations for feed intake, and showed the same trend to decrease with increasing interval between measurements. The repeatability of residual feed intake was also lower at 0.52. Genetic correlations between periods were higher than the phenotypic correlations, and did not decrease as the intervening period increased, although there was variation between periods in the estimates.

4.3.3 Length of test analysis

The variance components for residual feed intake calculated over different length tests are given in Figure 4.2, with the resultant heritability given in Figure 4.3. The results show that the environmental variation decreased as the length of the test increased to 10 weeks, suggesting that extra data were helpful in reducing the variance in residual feed intake attributable to random errors and temporary environmental effects. After 10 weeks the additional data included did not decrease the environmental variance to any significant extent. Consequently the heritability increased to 10 weeks and then remained constant as further data were added.

The phenotypic and genetic correlations of the shortened test with the full 17 week test are given in Figure 4.4. It should be noted that the correlation must converge to 1 at 17 weeks by definition, and so the points of interest are the magnitude at which the correlation starts, and how quickly it approaches 1. The results for residual feed intake showed that the genetic correlation was always higher than the phenotypic correlation, and although the genetic correlation starts at 0.7, it quickly increases and is greater than 0.95 after 7 weeks. The phenotypic correlation increased slower than the genetic correlation, and only reached 0.95 after 12 weeks. In Figure 4.5 the efficiency of indirect selection for residual feed intake measured over 17 weeks based on a shortened test is compared to direct selection on residual feed intake measured over 17 weeks. The results showed that selection efficiency greater than 95% was achieved using a 9 to 10 week test, and thus there is very little improvement made in the accuracy of selection decisions by increasing the length of test for residual feed intake past 10 weeks.

Figure 4.6 to Figure 4.9 show the results for daily feed intake. The environmental variation for daily feed intake did not decrease significantly when the test was extended past a 3 week test, and the heritability of daily feed intake reached its maximum at 3 weeks. However, the genetic and phenotypic correlations increased more slowly (Figure 4.8) and were not greater than 0.95 until 6 and 10 weeks respectively. Figure 4.9 shows that for daily feed intake, selection efficiency of 95% was reached using a 5 week test.

The results obtained for average daily gain measured over 1, 2 or 3 weeks are not presented as problems experienced with the analyses of this data meant that sensible estimates were not obtained. The heritability of average daily gain was generally lower than that of daily feed intake or residual feed intake, and consequently there was more variation in the parameter estimates, making the results more difficult to interpret. Figure 4.10 shows that as test length increased, the amount of environmental variance decreased to approximately 10 weeks and then remained constant as extra data was added. However, small variation in the amount of additive genetic variation partitioned meant that the maximum heritability for average daily gain was produced with 8 weeks of data (Figure 4.11). The estimates of the genetic correlation with average daily gain calculated from 17 weeks of data were also variable, although for tests longer than 6 weeks the correlations were very high (Figure 4.12). The variation in the parameter estimates meant that the response in efficiency of selection as extra data was added was also variable and difficult to interpret. The maximum efficiency was reached with 8 weeks of data (Figure 4.13). However in view of the variability in the parameter estimates for average daily gain it may be more appropriate to judge the optimum test length for measuring average daily gain by the point where the environmental variance is minimised (10 weeks) rather than by the point where maximum selection efficiency was achieved.

Figure 4.2 Additive genetic, environmental and phenotypic variances of residual feed intake calculated from tests of different length.

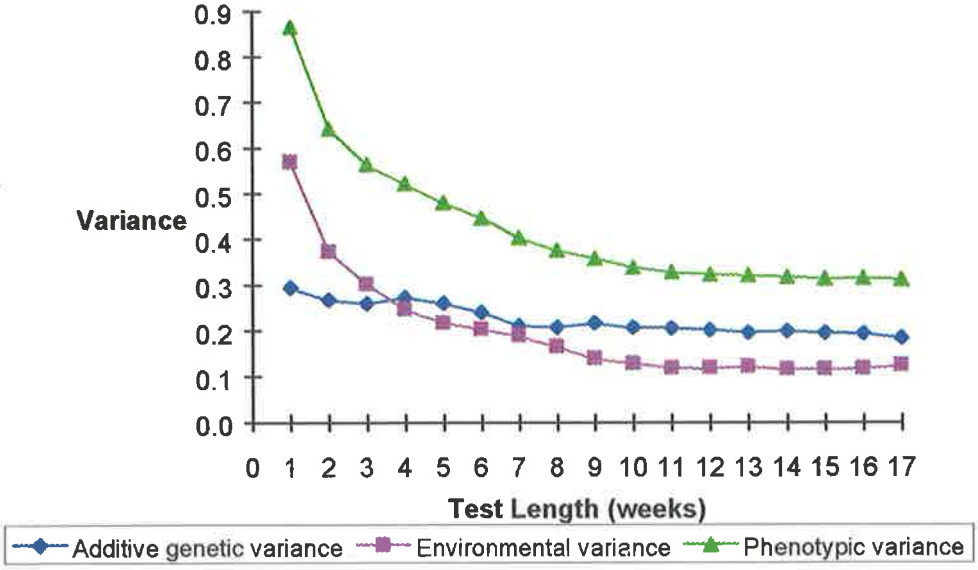


Figure 4.3 Heritability of residual feed intake calculated from tests of different length.

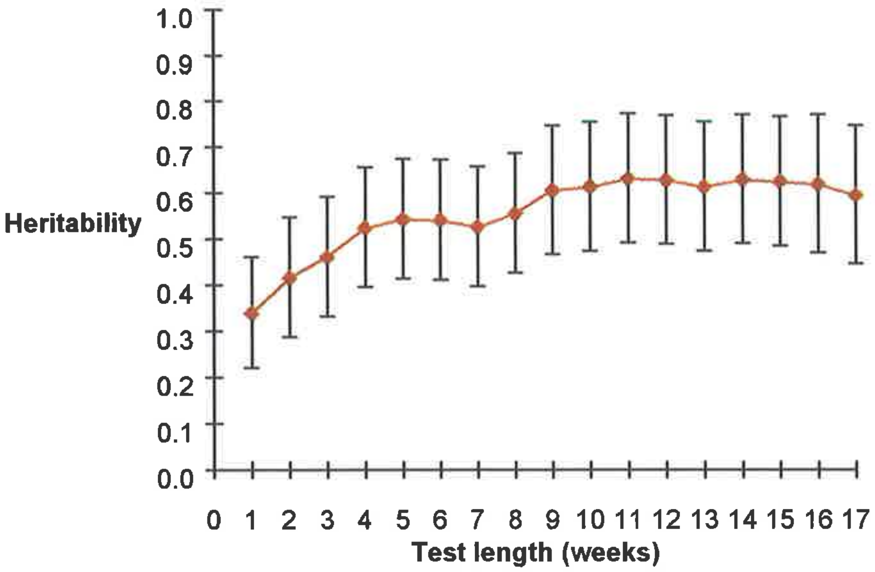


Figure 4.4 Phenotypic and genetic correlations between residual feed intake calculated from shortened tests and the full 17 week test.

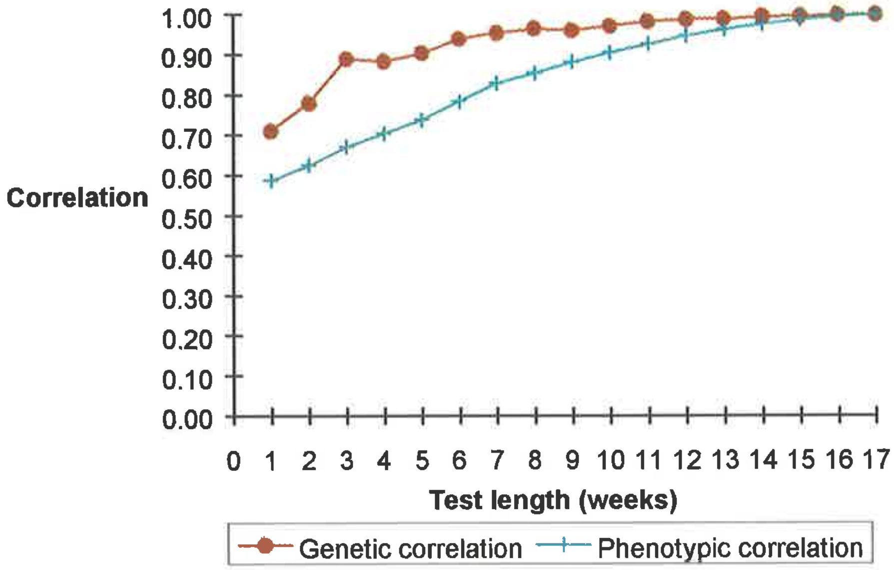


Figure 4.5 Efficiency of indirect selection for residual feed intake using a shortened test relative to direct selection on a 17 week test.

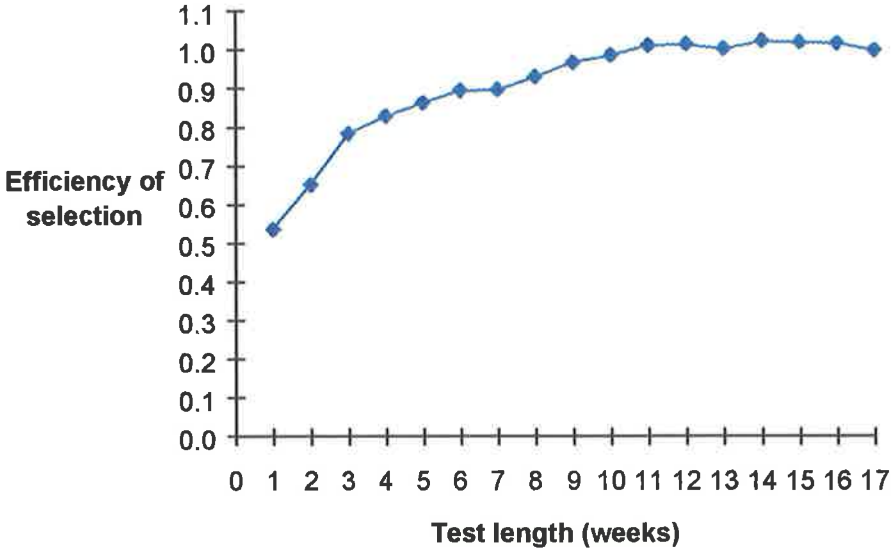


Figure 4.6 Additive genetic, environmental and phenotypic variances of daily feed intake calculated from tests of different length.

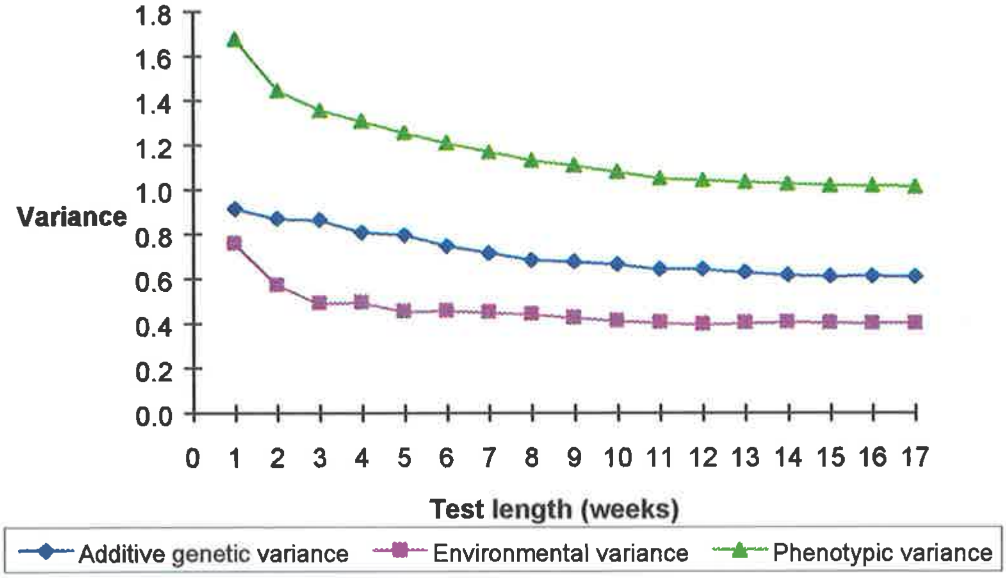


Figure 4.7 Heritability of daily feed intake calculated from tests of different length.

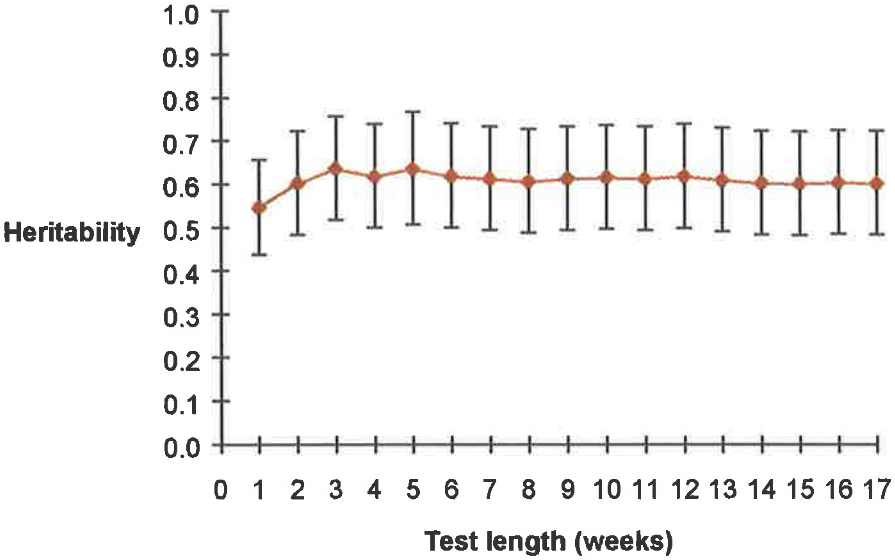


Figure 4.8 Phenotypic and genetic correlations between daily feed intake calculated from shortened tests and a 17 week test.

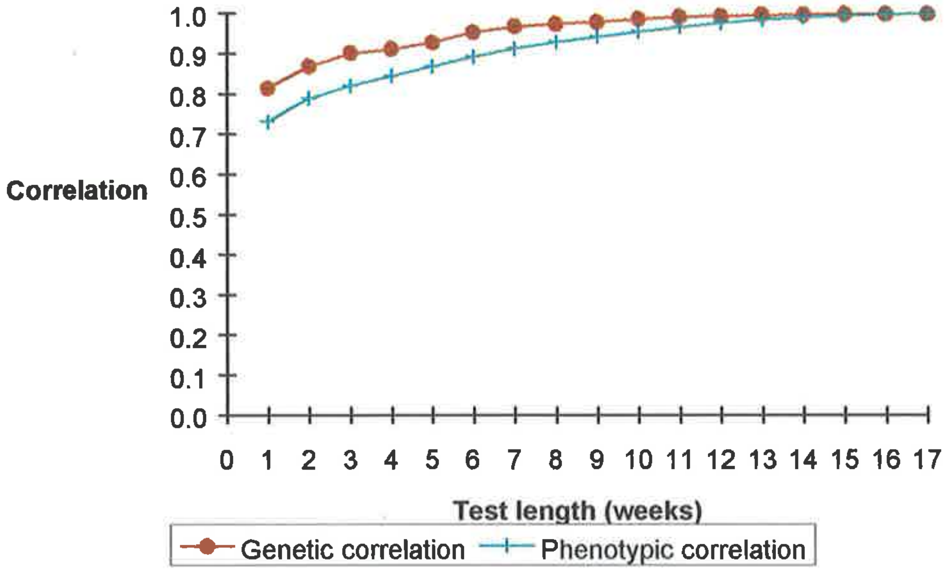


Figure 4.9 Efficiency of indirect selection for daily feed intake using a shortened test relative to direct selection on a 17 week test.

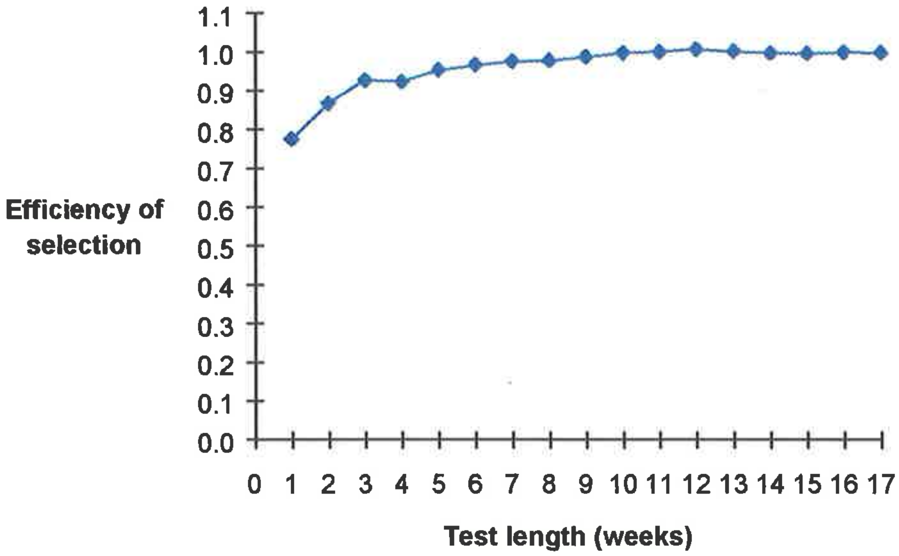


Figure 4.10 Additive genetic, environmental and phenotypic variances of average daily gain calculated from tests of different length.

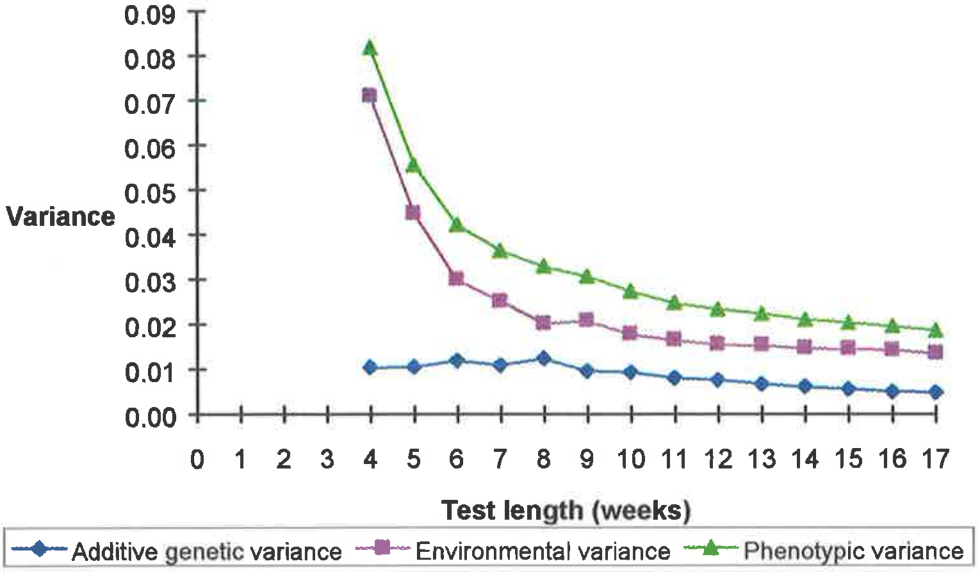


Figure 4.11 Heritability of average daily gain calculated from tests of different length.

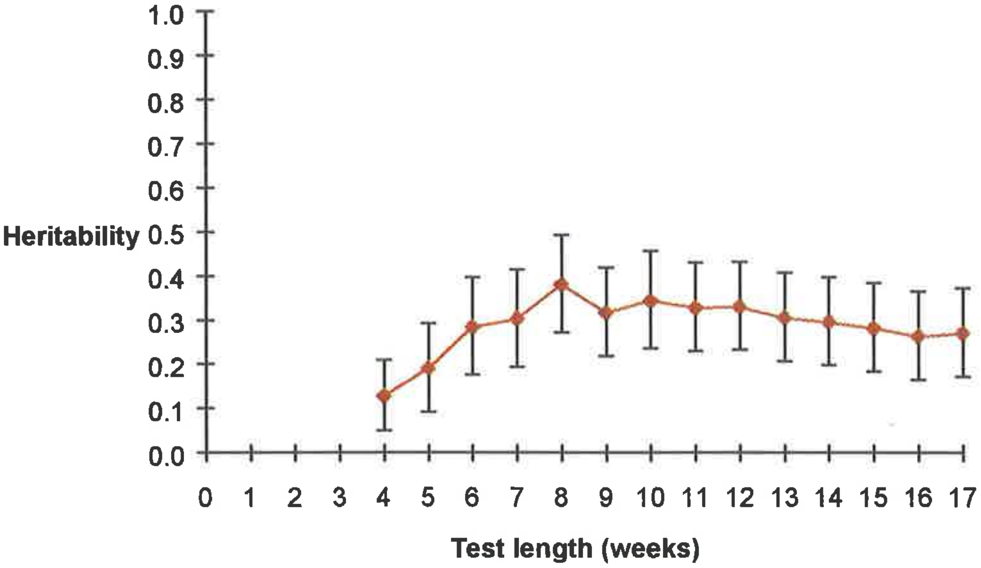


Figure 4.12 Phenotypic and genetic correlations between average daily gain calculated from shortened tests and a 17 week test.

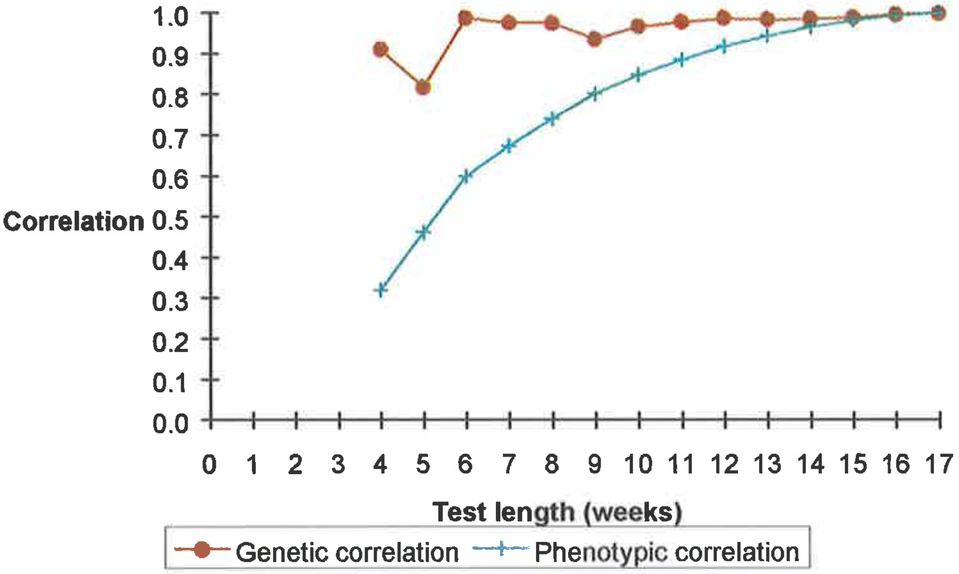
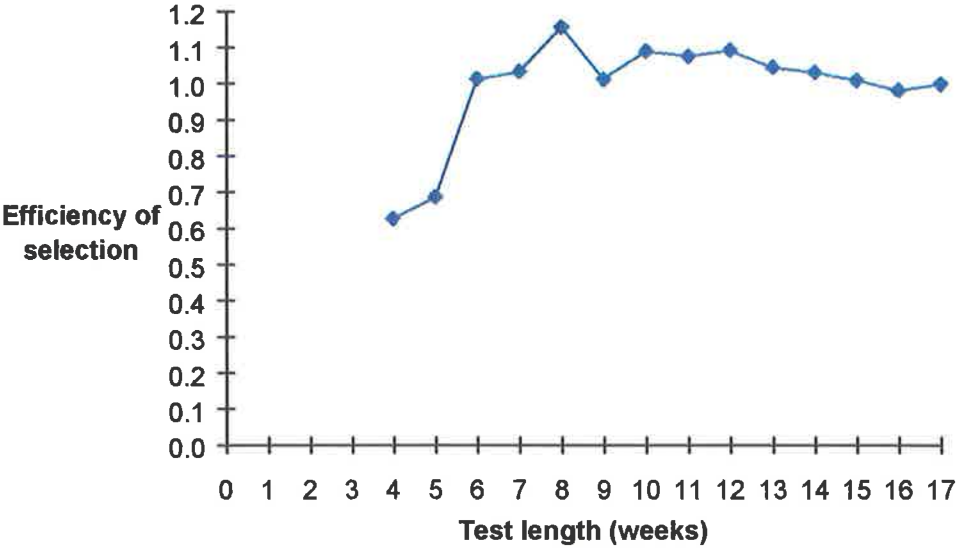


Figure 4.13 Efficiency of indirect selection for average daily gain using a shortened test relative to direct selection on a 17 week test.



4.4 Discussion

Comparison with Bull data from Chapter 3.

Comparison of the phenotypic correlations in Table 4.3 with the equivalent correlations from the analysis of the Angus bull data (Table 3.4) is very informative. One of the major questions arising from Chapter 3 was the effect of the feeding regime on the feed intake of the bulls. The correlations between feed intake over four week periods calculated from the data set analysed in this chapter (where feed intake was *ad libitum*) were remarkably similar to those calculated in Chapter 3 from bulls on "restricted *ad libitum*" feed. The largest difference between corresponding correlations for feed intake was only 0.07. This suggests that the results from Chapter 3 were not greatly influenced by the feeding regime the bulls were on, and that confidence can be placed in the estimates obtained. The repeatability of feed intake measured over 4 weeks estimated from this data set (0.75) was very similar to that obtained from the bull data in Chapter 3 (0.77) and both data sets suggest that feed intake over a four week period is able to predict feed intake over a longer period.

The phenotypic correlations for feed intake and residual feed intake calculated from the present data set showed the same trend observed with the bull data, with correlations between close periods being higher than those between measurements separated by a longer period of time. In Chapter 3 it was hypothesised that this decrease might be a result of temporary environmental effects on feed intake and residual feed intake, producing a decrease in phenotypic correlations with increasing interval of time, and that the genetic correlations may not show the same decrease as the animals mature. The fact that there was no decrease in the genetic correlations between periods estimated in this data set supports that hypothesis, as it indicates that the decrease in phenotypic correlations as the interval between measurements increased was caused by a decrease in the environmental correlations between periods. This suggests that there are temporary environmental effects which influence feed intake and efficiency, but that these effects are relatively short-lived. This agrees with the literature on the biology of feed intake which indicate that factors (such as the level of previous nutrition) can have transient effects on feed intake and efficiency (e.g. Ledger and Sayers 1977).

Comparison of the correlations for residual feed intake between periods with those obtained from the bull data in Chapter 3 shows that the correlations obtained with the current data set were considerably higher than those calculated from the bull data. This was also reflected in the repeatability estimate (0.52) which was higher than that found for the bulls (0.35). As the correlations for feed intake showed that the quality of the feed intake data was similar for both data sets, the differences in residual feed intake between the two data sets is likely to be due to the quality of the liveweight data which was used to model feed intake in order to calculate residual feed intake.

The weight data for the bulls in Chapter 3 was collected less frequently and was more variable between measurements than the current data set, and consequently the description of the growth of the bulls was less accurate. As pointed out in section 2.3.4.2 residual feed intake is partly composed of random and measurement errors as well as reflecting real differences in efficiency between individuals. Thus a poor description of growth would naturally lead to a reduction in phenotypic correlations between residual feed intake measurements as a greater proportion of the variation in residual feed intake will be simply due to errors in the feed intake model. In a genetic context, this will also cause the heritability of residual feed intake to decrease as more error variation is present. Hence the poor description of growth of the bulls may explain why the heritability estimates in Chapter 3 were lower than most estimates found in the literature.

A consideration of the role of measurement error in residual feed intake suggests that it is possible or even likely that genetic correlations between residual feed intake at different times will be significantly higher than the corresponding phenotypic correlations. This may occur because the genetic correlations calculated on a suitable data set should be free of the effects of measurement error which lower the phenotypic correlations. Although this principle applies to any trait, measurement error is likely to be of particular importance for residual feed intake as it is calculated as an unexplained deviation from a relationship between two or more traits. Consequently there is greater opportunity for errors of measurement to occur, and the manner in which residual feed intake is calculated may exaggerate the effects of these errors. It is, therefore, conceivable that the genetic correlation between residual feed intake post weaning and at maturity could be significantly higher than the phenotypic correlation. Post-weaning residual feed intake may still be a suitable criteria for indirect selection for maintenance efficiency although it may not be a good phenotypic indicator of the maintenance efficiency of an individual as an adult.

The difference between the repeatability of residual feed intake for the two data sets demonstrates that in order to measure residual feed intake it is important not only to have accurate feed intake data, but also to have sufficient data to accurately describe the liveweight of the animal during the period in which feed intake measurements are made. The approach used in this study to describe growth using a regression equation has the advantage of removing some of the error associated with weight measurements and hence improving the description of growth. The approach is made easier when considering growth over a period where growth is linear. If growth was considered over a period where a linear description was inadequate, then a non-linear function could be used and integrated to determine the body weight maintained over the period.

Length of efficiency test

In the context of selection decisions, the heritability and the efficiency of indirect selection, incorporating the heritability and genetic correlation with the 17 week test, are the most relevant criteria by which to assess the optimum length of test. The phenotypic correlations are also of some practical interest as these provide an indication of the likelihood of the re-ranking of animals if the test was continued on to 17 weeks. The results obtained here suggest the optimum test lengths are 5 weeks for measurement of feed intake alone, and 10 weeks for measurement of average daily gain and residual feed intake. However the response surfaces were not steep, indicating that small changes in test length would have little effect on the predicted genetic progress. At these points the phenotypic correlations were all greater than 0.8, and thus while some re-ranking of animals may occur over a longer test the changes will be relatively minor. Hence the recommendations appear to be appropriate based on the phenotypic correlations as well.

There are very few counterparts in the literature describing optimum test length for daily feed intake or residual feed intake with which the results obtained here can be compared. However, some comparison with other results for average daily gain are possible. Most of the literature examining optimum test length has come out of North America where a 140 day test is the standard and hence this has been the benchmark against which shortened tests have been compared. This is a longer test than the 17 week test which has been used as the benchmark in this study, which may have some influence on the outcome. McPeake and Buchanan (1986) and Kemp (1990) recommended that a 112 day (16 week) test for growth rate is a satisfactory alternative to a 140 day test. Swiger and Hazel (1961) and Liu and Makarechian

(1993a,b) suggested a shorter test of 84 days (12 weeks) which is closer to the 10 week test suggested by the present study. The frequent collection of weight data and the regression approach used to measure growth rate in this study may explain why a shorter test was recommended here, as more data is used to calculate growth rate and therefore the accuracy of measurement is greater (Liu *et al.* 1991; Liu 1994).

Kemp (1990) and Liu and Makarechian (1993a,b) also recommended that the pre-test adjustment period be extended from 28 to 56 days to minimise the effects of herd of origin on test performance. Numerous studies have found significant herd of origin effects on performance test results for average daily gain (Amal and Crow, 1987), feed efficiency (gross efficiency) and backfat (Liu *et al.* 1995), although other studies have not found herd of origin effects on growth rate after an adjustment period (Mohammed Ali and Crow 1984; Tong *et al.* 1986). This study did not examine the herd of origin effects and the length of pre-test adjustment period required, as the data enabled statistical adjustment for these effects. However, if commercial testing of animals is implemented the number of animals from each herd may be insufficient to allow statistical adjustment and a pre-test adjustment period will be important to allow fair comparison between animals.

The fact that feed intake requires only 5 weeks of data to obtain an accurate measurement, while residual feed intake requires 10 weeks suggests that measurement of residual feed intake is not limited by obtaining accurate feed intake data. The results presented suggest that the limitation in measuring residual feed intake lies in obtaining an accurate measure of growth rate, which requires 10 weeks of data. This agrees with the conclusions made from the comparison between the analyses in Chapter 3 and the current data set, and provides an explanation for the high repeatability of feed intake in the previous analyses, as the four week test is close to being sufficient for an accurate evaluation of feed intake. On the other hand, residual feed intake and average daily gain had lower repeatability in the previous analysis as four weeks is insufficient to obtain a repeatable measure of these traits.

The results raise some other possibilities for the measurement of residual feed intake. As feed intake is the most difficult and expensive trait to measure it is desirable to minimise the length of test for feed intake, and the results here suggest that 5 weeks is sufficient time. However, to accurately measure efficiency, growth must be measured over at least 10 weeks. Hence it may be possible to devise some test where individual feed intakes are measured for 5 weeks, after which the animals remain on the same diet for a further 5 weeks while more weight measurements are collected. Such a test would reduce the expense of testing and allow the feed intake measurement facility to be used for testing other animals in the second 5 weeks, thereby increasing the number of animals able to be measured. Also, it may not be necessary to collect weight data weekly, as visual examination of the plots in Figure 4.1 indicates that average daily gain calculated from weight measurements at the beginning and end of the 10 week test is likely to be highly correlated with average daily gain calculated from regression on weekly measurements.

Another possibility which should be explored is the use of alkane marker capsules to measure feed intake of animals at pasture. The advantage of these capsules are that they would allow on-farm testing of animals at a lesser cost, although testing is still not cheap. However the capsules are limited in that they can only measure feed intake over a period of 1 to 2 weeks (R. Herd, personal communication 1996). The results presented in this chapter indicate that a test of 1 to 2 weeks would result in approximately 60 % selection efficiency for residual feed intake (compared to direct selection based on a 17 week test) and 80 % for feed intake, assuming that the selection intensity was the same for direct and indirect selection. However, as the alkane capsules are cheaper and more convenient to use, it may be possible to test a much larger number of animals using alkane capsules. Thus if the alkane capsule can be developed sufficiently to provide an accurate measurement of feed intake, the increased selection intensity able to be applied may compensate for the reduction in selection efficiency, and so the selection response in feed intake may be equal to or greater than that obtained using selection based on a 17 week test in a centralised feed intake measurement facility.

The value of a shorter test with higher selection intensity may be demonstrated by use of an example. If selection based on a 17 week test allowed 20% of animals to be selected, but the increased numbers tested using alkane capsules allowed 5% of animal to be selected, then the selection intensity (i) applied would increase from $i=1.400$ to $i=2.064$. Using the heritabilities and genetic correlations estimated from a 2 week test, the efficiency of selection for feed intake compared to direct selection based on a 17 week test is given by:

$$\begin{aligned}\frac{CR_{17}}{R_{17}} &= r_g.\frac{i_2}{i_{17}}.\frac{h_2}{h_{17}} \\ &= 0.87.\frac{2.064}{1.400}.\frac{\sqrt{0.60}}{\sqrt{0.60}} \\ &= 1.28\end{aligned}$$

The efficiency of selection for residual feed intake based on a 2 week test is:

$$\begin{aligned}\frac{CR_{17}}{R_{17}} &= r_g.\frac{i_2}{i_{17}}.\frac{h_2}{h_{17}} \\ &= 0.78.\frac{2.064}{1.400}.\frac{\sqrt{0.42}}{\sqrt{0.60}} \\ &= 0.96\end{aligned}$$

It can be seen that even though the accuracy of measurement is compromised with a shorter test, the higher selection intensity available means that there is very little reduction in genetic progress in residual feed intake, and the genetic progress in feed intake is actually increased by 28%. The accuracy of measurement of residual feed intake using a 2 week measurement of intake might be further improved by the use of a longer period for measurement of growth rate. In addition, the improved accuracy of genetic evaluation resulting from records on a greater number of relatives may offset the inaccuracy of measurement. Thus although the analysis in this chapter has been able to provide recommendations as to the optimum test length to provide accurate measurements, other factors will need to be considered when deciding on the best test to use for commercial purposes.

The heritability estimates for residual feed intake measured over a 10 to 17 week test were higher than most estimates for residual feed intake of beef cattle in the published literature which generally fall in the range 0.2 to 0.3 (see section 2.4.4.3). The higher estimate found here may be due to the quality of the data on which the estimates were based as well as the approach of describing growth using linear regression used, as this approach minimises the effect of variation in weight measurements. This suggests that with accurate measurement of residual feed intake it should be possible to make significant gains in residual feed intake by selection.

4.5 Summary

This chapter presents the analysis of feed intake and weight data from another cattle data set in order to compare the results obtained with the bull data in Chapter 3. Results for feed intake were almost identical to those found in Chapter 3 and it was concluded that the restricted *ad* libitum feeding regime of the bulls in Chapter 3 did not produce significant differences in feed intake from that observed on a true *ad libitum* regime. Residual feed intake was more repeatable in the data set analysed in this chapter. It was hypothesised that the higher repeatability and heritability estimates were due to the better description of growth which was obtained with more accurate weight data, thus reducing the influence of measurement errors in residual feed intake. The quality of the data from which residual feed intake is estimated is important if residual feed intake is to be an accurate reflection of differences in efficiency between individuals, and the effect of measurement error on the results deserves attention, particularly as residual feed intake is a composite trait incorporating both growth and feed intake, and thus will reflect errors of measurement in both traits.

A decrease in phenotypic correlations between periods as the interval between periods increased was observed for feed intake and residual feed intake in a similar manner to that observed in Chapter 3. However, this was not accompanied by a decrease in genetic correlations, and hence it was concluded that the observed decrease in phenotypic correlations was attributable to temporary environmental effects on feed intake and residual feed intake. The results suggested that although the phenotypic correlation between residual feed intake post-weaning and at maturity may be low, it is possible that a genetic relationship may exist.

The optimum length of test required for accurate measurement of feed intake, average daily gain and residual feed intake was investigated. The results suggested that a 5 week test is appropriate for measurement of feed intake, but 10 weeks of data are required to accurately measure average daily gain and residual feed intake. The results support the previous conclusion that the limitation in obtaining an accurate measure of residual feed intake is the data required to accurately describe growth, and not the length of time required to collect feed intake data. The most appropriate test to use in commercial evaluation of feed intake and efficiency will also depend upon a number of factors other than which test provides the most accurate measure of the desired traits.

Chapter 5. Phenotypic variation in feed efficiency of mice

5.1 Introduction

In Chapters 3 and 4 post-weaning feed intake data from cattle was analysed to examine the repeatability of feed intake and residual feed intake. The results from these analyses indicated that, with accurate data collection, the repeatability of feed intake and residual feed intake is moderate to high. However, both analyses showed that for feed intake and residual feed intake, phenotypic correlations between periods decreased as the interval between the periods increased. This suggested that there may be systematic changes in the ranking of bulls for efficiency as the bulls mature, and that post-weaning residual feed intake may not be a good predictor of maintenance efficiency at maturity. Nevertheless, the genetic correlations between periods estimated in Chapter 4 suggested that post-weaning residual feed intake may be genetically related to maintenance efficiency.

The ability of an efficiency test on a young animal to predict the efficiency of the animal as an adult is of considerable interest in the context of selection for efficiency. There are no published reports of changes in residual feed intake which occur as animals grow from weaning to maturity, either at a phenotypic or genetic level. Knowledge of the relationship between post-weaning efficiency and lifetime efficiency is important as this will play a large part in determining the value of selection as a means of improving efficiency.

A major limitation in the use of any performance test conducted over a short period is that the test only considers a snapshot of the performance of an individual during its lifetime. This snapshot may not always be an appropriate measure of performance over a lifetime of production. An alternative approach can be to fit curves to data in order to describe lifetime performance. This approach avoids some problems associated with snapshot performance tests, and if the curves fitted are chosen carefully the curve parameters can have biological significance.

Parks (1982) suggested a series of curves which can be used to describe the relationship between feed intake, body weight and time, the parameters of which can be used to describe some of the biological aspects of feed intake and growth in animals. His approach involved describing the relationship of body weight with cumulative feed intake and daily feed intake with time as asymptotic relationships. These two relationships can be combined to describe weight in terms of time and produce a sigmoid shape growth curve often associated with the description of growth.

The first of Parks' (1982) equations which describes the asymptotic relationship between daily feed intake and time is shown below.

$$\frac{dF}{dt} = C(1 - e^{\frac{-t}{t^*}}) \qquad 5.1$$

where:

F = cumulative feed intake (and its derivative with respect to time is daily feed intake);
t = time;
C = daily feed intake at maturity;
$\frac{1}{t^*}$ = rate of maturity of daily feed intake with respect to time.

The same mathematical relationship is used to describe the relationship between body weight and cumulative feed intake, shown below.

$$W = A(1 - e^{-BF}) \qquad 5.2$$

where:

W = body weight;
A = asymptotic body weight at maturity;
B = rate of maturation of body weight with respect to cumulative feed intake.

From the parameters of the curves, Parks described two aspects of feed efficiency. Firstly, the efficiency of growth (AB) was calculated as the product of the A and B parameter estimates from equation 5.2. AB is the first derivative of W with respect to F in equation 5.2 at the point where liveweight equals zero (i.e. W=0), and hence represents the instantaneous efficiency with which feed is converted to liveweight when there is no maintenance component. The second measure of feed efficiency derived from Parks' equations is the maintenance requirement per unit body weight (or its inverse, maintenance efficiency) and is calculated by dividing the C parameter estimate from equation 5.1 by the A parameter estimate from equation 5.2 to produce an estimate in g(feed).g(liveweight)$^{-1}$.

The biological meanings assigned to the parameters of Parks curves mean that this is a useful model with which to compare efficiency from a snapshot performance test with lifetime performance as described by curves. However, fitting such curves requires data over a considerable period of the growth of an animal, and hence collection of suitable data is slow. This means that it is difficult to obtain data on sufficient animals to enable a genetic analysis of the curve parameters, and unless a large amount of time and resources are available this approach is restricted to making comparisons at a phenotypic level. Hence the aim of this chapter is to investigate the phenotypic variation in efficiency from weaning to maturity and to compare residual feed intake measured in short performance tests with estimates of growth efficiency and maintenance efficiency derived using the principles of Parks' model.

Due to the time and resources required in order to perform such an experiment in livestock species where maturation is relatively slow, it was decided to use the laboratory mouse as a model species in this investigation. The mouse has been used for investigation of aspects of feed intake and growth many times in the past (e.g. Timon and Eisen 1970; Eisen 1977; Gunsett *et al.* 1981; Sharp *et al.* 1984; Stephens 1991) and has proved to be a convenient and valuable tool in investigating the biology of growth and in developing concepts able to be applied to livestock species. Hence the mouse was used here in the hope that the results may provide some direction as to the most appropriate path to proceed on in the selection for efficiency in livestock.

5.2 Materials and methods

5.2.1 Animals

The experiment was conducted using 119 mice from a 3-way cross. The dams of the mice were the F_1 progeny from a cross of C57/bl6 and BALB/c inbred lines, and were mated to Swiss outbred males. The mice were from 13 litters by 12 sires, and all surviving mice from each litter were used in the experiment. All mice were weaned at 21 days, with the exception of mice from one litter where the dam died when the young mice were 16 days old.

After weaning the mice were placed in individual cages to allow measurement of individual feed intake. Feeders were constructed which allowed the mice access to the feed through slits in the sides of the feeders, but prevented the mice from mixing the feed with the sawdust which was used for litter. The mice were fed a standard laboratory animal ration (Joint Stock Diet, Milling Industries Pty Ltd) and were allowed constant access to the feed and to water.

Feed intake and body weight were recorded daily for the first three weeks after weaning (weeks 4 to 6), and then twice weekly until the mice were 18 weeks old and had reached an asymptotic weight. The mice then remained on *ad libitum* intake until they were 29 weeks old when body composition was measured by isotope dilution. The large gap between the last feed intake measurement and the measurement of body composition was due to the failure of the first attempt to measure body water content and it was necessary to wait until all the radio-isotope had been excreted by the mice and background counts were zero before the procedure could be repeated. Feed intake was measured again for one week prior to the body water content measurement to confirm that no major changes in feed intake had occurred.

Body composition was estimated from body water content using an adaptation of the isotope dilution technique of Holleman and Dieterich (1973) using tritiated water. The body water content was calculated and expressed as a percentage of body weight for use in subsequent analyses. Percentage body water is an indicator of the lean content of an animal as lean tissue has a constant water composition. Fat has a lower water content than lean tissue and thus a lower body water content represents a higher proportion of fat.

5.2.2 Calculation of growth and feeding parameters

Curves were fitted to the data for each individual in order to give estimates of growth and feed intake parameters for comparison with residual feed intake. The first curve fitted was a modification of Parks' (1982) curve fitted to bodyweight and cumulative feed intake data. Parks' original curve for fitting to this data (equation 5.2) is fixed through the origin, as weight must equal zero when cumulative feed intake (F) is zero. Because feed intake data is often not available until after weaning, the cumulative feed intake data does not start when body weight is zero, but rather starts when body weight is the weight of the animal at weaning. To allow for this, Parks modified the first curve by fixing the curve through weaning weight. The resultant curve was:

$$W = (A - W_0).(1 - e^{-BF}) + W_0 \qquad 5.3$$

This approach has a problem in that the weaning weight of the animal is given an undue influence over the resulting shape of the curve, as the curve is fixed through this point. Hence any measurement errors in the weaning weight will not be removed when the curve is fitted and may potentially bias the estimates of other parameters. This is also a problem when a temporary weight loss occurs after weaning, as occurred with some mice in the data set used in this chapter. In this case a curve fitted through weaning weight does not always provide the best description of the data. In order to avoid fixing the curve through either the origin or weaning weight, an alternative modification of the curve to that suggested by Parks was used here. The new modification involved adding an extra parameter (F_0) to the curve, which is essentially the intercept of the curve with the X-axis. The curve used was:

$$W = A(1 - e^{-B(F+F_0)}) \qquad 5.4$$

This curve still allowed the calculation of growth efficiency (AB) from the parameters in the same way as Parks' original curve, as the first derivative at the point where liveweight is zero (i.e. where $F = -F_0$) was not altered. The curve was fitted to data from individual mice using the non-linear regression procedure of Genstat (1987). An example of the curve fitted to the data of a male mouse is shown in Figure 5.1.

A second curve was fitted to cumulative feed intake and age data for each mouse in order to estimate the daily feed intake of the mice at maturity. Parks' (1982) approach was to fit an asymptotic curve to daily feed intake and time data, which allows the description of both the feed intake at maturity and the rate of maturation of feed intake. This approach was not used here as examination of the data showed that most mice had daily intakes similar to their mature intakes within one week of weaning, and hence estimates of rate of maturation of feed intake were unlikely to provide meaningful information. Instead it was decided to fit a linear regression to cumulative feed intake and age data to estimate a slope (C) which was the feed intake per day at maturity as shown below.

$$F = a + C.t \qquad 5.5$$

In order to remove any bias from those mice where daily feed intake increased after weaning, the regression was fitted using data from the mice at ages greater than 60 days. The regression was performed using Genstat (1987). An example of the regression fitted to data from a male mouse is shown in Figure 5.2.

The estimates from the growth and feeding curves were used to calculate the efficiency of maintenance and growth of each mouse. Maintenance requirement was calculated as the estimate of mature feed intake (from equation 5.5) divided by the estimate of mature body weight (from equation 5.4) to produce a value in $g(feed).day^{-1}.g(body\ weight)^{-1}$. Maintenance requirement was also calculated per unit of metabolic body weight ($C/A^{0.75}$) in order to express results according to the procedure used in most feed requirement prediction equations. Growth efficiency was calculated as the product of mature weight (A) and the rate of maturity of body weight with respect to feed intake (B). These efficiencies are based on the principles behind Parks' (1982) model, although they differ slightly from Parks due to the modifications in the curves used. In addition to Park's efficiency parameters, stage of maturity for each week was calculated as the mean liveweight during the week divided by the estimate of mature weight (A) from equation 5.4.

Figure 5.1 Body weight and cumulative feed intake data from a male mouse with the fitted curve from equation 5.4 shown.

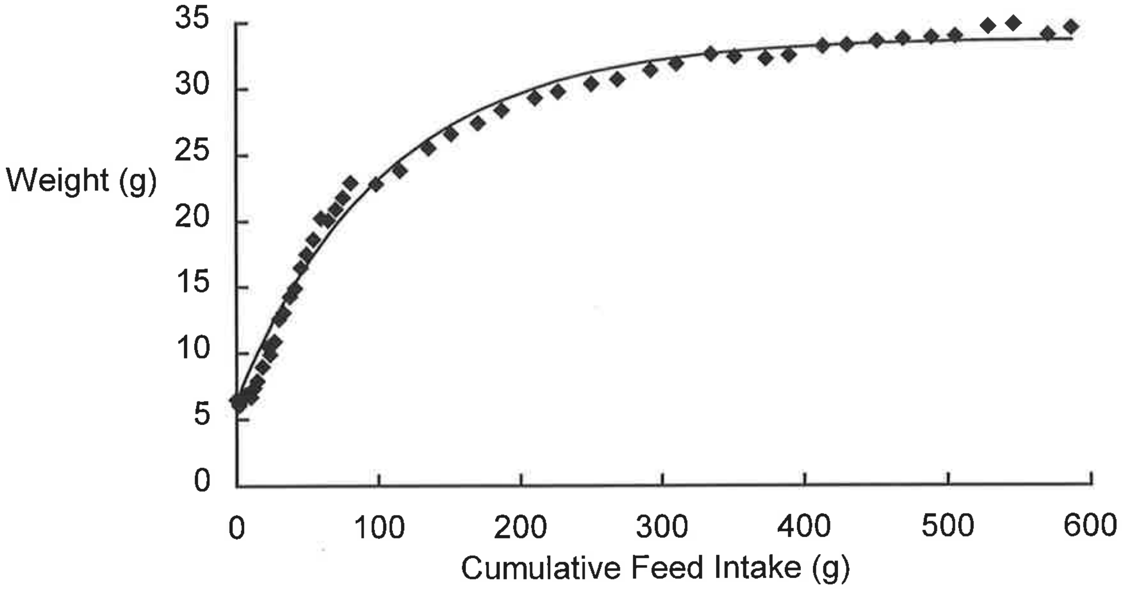
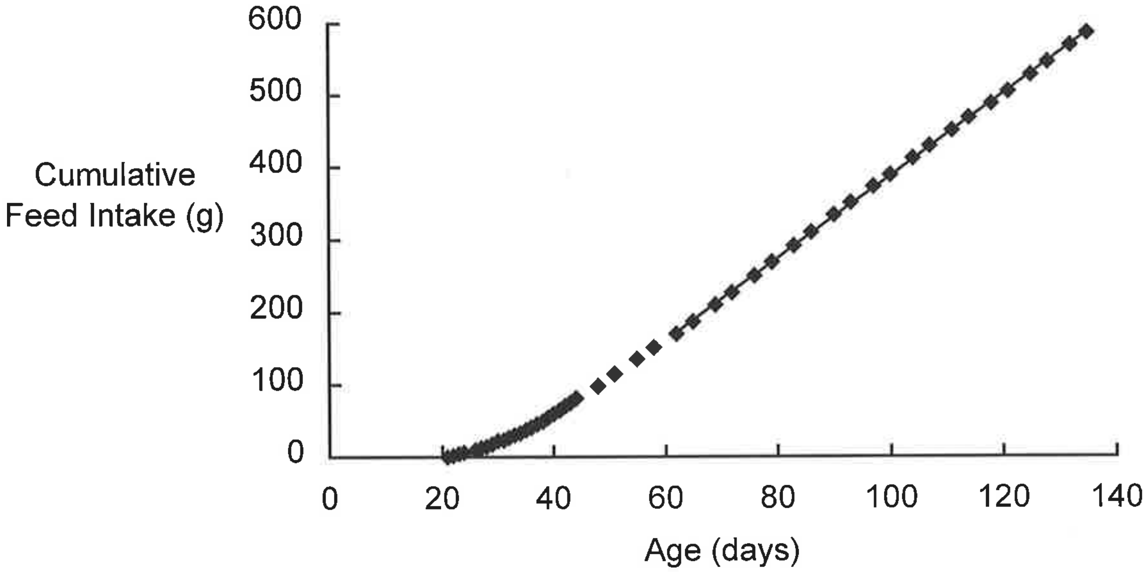


Figure 5.2 Cumulative feed intake and age data from a male mouse with the fitted linear regression from equation 5.5 shown.



5.2.3 Calculation of Residual Feed Intake

The calculation of residual feed intake was performed using feed intake data from periods of one week. Data from the first two days after weaning were discarded, as intake was lower than expected from the other intake data during the first day after weaning. This was considered to be a result either of the process of weaning itself or of the mice adjusting to the new feeding system. After removing this data, the remaining data was collated for analysis on a weekly basis, so that week 4 consisted of data from days 23 to 30, week 5 of days 30 to 37, and so on. At each measurement time the age of each mouse was within one day of the mean age, so that at the end of week 4 the mice were 29, 30 or 31 days old.

To calculate residual feed intake, daily feed intake for each week was modelled (PROC GLM, SAS 1989). The model fitted was:

$$Y_{ij} = \mu + \beta_1(G_i - \overline{G_.}) + \beta_2(M_i - \overline{M_.}) + S_j + S_j * \beta_{2j}(M_{ij} - \overline{M_{.j}}) + e_{ij} \qquad 5.6$$

where:

Y_{ij} = daily feed intake of mouse i;
μ = mean daily feed intake;
G_i = average daily weight gain of mouse i during the feed intake period;
M_i = metabolic midweight of mouse i ;
β_1, β_2 = partial regression coefficients of feed intake on average daily weight gain and metabolic midweight respectively;
S_j = sex of mouse;
e_{ij} = residual variation in daily feed intake.

The interaction between sex and weight gain was not included in the final model as preliminary analysis found that it did not account for a significant amount of variation in feed intake during any period. Residual feed intake was calculated as the residual error term in the model. The coefficient of variation in residual feed intake was calculated as the standard deviation in residual feed intake divided by the mean actual feed intake.

5.2.4 Analyses

Partial correlations and least square means for various parameters were calculated after adjustment for the sex of the mouse using PROC GLM (SAS 1989). Where correlations were calculated separately within sex PROC CORRELATE (SAS 1989) was used.

5.3 Results

Summary of animal performance

A summary of the growth performance and feed intake of the mice for each week is given in Table 5.1. During week 4 (immediately after weaning) there was no sex difference in mid weight or feed intake. However, males had significantly higher average daily gains than females in weeks 4 to 6, and this was accompanied by significantly higher intakes during weeks 5 to 7. After this early period of growth there were no significant sex differences for feed intake and average daily gain, with one exception. After week 4 males were significantly heavier than females due to the higher average daily gains in weeks 4 to 6, and this difference was maintained to maturity. Males were less mature than females during week 4 as there was no difference in mid-weight at this time but males were significantly heavier at maturity (see Table 5.4). However, in weeks 5 to 18 when the males were heavier than females there was no significant difference in maturity between males and females.

Calculation of residual feed intake

The amount of variation accounted for by the terms in the model of feed intake is shown in Table 5.2. A large amount of the total variance in feed intake of young mice was explained by the model, but as the mice matured the proportion of the variation declined rapidly, and only a small amount (10 to 20%) of the variation in feed intake of mature mice was accounted for by the model. This was also reflected by the coefficient of variation in residual feed intake which increased as the mice grew older.

Metabolic mid-weight accounted for a significant amount of variation in daily feed intake in all weeks, while average daily gain, sex and the interaction of sex with metabolic mid-weight were significant in some periods but not in others. Table 5.3 shows the regression coefficients for the model of feed intake in each week. As the male mice matured, the intercept term increased in magnitude, while the coefficient for metabolic mid-weight decreased. However, in female mice the intercept and coefficient for metabolic mid-weight did not appear to change as the mice matured. The trends observed with the regression coefficients were general trends, while there was a large amount of variation in the coefficients between weeks. This variation was probably a function of the reasonably large standard errors associated with many of the regression coefficients as there was a large amount of unexplained variation in feed intake of older mice.

Table 5.1 Least squares means (± s.e.) by sex for daily feed intake, weight gain, mid-weight and stage of maturity of mice during weeks 4 to 18.

Week	Sex	Daily feed intake	sig.†	Average daily gain	sig.†	Mid-weight	sig.†	Stage of maturity	sig.†
4	male	3.76 ± 0.10	n.s.	0.99 ± 0.04	***	13.5 ± 0.4	n.s.	0.42 ± 0.01	***
	female	3.65 ± 0.09		0.64 ± 0.03		12.6 ± 0.3		0.49 ± 0.01	
5	male	4.71 ± 0.10	***	0.82 ± 0.04	***	19.8 ± 0.5	***	0.65 ± 0.02	n.s.
	female	4.23 ± 0.09		0.50 ± 0.03		16.5 ± 0.4		0.61 ± 0.02	
6	male	4.54 ± 0.08	**	0.33 ± 0.03	***	23.8 ± 0.5	***	0.74 ± 0.02	n.s.
	female	4.23 ± 0.07		0.15 ± 0.03		18.8 ± 0.4		0.73 ± 0.02	
7	male	4.93 ± 0.07	*	0.27 ± 0.03	n.s.	26.1 ± 0.4	***	0.80 ± 0.02	n.s.
	female	4.74 ± 0.06		0.21 ± 0.03		20.0 ± 0.4		0.78 ± 0.01	
8	male	4.85 ± 0.07	n.s.	0.15 ± 0.02	n.s.	27.5 ± 0.4	***	0.85 ± 0.01	n.s.
	female	4.89 ± 0.06		0.09 ± 0.02		21.1 ± 0.3		0.82 ± 0.01	
9	male	5.01 ± 0.08	n.s.	0.15 ± 0.02	n.s.	28.4 ± 0.3	***	0.88 ± 0.01	n.s.
	female	5.01 ± 0.07		0.12 ± 0.02		21.8 ± 0.3		0.85 ± 0.01	
10	male	5.10 ± 0.08	n.s.	0.11 ± 0.02	n.s.	29.4 ± 0.3	***	0.90 ± 0.01	n.s.
	female	5.16 ± 0.07		0.14 ± 0.01		22.8 ± 0.3		0.89 ± 0.01	
11	male	5.27 ± 0.08	n.s.	0.09 ± 0.01	*	30.1 ± 0.3	***	0.92 ± 0.01	n.s.
	female	5.40 ± 0.07		0.05 ± 0.01		23.4 ± 0.3		0.91 ± 0.01	
12	male	5.39 ± 0.07	n.s.	0.05 ± 0.01	n.s.	30.6 ± 0.3	***	0.94 ± 0.01	n.s.
	female	5.36 ± 0.07		0.07 ± 0.01		23.9 ± 0.3		0.93 ± 0.01	
13	male	5.13 ± 0.09	n.s.	0.08 ± 0.01	n.s.	31.1 ± 0.3	***	0.96 ± 0.01	n.s.
	female	5.28 ± 0.08		0.08 ± 0.01		24.4 ± 0.3		0.95 ± 0.01	
14	male	5.28 ± 0.08	n.s.	0.07 ± 0.01	n.s.	31.7 ± 0.3	***	0.97 ± 0.01	n.s.
	female	5.24 ± 0.08		0.05 ± 0.01		24.8 ± 0.3		0.97 ± 0.01	
15	male	5.04 ± 0.09	n.s.	0.02 ± 0.02	n.s.	32.0 ± 0.3	***	0.98 ± 0.01	n.s.
	female	5.04 ± 0.08		-0.01 ± 0.02		25.0 ± 0.3		0.97 ± 0.01	
16	male	5.08 ± 0.09	n.s.	0.09 ± 0.02	n.s.	32.4 ± 0.4	***	0.99 ± 0.01	n.s.
	female	5.11 ± 0.08		0.07 ± 0.02		25.2 ± 0.3		0.98 ± 0.01	
17	male	5.16 ± 0.11	n.s.	0.08 ± 0.02	n.s.	33.0 ± 0.4	***	1.01 ± 0.01	n.s.
	female	5.11 ± 0.10		0.04 ± 0.02		25.6 ± 0.3		0.99 ± 0.01	
18	male	4.98 ± 0.11	n.s.	0.02 ± 0.02	n.s.	33.3 ± 0.4	***	1.02 ± 0.01	n.s.
	female	5.02 ± 0.10		0.00 ± 0.02		25.7 ± 0.3		1.00 ± 0.01	

† significance level of sex difference; n.s. $P>0.05$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$

Table 5.2 Percentage variation accounted for by terms in the model of daily feed intake[†] and the residual standard deviation and coefficient of variation in feed intake.

Week	Average daily gain	Midwt$^{0.75}$	Sex	Sex by Midwt$^{0.75}$	Residual feed intake	Residual s.d.	Residual c.v.
4	1*	36***	0	0	14	0.278	7.5
5	1**	74***	0	0	10	0.257	5.8
6	5***	52***	1	1*	39	0.377	8.6
7	2	46***	1	2*	46	0.345	7.1
8	1	40***	2	4**	59	0.372	7.6
9	0	28***	2	4*	70	0.453	9.1
10	1	31***	3*	5**	67	0.505	9.8
11	1	28***	4*	6**	69	0.480	9.0
12	5**	32***	2	4*	67	0.442	8.2
13	2	8**	1	2	88	0.666	12.8
14	2	15***	2	2	82	0.563	10.7
15	5**	10***	2	2	83	0.633	12.5
16	1	11***	2	3*	88	0.624	12.2
17	7**	13***	1	2	80	0.752	14.6
18	0	7**	2	3	91	0.797	15.9

[†] Type III Sums of Squares. Each term in the model accounted for 1 degree of freedom. Residual degrees of freedom varied from 110 to 114 due to incidentally missing values in some weeks.

* P<.05;** P<.01;***P<.001

Table 5.3 Regression coefficients and standard errors from the model of daily feed intake. Significance levels for each term are given in Table 5.2.

Week	Intercept	se	Average daily gain	se	Midwt$^{0.75}$	se	Sex - F[a]	se	Sex - F[a] by Midwt$^{0.75}$	se
4	-0.27	0.24	0.28	0.14	0.54	0.04	-0.03	0.32	0.03	0.05
5	-0.02	0.22	0.23	0.09	0.49	0.02	-0.39	0.32	0.07	0.04
6	0.93	0.38	0.63	0.17	0.32	0.03	-0.76	0.57	0.12	0.06
7	1.19	0.54	0.33	0.17	0.32	0.04	-0.97	0.71	0.15	0.07
8	1.78	0.66	0.37	0.23	0.25	0.05	-1.62	0.91	0.23	0.08
9	1.67	0.90	0.20	0.26	0.27	0.07	-2.21	1.25	0.28	0.11
10	1.32	1.05	0.50	0.42	0.30	0.08	-3.64	1.58	0.42	0.14
11	2.03	1.04	0.42	0.49	0.25	0.08	-4.00	1.57	0.44	0.14
12	1.31	0.96	-1.18	0.41	0.32	0.07	-2.71	1.47	0.32	0.13
13	2.89	1.35	0.89	0.63	0.16	0.10	-2.37	2.11	0.26	0.18
14	2.46	1.11	0.81	0.50	0.21	0.08	-2.64	1.77	0.28	0.15
15	2.96	1.19	1.17	0.43	0.15	0.09	-2.88	1.96	0.29	0.16
16	3.27	1.13	-0.46	0.42	0.14	0.08	-3.36	1.90	0.33	0.16
17	1.45	1.39	1.54	0.51	0.26	0.10	-2.79	2.30	0.30	0.19
18	3.44	1.48	0.44	0.57	0.11	0.11	-3.92	2.39	0.37	0.20

[a] Regression coefficient for females. The coefficients of the sex effects for males were zero.

Growth and feeding curves

The curve in equation 5.4 fitted to the weight and cumulative feed intake data of individual mice accounted for 88 to 99 % of the variance. The linear regression of age on cumulative feed intake accounted for 99 to 100 % of the variation in cumulative feed intake. As both curves explained a high proportion of the variation the parameter estimates obtained were accurate with relatively small standard errors. Table 5.4 shows the least squares means by sex and the standard errors for the between animal variation in the parameter estimates and the traits derived from the estimates (i.e. growth efficiency (AB) and maintenance requirement (C/A and $C/A^{0.75}$), as well as the body water content measurement from the isotope dilution study. The mature weight of males was significantly higher than that of the females, but there was no significant sex difference for mature feed intake. Hence males had significantly lower maintenance requirements per unit body weight than females.

Correlations between the parameters were calculated separately for each sex and are given in Table 5.5. Correlations were generally similar for males and females except for correlations involving mature feed intake or body composition. The relationship between mature feed intake and mature weight differed for males and females and is plotted in Figure 5.3. The correlation between mature weight and mature intake was not significantly different from zero for females but was significant (P=0.001) for males. There were several females which had very high mature feed intakes. The intakes of these individuals appeared to be normal during growth, but after week 8 or 9 the intakes rose to the levels shown in Figure 5.3. The high mature intakes were not an artefact of the curve fitting as examination of the raw data showed that the high intakes observed were consistent from week to week in mature animals. There did not appear to be any individuals with exceptionally low feed intake at maturity.

In males mature weight was negatively correlated with body composition, and so heavier mice were fatter, whereas there was no relationship between mature weight and body composition in females. Conversely, mature feed intake of females was positively correlated with body composition, indicating that fatter females had lower intakes, whereas there was no relationship between mature feed intake and body composition in males. Hence the correlation of maintenance efficiency with body composition was of similar magnitude in males and females, but appears to be a consequence of different relationships as the response surface of mature weight, mature feed intake and body composition are different for males and females.

Table 5.4 Least-squares means by sex for estimates of mature weight (A), rate of maturity of bodyweight (B), F_0 term from equation 5.4, mature feed intake (C), maintenance requirement (C/A and $C/A^{0.75}$), growth efficiency (AB) and body water content (BWC).

Trait	Units	Male		Female		
		Mean	s.e.	Mean	s.e.	sig. [†]
A	g (bodyweight)	32.62	1.01	26.58	0.90	***
B	$g\ (feed)^{-1}$	0.0135	0.0006	0.0115	0.0006	*
F_0	g (feed)	27.83	4.59	58.34	4.12	***
C	$g\ (feed).day^{-1}$	5.15	0.08	5.19	0.08	n.s.
AB	$g\ (bodyweight).g\ (feed)^{-1}$	0.429	0.016	0.290	0.015	***
C/A	$g\ (feed).g\ (bodyweight)^{-1}.day^{-1}$	0.159	0.004	0.202	0.004	***
$C/A^{0.75}$	$g\ (feed).g\ (bodyweight)^{-0.75}.day^{-1}$	0.379	0.008	0.455	0.007	***
BWC	% H_2O	64.5	0.8	66.2	0.7	n.s.

[†] significance level for sex difference.

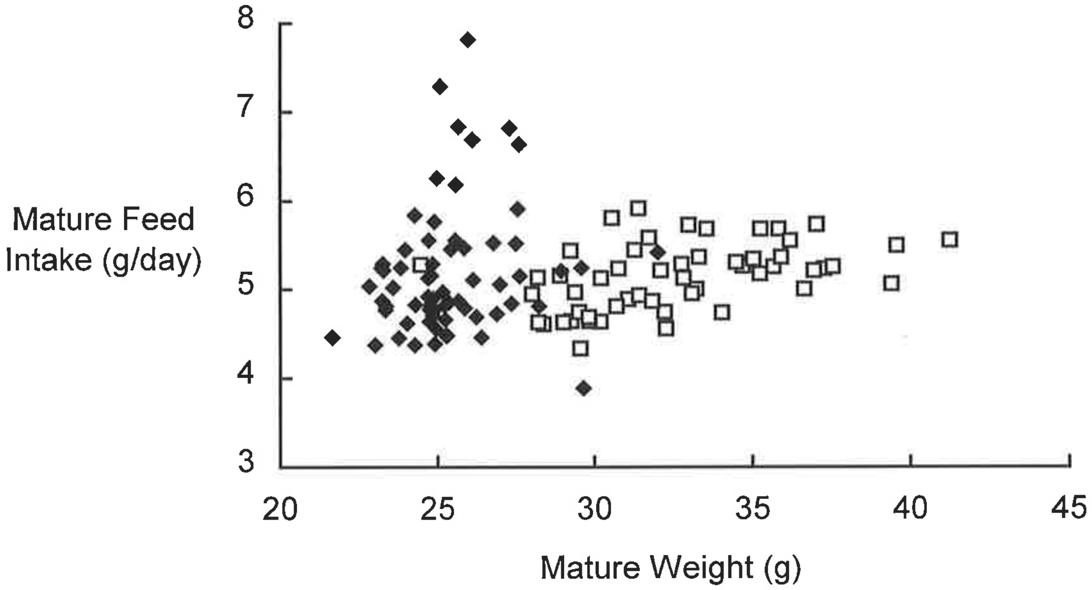
* P>.05; *** P>.001

Table 5.5 Phenotypic correlations within sex for parameter estimates, maintenance requirement, growth efficiency and body water content[†]. Correlations for males are given on the upper diagonal and females on the lower diagonal.

	A	B	F_0	C	AB	C/A	$C/A^{0.75}$	BWC
A		-0.61	0.45	0.44	-0.42	-0.72	-0.56	-0.49
B	-0.40		-0.68	-0.18	0.97	0.49	0.41	0.39
F_0	0.48	-0.81		0.11	-0.67	-0.38	-0.33	-0.15
C	-0.09	0.12	-0.06		-0.06	0.30	0.49	-0.04
AB	-0.37	0.98	-0.81	0.18		0.36	0.32	0.33
C/A	-0.59	0.42	-0.38	0.80	0.41		0.98	0.44
$C/A^{0.75}$	-0.54	0.37	-0.34	0.86	0.38	0.99		0.40
BWC	-0.02	0.07	-0.07	0.31	0.03	0.32	0.32	

[†] Abbreviations and units given in Table 5.4.

Figure 5.3 Plot of mature feed intake against mature weight by sex. Males are shown as open squares, females as shaded diamonds.



Growth efficiency (AB) was positively correlated with maintenance requirement in both males and females, and so animals with high growth efficiency were less efficient at maintaining bodyweight at maturity. However the correlation between growth efficiency and maintenance efficiency was weak (0.32 to 0.41) and so it should be possible to identify animals which are superior for both growth and maintenance efficiency.

Repeatability of feed intake and residual feed intake

Partial correlations between weeks for feed intake and residual feed intake are given in Table 5.6. The correlations for feed intake were considerably higher than for residual feed intake in young mice. However while the correlations for feed intake increased slightly as the mice matured, the correlations for residual feed intake increased rapidly as mice matured, and were of a similar magnitude to those for feed intake at maturity. Repeatability from weeks 13 to 18 was 0.81 for daily feed intake and 0.80 for residual feed intake. Correlations between actual feed intake and residual feed intake were low to moderate for young animals (0.35 to 0.70), but were high in mature animals (>0.90, results not shown).

Relationship of feed intake and residual feed intake with efficiency parameters and body composition

Partial correlations of daily feed intake and residual feed intake with maintenance requirement, growth efficiency, body water content and stage of maturity are given in Table 5.7 and Table 5.8 respectively. Maintenance requirements were poorly correlated with feed intake or residual feed intake in weeks 4 and 5. However as the mice matured the correlations increased, and both feed intake and residual feed intake in mature mice were reasonable predictors of maintenance efficiency. Growth efficiency was significantly correlated with feed intake in weeks 5 to 7, 9, 10 and 18, and with residual feed intake in weeks 4, 5, 17 and 18. However, most of the correlations with growth efficiency were low. Percentage body water was poorly correlated with daily feed intake, but was significantly correlated with residual feed intake for mice in week 9 and onwards. The correlations were low and there was still a large amount of variation in residual feed intake which was independent of body composition. Stage of maturity was significantly correlated with daily feed intake in all weeks except weeks 13 to 15. In young mice the correlations were high, but decreased as the mice matured and there was less variation in maturity. In contrast to the results with daily feed intake, residual feed intake was independent of stage of maturity at all ages.

Table 5.6 Partial correlations (adjusted for sex) between adjacent weeks for daily feed intake and residual feed intake.

Weeks	Daily Feed Intake	Residual Feed Intake
4 & 5	0.80***	0.24 *
5 & 6	0.61***	0.11 ^{ns}
6 & 7	0.64***	0.37***
7 & 8	0.73***	0.61***
8 & 9	0.66***	0.52***
9 & 10	0.82***	0.76***
10 & 11	0.85***	0.78***
11 & 12	0.87***	0.79***
12 & 13	0.74***	0.69***
13 & 14	0.84***	0.82***
14 & 15	0.91***	0.91***
15 & 16	0.92***	0.93***
16 & 17	0.88***	0.83***
17 & 18	0.86***	0.79***

^{ns} P>0.05; * P<0.05; *** P <0.001

Table 5.7 Partial correlations of daily feed intake with maintenance requirement (C/A and C/A$^{0.75}$), growth efficiency (AB), body water content (BWC) and stage of maturity.

Week	C/A	C/A$^{0.75}$	AB	BWC	Stage of maturity
4	0.11^{ns}	0.13^{ns}	-0.02^{ns}	0.00^{ns}	0.83***
5	0.18^{ns}	0.21*	0.30**	-0.04^{ns}	0.84***
6	0.32***	0.35***	0.40***	-0.03^{ns}	0.66***
7	0.48***	0.51***	0.39***	0.14^{ns}	0.60***
8	0.42***	0.48***	0.11^{ns}	-0.02^{ns}	0.32***
9	0.55***	0.61***	0.27**	0.17^{ns}	0.32***
10	0.59***	0.66***	0.23*	0.11^{ns}	0.27**
11	0.62***	0.69***	0.09^{ns}	0.18^{ns}	0.22*
12	0.67***	0.74***	0.15^{ns}	0.20*	0.26**
13	0.61***	0.68***	-0.04^{ns}	0.13^{ns}	0.08^{ns}
14	0.69***	0.76***	0.07^{ns}	0.20*	0.17^{ns}
15	0.70***	0.78***	0.05^{ns}	0.23*	0.17^{ns}
16	0.71***	0.78***	0.10^{ns}	0.18^{ns}	0.19*
17	0.67***	0.74***	0.15^{ns}	0.20*	0.18*
18	0.68***	0.74***	0.25*	0.22*	0.22*

^{ns} P>0.05;* P<0.05; ** P<0.01; *** P<0.001;

Table 5.8 Partial correlations (adjusted for sex) of residual feed intake with maintenance requirement (C/A and C/A$^{0.75}$), growth efficiency (AB), body water content (BWC) and stage of maturity.

Week	C/A	C/A$^{0.75}$	AB	BWC	Stage of maturity
4	-0.15^{ns}	-0.15^{ns}	-0.48***	-0.02^{ns}	-0.03^{ns}
5	-0.02^{ns}	-0.02^{ns}	-0.22*	0.00^{ns}	-0.02^{ns}
6	0.30**	0.30**	0.11^{ns}	0.01^{ns}	0.10^{ns}
7	0.44***	0.45***	0.06^{ns}	0.26**	0.15^{ns}
8	0.36***	0.40***	-0.19^{ns}	0.01^{ns}	-0.03^{ns}
9	0.53***	0.56***	0.09^{ns}	0.26**	0.10^{ns}
10	0.60***	0.63***	0.15^{ns}	0.21*	0.10^{ns}
11	0.62***	0.65***	0.02^{ns}	0.32**	0.10^{ns}
12	0.67***	0.71***	0.02^{ns}	0.34***	0.13^{ns}
13	0.68***	0.73***	-0.01^{ns}	0.22*	0.04^{ns}
14	0.77***	0.81***	0.08^{ns}	0.34***	0.11^{ns}
15	0.76***	0.81***	0.08^{ns}	0.32**	0.10^{ns}
16	0.76***	0.80***	0.12^{ns}	0.26**	0.12^{ns}
17	0.76***	0.80***	0.21*	0.38***	0.15^{ns}
18	0.73***	0.77***	0.28**	0.33***	0.15^{ns}

^{ns} P>0.05; * P<0.05; ** P<0.01; *** P<0.001;

5.4 Discussion

The approach that fits curves to data in order to describe growth, feed intake and efficiency is a very useful way of looking at the processes involved, as it accounts for patterns which occur over the growth of an animal from weaning to maturity and which are difficult to describe and investigate using the “snapshot performance test” approach. However care must be taken to ensure that the parameters of the curves fitted are useful for describing the data and have biological meaning. An improper understanding of the models used and the description of the data can lead to incorrect inferences being drawn. For example, it may be tempting to analyse the variation in the F_0 parameter from equation 5.4 and make conclusions on the basis that this parameter represents the amount of feed consumed from conception to weaning. However, this conclusion is based on the assumption that the pattern of feed intake and growth pre-weaning follows the same asymptotic relationship used to describe the post-weaning data, an assumption which is not able to be verified by experimental data. Hence it is unwise to assign biological meaning to the F_0 parameter which is used here simply as a statistical tool to improve the description of the post-weaning data by increasing the flexibility of the curve fitted to the data.

The measure of growth efficiency used by Parks (1982) in the model of feed intake and growth is obtained by multiplying the mature weight (A) by the rate of maturation of weight with respect to feed intake (B) from equation 5.2. Parks used this measure as it represented the slope of the curve at the point where it crosses the x-axis, and hence represents the instantaneous efficiency of growth when weight is zero and all feed is directed towards growth. This reasoning also incorporates the assumption mentioned previously that pre-weaning feed intake and growth can be described using post-weaning data and an asymptotic relationship. This assumption is difficult to verify and may be somewhat unreliable, and caution should be used in placing a rigid biological interpretation on AB. However, AB may still be a useful index for describing an aspect of the relationship between growth and feed intake, and is still worth examining as Thompson and Barlow (1986) showed that changes made in AB may still have an impact on the biological efficiency of real production systems.

In addition to concerns with the extrapolation of post-weaning feed intake to estimate growth efficiency, it is conceptually difficult to identify what the efficiency of growth represents as growth is a compound result of many separate but inter-related processes, including synthesis and degradation of protein, adipose tissue and bone. These processes have different energetic inputs and the relative importance between processes can change as an animal grows towards its mature equilibrium state, and hence a representation of growth efficiency as a single value constant across a wide range of maturity is incomplete. Thus from a theoretical consideration of the processes of growth it also appears to be wiser to consider the AB parameter of Parks (1982) as an index describing a relationship between post-weaning feed intake and growth, rather than as the efficiency of growth.

The correlation between AB and maintenance requirements suggests that the two measures are antagonistic, and that improving one may lead to a decline in the other. This antagonistic relationship was alluded to by Thompson and Barlow (1986). However this observation is made at the phenotypic level and is not informative as to changes which occur if selection pressure is placed on maintenance efficiency. Stephens (1991) found that selection for maintenance efficiency in mice did not produce a significant correlated change in AB, although a trend for high maintenance efficiency animals to exhibit higher AB values was observed. These relationships between growth and maintenance efficiency suggest that indirect selection for maintenance efficiency using post-weaning efficiency may have different biological consequences from direct selection on maintenance efficiency and it is important to evaluate these consequences before a recommendation as to the most appropriate method of selection for efficiency can be made.

The different relationship between mature feed intake and mature weight for male and female mice was also found by Stephens (1991). This study has found that the differences also extend to the relationship with body composition, and that the response surface for these three components is a different shape for males and females. Stephens *et al.* (1988) alluded to this difference in response surface when they reported interactions of sex with body weight and body composition when modelling feed intake. The reason for this difference in response surface is unknown and to the author's knowledge these observations have not been made in other species.

The increase in the amount of variation in feed intake not able to be explained by the model is of interest. This represented an increase in the coefficient of variation for residual feed intake from around 6 to 9% in growing mice to 11 to 16% in mature mice. Similar coefficients of variation to that found here in growing mice have been reported for livestock species and include estimates of 4% (Brelin and Brannang 1982) and 8% (Korver *et al.* 1991) in growing cattle, 5% in growing pigs (Foster *et al.* 1983) and 5 to 6% (Luiting 1991) and 6 to 10% (Bentsen 1983) in laying hens from 20 to 30 weeks of age.

At maturity the coefficient of variation in residual feed intake of mice was greater than many of the estimates in the literature for livestock species. Luiting (1991) found that the coefficient of variation in residual feed consumption increased with age in laying poultry to 7-8%. Estimates in lactating cows include 5% (van Arendonk *et al.* 1991) and 8% (Ngwerume and Mao 1992). However, Bordas and Merat (1984) working with poultry found more variation in residual feed intake of mature males than in mature laying hens. The greater variation in male poultry may be due to differences in the physiological state of non-producing and producing animals. If this is the case then a higher coefficient of variation would be expected for the mature non-producing mice in this study than is observed in lactating or laying females. This observation would support the hypothesis of Taylor *et al.* (1986) who suggested that when animals are operating at their maximum production potential there may be no difference in efficiency between animals which differ in efficiency at maintenance. This hypothesis has significance for selection to improve maintenance efficiency as it suggests that no difference in efficiency of production may occur, but that the only change may be a decrease in production potential.

The increase in the coefficient of variation in residual feed intake with age may be a reflection of a greater component of maintenance in older animals, with less feed being used for growth. The literature contains reports suggesting that there is more genetic variation in the efficiency with which animals use feed for maintenance than for growth (e.g. Herd *et al.* 1990), and if so it might be expected that mature animals would show more residual variation in feed intake due to a larger component of genetic variance. However the results of Luiting (1991) with poultry suggest that the greater phenotypic variation in residual feed intake of old animals is due to an increase in the environmental variance in older animals with the amount of additive genetic variance remaining constant. It was not possible to partition the genetic variance from the environmental variance in this data and so the cause of the increase in variation is not able to be determined from the current data.

The repeatability of feed intake was high even for young mice and reflects the fact that many of the mice had reached their mature feed intake very shortly after weaning. It is known that feed intake matures appreciably faster than bodyweight in other species, as found by Thompson *et al.* (1985) in sheep, and the fast rate at which mature feed intake was attained in the mice is likely to be a function of their lower mature size and higher metabolic rate. This would suggest that mature feed intake can be measured much earlier than mature weight and on animals which are still growing. Although this is the case phenotypically, the corresponding genetic correlation between feed intake during growth and at maturity may not be as high as the phenotypic correlation as it is possible to envisage different factors controlling feed intake during late growth and at maturity.

In comparison to feed intake, residual feed intake was poorly repeatable at young ages, but became repeatable as the mice matured and reached a stable state with little change in either feed intake or weight occurring. Post-weaning residual feed intake was phenotypically a poor indicator of maintenance efficiency at maturity. If the phenotypic correlations are taken as a first approximation of the unknown genetic correlations they would suggest that selection on post-weaning residual feed intake is unlikely to change maintenance efficiency, and that a greater selection response would be achieved by measuring residual feed intake on older animals. However, it is possible that the genetic correlations are significantly higher than the phenotypic correlations, and hence to predict the value of selection on residual feed intake knowledge of the genetic parameters is required. There is little information in the literature concerning genetic correlations of residual feed intake measured at different ages. Jensen *et al.* (1992) examined residual feed intake of bulls over two periods and estimated phenotypic and genetic correlations between the periods of 0.10 and 0.19 respectively. However in Jensen's study the feeding regime of the bulls differed between periods and it was not possible to separate the effects of age and feeding regime.

In mature mice residual feed intake was highly repeatable and was correlated with maintenance efficiency as calculated from the growth and feeding curves. The high repeatability suggests that the factors causing differences in feed utilisation between animals were consistent between weeks. These differences were not able to be explained by body composition as body composition was only able to explain a small proportion of the variation in residual feed intake and maintenance requirements. It was not possible to determine whether the variation between animals in residual feed intake and maintenance efficiency was due to genetic variation or to permanent environment effects.

The correlation of body composition with residual feed intake and maintenance requirements found here suggest that at maturity leaner mice have higher residual feed intake and higher maintenance requirements. This relationship is similar to that found in the poultry literature as summarised by Luiting (1991) who suggested that the effect of body composition on residual feed intake of poultry appears to be small, but that fatter poultry tend to have lower residual feed intake at maturity. These results agree with conventional thought (eg Webster 1981; Tess *et al.* 1984) which suggests that in mature animals at maintenance, fat tissue is metabolically less active than lean tissue, and hence energy requirements per unit body weight are lower in fatter animals. This relationship does not necessarily hold for growing animals as fat is energetically more expensive to deposit than lean (Webster 1980), and hence there is a conflict of the lower energy required to maintain fat with the greater amount of energy required to deposit fat. There has been little published relating residual feed intake to body composition in ruminants. The only study with this information to the authors knowledge is that of Jensen *et al.* (1992) who found that in growing cattle the phenotypic correlation of body composition with residual feed intake was low, but fatter animals tended to have higher residual feed intakes. However the genetic correlation in Jensen's study was of the opposite sign, suggesting that genetically fat animals were more efficient. The difference between the phenotypic and genetic correlations may be a function of the conflict between deposition and maintenance in body composition of growing animals. This situation again provides a warning that selection for efficiency post-weaning may have a different biological outcome to selection at maturity.

The results of this study raise the question as to why residual feed intake of young animals is such a poor phenotypic predictor of the efficiency of maintenance of mature animals. This may be due to inadequacies in the model used as the basis of residual feed intake. The basic model used by nutritionists for predicting feed requirements partitions energy requirements into those for maintenance of body weight and growth. The model used in calculating residual feed intake is based on the nutritional model of feed requirements, as it includes adjustments of feed intake data for weight maintained and weight gain to represent maintenance and growth. However, partitioning of feed requirements into maintenance and growth is essentially conceptual, as the physiological processes occurring in the body involve both synthesis and degradation of protein and fat, even in a rapidly growing animal. The difficulty and inappropriateness of partitioning feed requirements into those for maintenance and those for growth are shown in experiments by Koong *et al.* (1982; 1985) where fasting heat production of pigs, rats and sheep was shown to vary with growth rate independent of body size. In addition, as discussed earlier, assigning a constant efficiency to growth consisting of both fat and protein deposition which differ in their energetic requirements is an oversimplification of the process and may lead to errors in prediction of feed requirements. Likewise the assumption that maintenance efficiency in a growing animal is related to maintenance efficiency at maturity may be false. Further knowledge of the processes regulating feed intake and growth may lead to improved models of feeding and growth and allow more accurate prediction of maintenance efficiency in young animals.

5.5 Summary

In this chapter the relationship between residual feed intake and efficiency from weaning to maturity was examined. Mice were used as a model species due to their short lifecycle. Curves were fitted to feed intake and growth data and the curve parameters were used to describe lifetime efficiency of the mice. The relationship between residual feed intake and lifetime efficiency was then examined to determine whether selection on post-weaning residual feed intake is likely to result in improved lifetime efficiency.

The results obtained indicated that the age at which residual feed intake is measured may be important in determining the outcome of selection for efficiency. Residual feed intake of young animals was poorly correlated with maintenance efficiency whereas residual feed intake of mature animals was highly correlated with maintenance efficiency. In addition there was more phenotypic variation in residual feed intake of mature animals and hence a greater selection response may be obtained if there is also more genetic variation present. If the genetic correlations follow the phenotypic correlations a greater correlated response in maintenance efficiency will occur if selection is based on residual feed intake of older animals. However an increase in the age at which residual feed intake is measured may increase the generation interval and hence reduce the rate of genetic progress in residual feed intake and other traits in the breeding objective. Only through knowledge of the relevant genetic parameters can the response to selection and the optimal age for measurement of residual feed intake be determined accurately.

Chapter 6. Genetic variation in feed efficiency of mice

6.1 Introduction

The potential for genetic improvement of production system efficiency in species where a relatively high proportion of feed resources is consumed by the breeding herd is dependant on the genetic variation in feed intake and growth traits both in growing and in mature animals. Many studies have examined the genetic variation in these traits for either growing or mature animals. However, with the exception of the study conducted in the Netherlands reported by Nieuwhof et al. (1992), there have been no studies which have examined the genetic relationship between growth and feed intake in growing and mature animals.

In Chapter 5 the phenotypic relationships between feed intake and growth traits in mice were examined from weaning to maturity. The results showed that post-weaning efficiency was poorly correlated phenotypically with maintenance efficiency, suggesting that a post-weaning test is unlikely to be informative as to the efficiency of an individual at maturity. It was also found that the amount of phenotypic variation in efficiency increased as the mice matured, and that most of the variation was independent of body composition.

While the phenotypic relationships found in Chapter 5 are valuable for increasing the understanding of the efficiency complex, knowledge of the genetic parameters is required in order to examine the potential for genetic improvement of efficiency. With knowledge of the genetic parameters it is possible to determine the amount of genetic variation in feed efficiency both post-weaning and at maturity, and to predict the likely correlated responses to selection for feed efficiency. This knowledge is extremely important in order to be able to predict the value of selection to make genetic improvements in efficiency.

The mouse model used in chapter 5 provided a quick and cheap way to collect data which is useful for increasing our understanding of the biology of efficiency in mammals. It can also provide valuable insight into the likely consequences of selection for efficiency in livestock species. This chapter extends the results of Chapter 5 by examining the genetic properties of feed intake, growth and efficiency in growing and mature mice.

6.2 Materials and methods

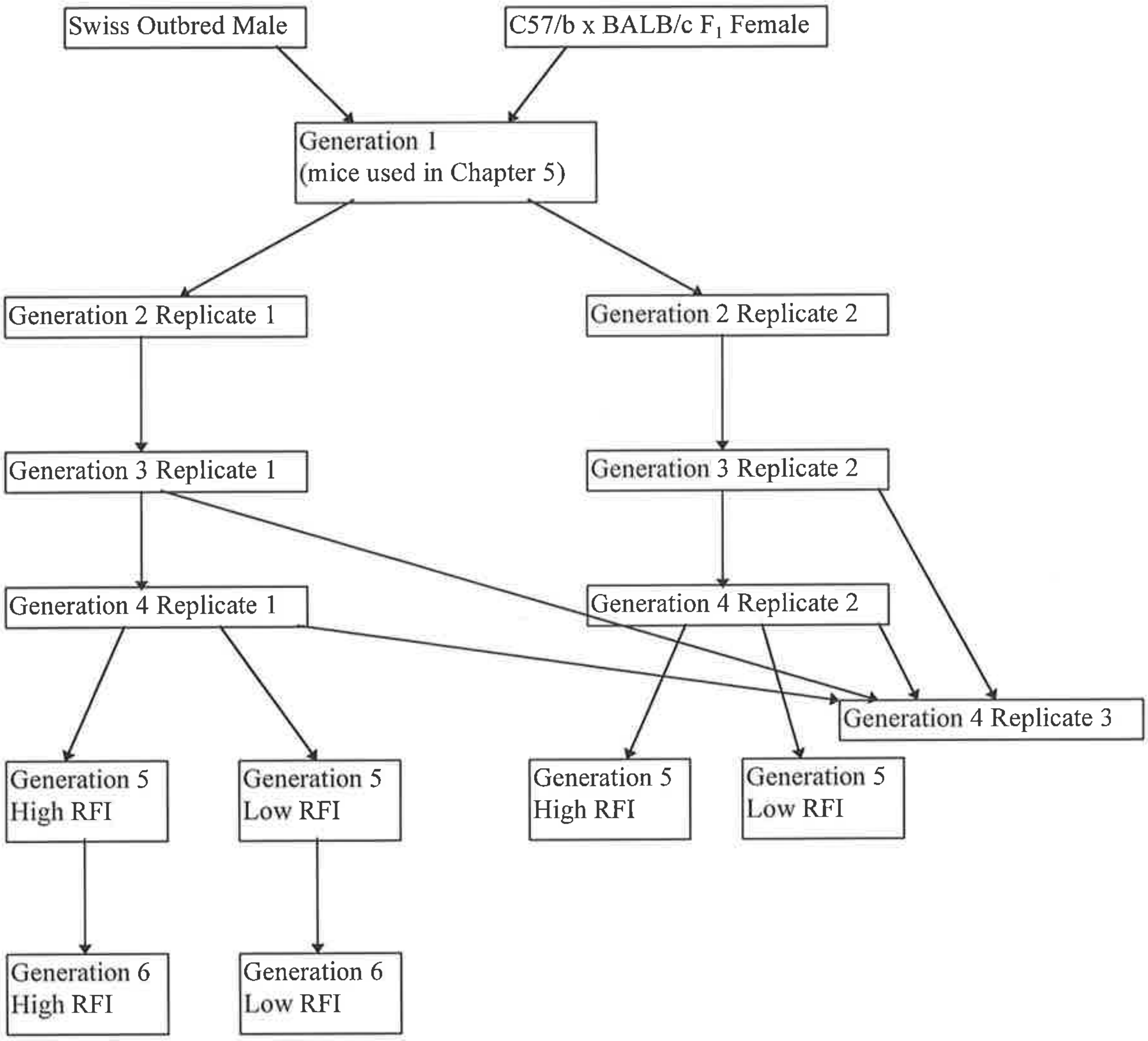
6.2.1 Animals

6.2.1.1 Population structure

The mouse population used in this study was derived from the three-way cross used in Chapter 5, which was termed generation 1 for the purposes of this experiment. The experiment was designed to produce a population structure from which accurate estimates of genetic parameters could be obtained. The overall mating system is represented in Figure 6.1. The population was split into two replicates for management reasons, and the lifecycle of the replicates were staggered to allow efficient use of the available resources. Both replicates were derived from a random mating of the population from chapter 5, to produce generation 2. From generation 2 to 4, sires were chosen at random and all dams were allocated to sires randomly but with full sib matings avoided. From generation 5 it was decided to initiate selection lines for high or low residual feed intake, and hence the parents of generation 5 were selected on the basis of their estimated breeding value for residual feed intake calculated using Best Linear Unbiased Prediction from the accumulated data set. Replicate 2 was not continued after generation 5. Generation 6 replicate 1 was a continuation of the selection lines, but little selection intensity was placed on the lines due to an error in the program written to sort mice by estimated breeding value which was not noticed until generation 6 mice had been measured post-weaning.

An extra group of animals was produced in generation 4 in order to improve the data structure for estimation of maternal effects and to strengthen the genetic linkage between the two replicate populations. This extra group (replicate 3 of generation 4) was produced by mating dams from both replicates of generation 3 which had already had progeny measured in generation 4, with sires chosen randomly from generation 3 replicate 2 and generation 4 replicates 1 and 2.

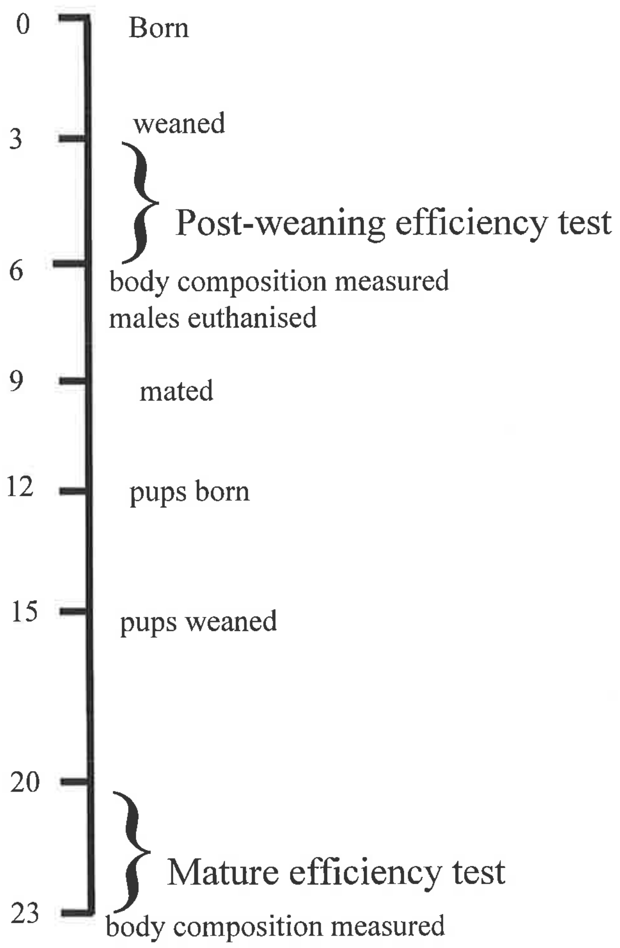
Figure 6.1 Mating design of mouse population



6.2.1.2 Husbandry

A summary of the lifecycle and measurements taken on the mice is shown in Figure 6.2. At mating, males were placed with the females for 7 days, after which they were removed. Before the females gave birth they were placed in individual boxes and given paper towelling material with which they could build a nest for the litter. Females began pupping 19 days after being exposed to the male, and were checked daily for litters until all pregnant females had given birth. One day after birth the number of pups in each litter was recorded and litters were standardised to six pups in generation 2 and five pups in subsequent generations. When standardising litters, equal numbers of male and females were kept if possible. When 5 pups were required, two males and two females were chosen, with the fifth pup being chosen at random. Care was taken not to bias the sample by ensuring that pups were selected at random without bias towards larger pups. In generation 2 replicate 1 the pups were born in 2 rounds of matings as insufficient numbers were obtained due to poor reproductive rates of the females. The poor reproductive rates of the three way cross females was probably due to the effect of being relatively old at the time of first mating. For the second replicate of generation 2 the litters were not standardised as sufficient numbers were required from one round of mating in order to keep the replicates synchronised.

Figure 6.2 Lifecycle and measurements taken on the mice (age is given in weeks).



6.2.1.3 Measurements

All mice were weaned at 21 days and liveweight at weaning was recorded. Approximately 200 mice from 40 litters were then put in individual cages for a post-weaning efficiency test, while any excess mice were euthanised humanely. All groups were measured post-weaning with the exception of generation 5 replicate 2 where only weaning weight was recorded. Litters for the post-weaning test were chosen at random, but it was attempted to use an equal number of litters from each sire where possible. All mice were fed a standard laboratory animal ration (Joint Stock Diet, Milling Industries). The energy concentration of the ration was not measured separately for each test group as the analysis included a term for management group which adjusted for differences between groups and hence differences in feed composition which may have occurred between groups were removed. Feed intake was measured using the same feeding system as used in chapter 5.

After weaning, feed intake and liveweight were recorded for mice placed on the post-weaning efficiency test. Measurements were taken at approximately 28 days of age and then for two periods of exactly seven days each after the 28 day measurement, so that the test concluded when the mice were approximately 42 days old. At the conclusion of the test the body composition of the mice was measured using an EM-SCAN Body Composition Analyser, and percentage body fat was estimated. Details of the method used for estimation of body composition are given in Appendix C. After the post-weaning test approximately 10 males were retained as future sires and the remainder of the males were euthanised.

The mice were mated at approximately 9 weeks of age, with litters being born at 12 weeks. Sires were euthanised after litters were born. After the pups were weaned (when the dam was approximately 15 weeks) the dams were group housed until 20 weeks. At 20 weeks all females were placed on a mature efficiency test. The mice were put in individual cages and were on the same feeding system used previously. An initial pre-test period was allowed for re-adjustment to the feeding system, after which feed intake and weight were measured weekly for 2 weeks. At the end of the mature test a second measurement of body composition was taken using the EM-Scan Body Composition Analyser. The females were then euthanised, with the exception of females from generation 3 which were retained to produce a second litter as described above. Mice from generation 4 replicate 3, generation 5 replicate 2 and generation 6 replicate 1 were not measured at maturity. A summary of the numbers of mice weaned and measured during the post-weaning test and mature test is presented for each generation in Table 6.1.

Table 6.1 Numbers of animals measured at weaning, post-weaning and maturity by sex, generation and replicate.

		Weaning		*Post-Weaning Test*		*Mature Test*	
Generation	Replicate	male	female	male	female	male	female
1	-	55	66	53	66	0	66
2	1	44	54	42	53	0	52
2	2	61	48	60	48	0	47
3	1	93	92	89	89	0	85
3	2	108	101	100	92	0	89
4	1	147	136	105	93	0	88
4	2	168	149	99	93	0	86
4	3	158	148	98	98	0	0
5	1	134	150	87	104	0	101
5	2	142	145	0	0	0	0
6	1	97	97	90	89	0	0
	Total	1207	1186	823	825	0	614

6.2.2 Definition of traits

The traits measured on the mice can be divided into two categories, those measured post-weaning and those measured at maturity. A summary of the traits used in the analyses is given in Table 6.2.

The data collected post-weaning consisted of weights at days 21 (weaning), 28, 35 and 42, feed intake from day 21 to 28, 28 to 35 and 35 to 42, and body composition at the end of the post-weaning test. The day of the year on which each measurement was made was recorded in Julian days from the 1st of January 1993, and are notated as $DOY_{21,\ etc}$. From this data other traits of interest were derived. The main period of interest in the post-weaning test was from days 28 to 42, as the first week was considered as a pre-test adjustment phase during which the mice were able to adjust to the stress of weaning and adapt to the feeding system. Average daily feed intake during this period, average daily gain, mid-weight and metabolic mid-weight were calculated according to the formulae given below. In addition, the exact age of the mouse at day 28 and at the measurement of body composition were calculated and subsequently used as covariates in the analyses as there was some variation in the actual age of the mice at these times.

Formulae used in calculation of Post-weaning Traits

$$\mathrm{DFI}_{\mathrm{PW}} = \frac{\mathrm{FI}_{28\text{-}35} + \mathrm{FI}_{35\text{-}42}}{\mathrm{DOY}_{42} - \mathrm{DOY}_{28}}$$

$$\mathrm{ADG}_{\mathrm{PW}} = \frac{\mathrm{Wt}_{42} - \mathrm{Wt}_{28}}{\mathrm{DOY}_{42} - \mathrm{DOY}_{28}}$$

$$\mathrm{MidWt}_{\mathrm{PW}} = 0.5(\mathrm{Wt}_{28} + \mathrm{Wt}_{42})$$

$$\mathrm{MidWt}_{\mathrm{PW}}^{0.73} = (0.5(\mathrm{Wt}_{28} + \mathrm{Wt}_{42}))^{0.73}$$

$$\mathrm{AGE}_{28} = \mathrm{DOY}_{28} - \mathrm{DOY}_{0}$$

The mature test started when mice were approximately 140 days old and continued for approximately 3 weeks. Measurements of weight were made on approximately days 140, 147, 154 and 161 and the feed intake between these days was recorded. Body composition was measured at the end of the test. The first period of this test (day 140 to 147) was used as a pre-test adjustment phase. The length of this period varied between management groups due to varying demands on available cages as this period was not included in the original experimental plan. The data used for the mature traits consisted of that collected between day 147 and 161. The traits calculated for use in analyses were average daily feed intake from day 147 to 161, average daily weight change during this period, mid-weight and metabolic mid-weight. Also the daily weight change during the pre-test phase was analysed. The exact age of the mouse at days 140, 147 and at measurement of body composition was calculated for use as a covariate in the analyses. The formulae used to calculate the traits from the mature test are given below.

Formulae used in calculation of Mature Traits

$$\mathrm{DFI}_{\mathrm{Mat.}} = \frac{\mathrm{FI}_{147\text{-}154} + FI_{154\text{-}161}}{\mathrm{DOY}_{161} - DOY_{147}}$$

$$ADWC_{\Pr e-Mat.} = \frac{Wt_{147} - Wt_{140}}{DOY_{147} - DOY_{140}}$$

$$ADWC_{Mat.} = \frac{Wt_{161} - Wt_{147}}{DOY_{161} - DOY_{147}}$$

$$MWt_{Mat.} = 0.5(Wt_{147} + Wt_{161})$$

$$MWt^{0.73}_{\mathrm{Mat.}} = (0.5(Wt_{147} + Wt_{161}))^{0.73}$$

In addition to the traits described above which were calculated using arithmetic functions, residual feed intake of the mice post-weaning and at maturity was calculated using a linear model (PROC GLM, SAS 1989). For calculation of post weaning residual feed intake the linear model was fitted to post-weaning daily feed intake and included terms for the class variables sex and management group, covariates average daily gain and metabolic mid-weight and the interaction of each class variable with the covariables. All 2-way interactions were retained in the model. Residual feed intake at maturity was calculated by fitting the linear model to mature daily feed intake and the terms in the model included management group, metabolic mid-weight, average daily weight change and the interaction of management group with metabolic mid-weight and average daily weight change. Residual feed intake post-weaning and at maturity was calculated as the residual error term in the respective models.

Records from mice in generation 1 used in chapter 5 were also included in the analyses. The data from the post-weaning test for generation one was able to be used in exactly the same way as data from the subsequent generations. However as the mice in generation 1 were not measured at 140 days, the records for the last 3 weeks on test (from 112 to 128 days of age) were used for calculation of mature traits on the female mice from generation 1. It was considered that the use of these records was unlikely to bias the results as the mice were mature and had not had a pregnancy at the time of measurement. These records made up approximately 60 of the total of 600 mature records. As the body composition of these mice was measured using a different method to that used in subsequent generations, body composition data on mice in generation 1 was not included.

Table 6.2 Summary of the traits used in the analyses with their abbreviations and units.

Abbreviation	Trait	Units
General		
Wt_x	Bodyweight on day x (where x refers to an approximate age at which a measurement was made)	g(bodyweight)
FI_{x-y}	Feed intake from day x to day y	g(feed)
DOY_x	Day of the year at day x	Julian days
AGE_x	Exact age of the mouse on day x	days
Post-weaning		
ADG_{PW}	Average daily gain during post-weaning test	$g(bodyweight).day^{-1}$
$MidWt_{PW}$	Mid-weight during post-weaning test	g(bodyweight)
$MidWt_{PW}^{0.73}$	Metabolic mid-weight during post-weaning test	$g(bodyweight)^{0.73}$
DFI_{PW}	Average daily feed intake during post-weaning test	$g(feed).day^{-1}$
RFI_{PW}	Residual feed intake during post-weaning test	$g(feed).day^{-1}$
$\%FAT_{PW}$	Fat % at end of post-weaning test	%(bodyweight)
Mature		
$ADWC_{Pre\text{-}Mat.}$	Average daily weight change in pre-mature test period	$g(bodyweight).day^{-1}$
$ADWC_{Mat.}$	Average daily weight change during mature test	$g(bodyweight).day^{-1}$
$MidWt_{Mat.}$	Mid-weight during mature test	g(bodyweight)
$MidWt_{Mat.}^{0.73}$	Metabolic mid-weight during mature test	$g(bodyweight)^{0.73}$
$DFI_{Mat.}$	Average daily feed intake during mature test	$g(feed).day^{-1}$
$RFI_{Mat.}$	Residual feed intake during mature test	$g(feed).day^{-1}$
$\%FAT_{Mat.}$	Fat % at end of mature test	%(bodyweight)

6.2.3 Analyses

Estimation of genetic parameters was performed using DFREML Version 2.14 (Meyer, 1993) which was operated using a series of front-end programs (Swan, 1995). Variance components were estimated for single traits by univariate analyses, and bivariate analyses were used to estimate co-variances between pairs of traits with starting values for variances taken from the univariate analyses.

The fixed effects fitted differed for each trait and are given in Table 6.3. Fixed effects included sex, management group (equivalent to generation x replicate combination, except for generation 2 replicate 1 where 2 management groups occurred), parity of the dam, parity of the individual at the mature test, the number of pups born in the litter from which the individual was taken, the number of pups kept after standardising the litter on day 1 and the number of pups in the litter at weaning. The latter three fixed effects were used to account for differences in the pre- and post-natal environment. Parity of the dam was classified as either first parity or second and greater parity, as the number of observations with parity greater than 2 was very low. Parity of the individual at the mature test was either 0 (had not had a litter) or 1 (had one litter), as the mice were only mated once before the mature test. Age at the time of measurement was used as a covariate in the model where appropriate. Generally the age used was either the age of the mouse at the beginning of the post-weaning or mature tests (day 28 or 147), or the age of the mouse on the day that body composition was measured.

The animal models used differed between traits and are given in Table 6.3. For traits measured post-weaning the model included terms for the additive genetic merit of each animal and a second uncorrelated random effect for the common environment within litters (model type 2 in DFREML). A model which included an additional term for additive maternal effects was also fitted, but univariate analyses found that the variance component attributed to the maternal effect was low and within one standard error of zero for all traits, and so the maternal effect was not included in the final model.

For traits measured at maturity the animal model included only a term for the additive genetic merit of each mouse (model type 1 in DFREML). Preliminary analyses indicated that the effect of common environment within litters was negligible (within one standard error of zero) for traits measured at maturity, and so this effect was not included in the final model.

A preliminary analysis was performed with post-weaning daily feed intake and residual feed intake analysed as different traits in males and females. However it was found that the correlations between males and females for additive genetic and common litter environment variance components were very close to unity (results not presented). Thus it was decided to treat daily feed intake and residual feed intake in both sexes as one trait in all other analyses.

6.2.4 Selection index approach to calculate residual feed intake

Kennedy *et al.* (1993) presented an alternative method for calculating residual feed intake using the estimated variance-covariance matrices of the component traits. This method allows residual feed intake to be calculated from a phenotypic regression of production on feed intake, or from a genetic regression of production on feed intake. The advantage of the genetic regression (called restricted residual feed intake by Kennedy *et al.*) is that the genetic correlation of restricted residual feed intake with production is zero and hence it reflects the true genetic variation in efficiency. Phenotypic residual feed intake may still be genetically correlated with production and hence some of the genetic variation is due to genetic variation in production traits and not to genetic variation in efficiency.

For comparison with residual feed intake estimated from the conventional regression approach, both phenotypic residual feed intake and restricted residual feed intake during the post-weaning and mature tests were also calculated using the method of Kennedy *et al.* (1993) based on the (co)variances of the component traits. Heritabilities of residual feed intake calculated from phenotypic and genetic parameters and the correlation between the two methods were calculated. The expected response to selection on residual feed intake in each of the component traits after one generation with selection intensity equal to one were calculated using selection index equations (Ponzoni 1992).

Table 6.3 Summary of the animal model fitted to each trait, the number of records available and the number of sires and dams with records on progeny. Fixed effects are sex, management group (MGRP), parity of dam (PAR), number born in litter (NOBORN), number kept in litter (NOKEPT), number weaned in litter (NOWEANED) and parity of the individual at the mature test (MPAR). Abbreviations for traits are given in Table 6.2.

		Post-weaning Traits									*Mature Traits*					
	Max. No. Levels	Wt_{21}	Wt_{28}	Wt_{35}	Wt_{42}	ADG_{PW}	$MidWt_{PW}$	DFI_{PW}	RFI_{PW}	$\%FAT_{PW}$	$ADWC_{Pre\text{-}Mat.}$	$MidWt_{Mat.}$	$ADWC_{Mat.}$	$DFI_{Mat.}$	$RFI_{Mat.}$	$\%FAT_{Mat.}$
Fixed Effects																
SEX	2	√	√	√	√	√	√	√	√	√	-	-	-	-	-	-
MGRP	12	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√
PAR	2	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√
NOBORN	16	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√
NOKEPT	13	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√
NOWEANED	13	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√
MPAR	2	-	-	-	-	-	-	-	-	-	√	√	√	√	√	√
Covariates																
AGE[†]		-	√	√	√	√	√	√	√	√	√	√	√	√	√	√
Random effects																
h^2	2423	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√
c^2	486	√	√	√	√	√	√	√	√	√	-	-	-	-	-	-
Data Structure																
No. Records		2392	1596	1642	1647	1579	1579	1553	1553	1021	613	610	601	607	607	421
No. Sires		91	84	84	84	84	84	84	84	55	71	70	70	70	70	49
No. Dams		409	289	289	290	289	289	289	289	189	246	246	244	246	246	192

[†] The covariate age used in the model was the age at which each trait was measured.

6.3 Results

Post-weaning traits

The mean and phenotypic standard deviation after adjustment for fixed effects is given for each trait in Table 6.4, along with the heritability and proportion of variation due to common environment within litters. Genetic parameters for metabolic midweight are not presented as the results were very similar to those for midweight. The heritability estimates of post-weaning traits were quite accurate, with standard errors of 0.05 to 0.07 for all traits except body composition where fewer records were available. Heritability was moderate for all post-weaning traits with the exception of average daily gain which had a low heritability. The litter effects were estimated accurately, with standard errors between 0.02 and 0.04. In general litter effects for traits measured during the post-weaning test (days 28 to 42) were small although significant. However there was a large (48%) variance component due to common environment within litters for weight at weaning (Wt_{21}).

Correlations among post-weaning traits are given for phenotypic, additive genetic, common litter environment and environmental variance components in Tables 6.5 to 6.8. Correlations between growth traits were generally positive and moderate to high for all variance components, with the exception of common environmental correlations between average daily gain and weight traits not used to derive average daily gain (i.e. Wt_{21}, Wt_{35}, and $MidWt_{PW}$) which were negatively correlated. Thus, where the litter environment was favourable for growth and the mice had higher weights at fixed ages, the growth rates of the mice tended to be lower. This suggests that mice from litters where nutrition was restricted probably exhibited compensatory growth after weaning. Pre-weaning environment has been shown to have similar effects on the shape of the growth curve in other species (Pitchford *et al.* 1993).

The additive genetic correlation between daily feed intake and the weight traits was high (Table 6.6), ranging from 0.7 to 0.9 depending on the individual trait, but was less than unity indicating that genetic variation in feed intake independent of variation in growth may exist. The common litter environmental correlations and environmental correlations between feed intake and growth were also moderate to high (Tables 6.7 and 6.8). The strong phenotypic relationship between feed intake and growth was reflected by the fact that the model of feed intake used to calculate residual feed intake accounted for 70 % of the variance in feed intake.

Table 6.4 Mean (μ), phenotypic standard deviation (σ_P), heritability (h^2) and common environmental effects (c^2) for traits[A] from univariate analyses.

	μ	σ_P	h^2	c^2
Post-weaning Traits				
Wt_{21}	14.2	1.66	0.33 ± 0.06	0.48 ± 0.03
Wt_{28}	20.6	2.67	0.23 ± 0.07	0.18 ± 0.03
Wt_{35}	24.3	2.84	0.26 ± 0.06	0.13 ± 0.03
Wt_{42}	25.7	2.70	0.40 ± 0.07	0.07 ± 0.02
ADG_{PW}	0.366	0.148	0.14 ± 0.05	0.11 ± 0.03
$MidWt_{PW}$	23.2	2.40	0.35 ± 0.07	0.14 ± 0.03
DFI_{PW}	4.65	0.431	0.32 ± 0.06	0.09 ± 0.03
RFI_{PW}	0.00	0.306	0.27 ± 0.06	0.16 ± 0.03
$\%FAT_{PW}$	15.3	1.66	0.22 ± 0.10	0.14 ± 0.04
Mature Traits				
$ADWC_{Pre\text{-}Mat.}$	-0.735	0.385	0.16 ± 0.08	-
$MidWt_{Mat.}$	32.0	3.89	0.78 ± 0.09	-
$ADWC_{Mat.}$	-0.071	0.135	0.29 ± 0.10	-
$DFI_{Mat.}$	4.25	0.654	0.36 ± 0.09	-
$RFI_{Mat.}$	0.00	0.581	0.24 ± 0.08	-
$\%FAT_{Mat.}$	16.6	2.18	0.31 ± 0.11	-

[A] Abbreviations for traits are given in Table 6.2.

While feed intake was correlated with growth, residual feed intake was phenotypically independent of growth as the growth traits were included in the model used to calculate residual feed intake. The genetic and environmental correlations between residual feed intake and growth traits were also low. Thus residual feed intake was independent of growth at a genetic level as well as at a phenotypic level.

The genetic relationship between body composition and other post-weaning traits differed from the environmental and common litter environmental relationships. The genetic correlations between body composition and most growth traits were positive, suggesting that genetically heavy mice were also genetically fatter. However the corresponding environmental and common litter environment correlations were close to zero. Conversely, while the genetic and environmental correlations of body composition with feed intake and residual feed intake were low, the common litter environmental correlation was positive, suggesting that pre-weaning environment has an influence on the relationship between these traits.

Residual feed intake calculated from the (co)variances of the component traits using the method presented by Kennedy *et al.* (1993) produced similar results to that calculated using the conventional regression approach. The small non-significant differences between the results from the two different approaches are able to be explained by the sampling variation of the estimates. When residual feed intake was calculated using phenotypic variance-covariances, the heritability was 0.26. The expected responses in the component traits after one generation of selection with selection intensity equal to one were calculated using selection index equations. The expected responses to selection on residual feed intake calculated from phenotypic (co)variances were -0.082 g.day^{-1} for daily feed intake, -0.011 g for mid-weight and 0.003 g.day^{-1} for average daily gain.

When restricted residual feed intake was calculated from genetic (co)variances so that the expected response in growth traits is zero, the resulting heritability was 0.25. The predicted response in daily feed intake to selection on restricted residual feed intake was -0.079 g.day^{-1}. Residual feed intake calculated from phenotypic or genetic (co)variances were very similar, with a correlation between the two methods of 0.98.

Table 6.5 Phenotypic correlations between traits[A] measured in the post-weaning test.

	Wt$_{21}$	Wt$_{28}$	Wt$_{35}$	Wt$_{42}$	ADG$_{PW}$	MidWt$_{PW}$	DFI$_{PW}$	RFI$_{PW}$
Wt$_{28}$	0.55							
Wt$_{35}$	0.43	0.83						
Wt$_{42}$	0.44	0.70	0.84					
ADG$_{PW}$	-0.16	-0.40	0.07	0.42				
MidWt$_{PW}$	0.58	0.92	0.91	0.91	-0.01			
DFI$_{PW}$	0.29	0.58	0.73	0.66	0.11	0.68		
RFI$_{PW}$	-0.11	0.00	0.09	-0.03	-0.04	-0.02	0.69	
%FAT$_{PW}$	0.04	0.05	0.14	0.21	0.20	0.14	0.11	-0.02

[A] Abbreviations for traits are given in Table 6.2.

Table 6.6 Additive genetic correlations between traits[A] measured in the post-weaning test.

	Wt$_{21}$	Wt$_{28}$	Wt$_{35}$	Wt$_{42}$	ADG$_{PW}$	MidWt$_{PW}$	DFI$_{PW}$	RFI$_{PW}$
Wt$_{28}$	0.51							
Wt$_{35}$	0.56	0.93						
Wt$_{42}$	0.57	0.88	1.00					
ADG$_{PW}$	-0.15	-0.21	0.64	0.58				
MidWt$_{PW}$	0.74	0.96	0.91	0.90	0.49			
DFI$_{PW}$	0.42	0.74	0.89	0.80	0.36	0.76		
RFI$_{PW}$	-0.16	0.03	0.10	-0.02	-0.06	0.00	0.64	
%FAT$_{PW}$	0.01	-0.07	0.33	0.34	0.57	0.24	0.09	-0.10

[A] Abbreviations for traits are given in Table 6.2.

Table 6.7 Common environment (c^2) correlations between traits[A] measured in the post-weaning test.

	Wt$_{21}$	Wt$_{28}$	Wt$_{35}$	Wt$_{42}$	ADG$_{PW}$	MidWt$_{PW}$	DFI$_{PW}$	RFI$_{PW}$
Wt$_{28}$	0.73							
Wt$_{35}$	0.64	0.93						
Wt$_{42}$	0.75	0.86	0.74					
ADG$_{PW}$	-0.54	-0.02	-0.69	0.00				
MidWt$_{PW}$	0.88	0.98	0.91	0.98	-0.76			
DFI$_{PW}$	0.38	0.50	0.46	0.02	-0.52	0.47		
RFI$_{PW}$	-0.26	-0.16	-0.19	-0.02	-0.03	-0.26	0.74	
%FAT$_{PW}$	0.12	0.16	0.00	0.00	-0.06	0.00	0.44	0.31

[A] Abbreviations for traits are given in Table 6.2.

Table 6.8 Environmental correlations between traits[A] measured in the post-weaning test.

	Wt$_{21}$	Wt$_{28}$	Wt$_{35}$	Wt$_{42}$	ADG$_{PW}$	MidWt$_{PW}$	DFI$_{PW}$	RFI$_{PW}$
Wt$_{28}$	0.26							
Wt$_{35}$	0.31	0.77						
Wt$_{42}$	0.28	0.59	0.79					
ADG$_{PW}$	-0.03	-0.52	0.03	0.45				
MidWt$_{PW}$	0.33	0.90	0.91	0.91	-0.05			
DFI$_{PW}$	0.24	0.54	0.72	0.67	0.13	0.67		
RFI$_{PW}$	0.04	0.04	0.15	0.00	-0.04	0.03	0.72	
%FAT$_{PW}$	0.03	0.07	0.10	0.19	0.15	0.13	0.06	-0.06

[A] Abbreviations for traits are given in Table 6.2.

Mature traits

When the mice were placed on the feed intake test at maturity there was a tendency for the mice to lose bodyweight during the first week. The cause of the weight loss was not known, but two factors changed when the mice were placed on the feed intake test. First the actual feeding system itself changed from feed placed on the top of the cage to the feeders used to measure feed intake, and the change in feeding system may have affected feed intake. Secondly the mice were put into individual cages, having been group housed prior to the mature test, and it is possible that changes in the level of social interaction, or the inability to huddle together for thermoregulation had an affect on feed intake and body-weight. It was decided to use this period as a pre-adjustment period and to analyse the changes in bodyweight occurring during this time as a separate trait ($ADWC_{Pre\text{-}Mat.}$). The mean daily weight change during the pre-test period was -0.74 $g.day^{-1}$ with a phenotypic standard deviation (after adjustment for fixed effects) of 0.39 $g.day^{-1}$. During the mature test period itself the bodyweight of the mice generally stabilised, with the mean daily weight change (± phenotypic s.d.) of -0.07 ± 0.14 $g.day^{-1}$.

The traits measured during the mature test were generally of low to moderate heritability (results in Table 6.4). The exception to this was midweight which was highly heritable ($h^2 = 0.78$). As was found for post-weaning traits, mature residual feed intake had a lower heritability than mature daily feed intake. The amount of phenotypic variation in mature body composition was greater than that for post-weaning body composition, and the heritability of body composition was also higher at maturity, although with large standard errors the estimates are not significantly different. Heritability of mature daily feed intake and mature residual feed intake were similar to the respective traits measured post-weaning.

The relationships between traits measured during the mature test for phenotypic, additive genetic and environmental variance components are presented in Tables 6.9 to 6.11. Although the phenotypic correlation between average daily weight change during the pre-test period and average daily weight change during the mature test was not high (0.29), the genetic correlation (1.00) showed that they were genetically the same trait. Both average daily weight change during the pre-test period and during the mature test were negatively correlated with midweight for all variance components, indicating that heavier mice tended to have greater weight losses. Mice with greater weight losses also had lower daily feed intake and residual feed intake and were fatter at the end of the test period.

The phenotypic correlations of daily feed intake at maturity with midweight (0.07) and average daily weight change (0.38) were only low to moderate, which is reflected in the fact that the model of feed intake used to calculate residual feed intake only accounted for 42 % of the variation. This meant that the phenotypic correlation between feed intake and residual feed intake was very high (0.88). The additive genetic and environmental correlations between feed intake and residual feed intake were also high (0.93 and 0.87 respectively), and so feed intake and residual feed intake were almost the same trait at maturity.

The genetic correlation between body composition and midweight was very high (0.87) which suggests that mature weight in this mouse population is strongly associated with the propensity of the animal to lay down fat. The environmental correlation between body composition and midweight was much lower (0.25). Mature body composition was not genetically related to feed intake or residual feed intake, although the environmental and phenotypic correlations were low and negative indicating that fatter mice had a tendency to have lower feed intakes and were more efficient.

The results for mature residual feed intake calculated from the (co)variances of the component traits were similar to those for residual feed intake calculated from the conventional regression approach. Mature residual feed intake calculated from phenotypic or genetic (co)variances had heritabilities of 0.29 and 0.25 respectively and the two methods were highly correlated (r = 0.96), indicating that similar results were obtained with phenotypic or genetic parameters. The expected responses in component traits after one generation of selection on phenotypic mature residual feed intake with selection intensity equal to one was -0.193 g.day^{-1} for daily feed intake, -0.044 g for mid-weight and -0.010 g.day^{-1} for average daily weight change. For mature residual feed intake calculated from genetic (co)variances the response in growth traits was restricted to zero, while the expected response in daily feed intake was -0.152 g.day^{-1}.

Table 6.9 Phenotypic correlations between traits[A] measured in the mature test.

	ADWC$_{\text{Pre-Mat.}}$	MidWt$_{\text{Mat.}}$	ADWC$_{\text{Mat.}}$	DFI$_{\text{Mat.}}$	RFI$_{\text{Mat.}}$
MidWt$_{\text{Mat.}}$	-0.18				
ADWC$_{\text{Mat.}}$	0.29	-0.26			
DFI$_{\text{Mat.}}$	0.20	0.07	0.38		
RFI$_{\text{Mat.}}$	0.14	-0.05	0.00	0.88	
%FAT$_{\text{Mat.}}$	-0.22	0.58	-0.19	-0.16	-0.23

[A] Abbreviations for traits are given in Table 6.2.

Table 6.10 Additive genetic correlations between traits[A] measured in the mature test.

	ADWC$_{\text{Pre-Mat.}}$	MidWt$_{\text{Mat.}}$	ADWC$_{\text{Mat.}}$	DFI$_{\text{Mat.}}$	RFI$_{\text{Mat.}}$
MidWt$_{\text{Mat.}}$	-0.39				
ADWC$_{\text{Mat.}}$	1.00	-0.25			
DFI$_{\text{Mat.}}$	0.58	0.19	0.53		
RFI$_{\text{Mat.}}$	0.39	0.00	0.24	0.93	
%FAT$_{\text{Mat.}}$	-0.23	0.87	-0.42	-0.04	-0.04

[A] Abbreviations for traits are given in Table 6.2.

Table 6.11 Environmental correlations between traits[A] measured in the mature test.

	ADWC$_{\text{Pre-Mat.}}$	MidWt$_{\text{Mat.}}$	ADWC$_{\text{Mat.}}$	DFI$_{\text{Mat.}}$	RFI$_{\text{Mat.}}$
MidWt$_{\text{Mat.}}$	-0.09				
ADWC$_{\text{Mat.}}$	0.07	-0.35			
DFI$_{\text{Mat.}}$	0.08	-0.08	0.30		
RFI$_{\text{Mat.}}$	0.08	-0.12	-0.10	0.87	
%FAT$_{\text{Mat.}}$	-0.22	0.25	-0.09	-0.22	-0.30

[A] Abbreviations for traits are given in Table 6.2.

Relationships between post-weaning and mature traits

The phenotypic, additive genetic and environmental correlations of the post-weaning traits with the mature traits are presented in Tables 6.12 to 6.14. The genetic correlations of midweight at maturity with weights measured during the post weaning test were high (0.76 to 0.86), while the environmental correlations were moderate (0.42 to 0.52). There was a reasonably strong genetic association ($r_g = 0.68$) between post-weaning feed intake and midweight at maturity, although the corresponding environmental correlation was low. Conversely the genetic correlations of mature feed intake with post-weaning weights were low, as were the phenotypic and environmental correlations.

The genetic correlation of post-weaning feed intake with mature feed intake was 0.51, while that between post-weaning residual feed intake and mature residual feed intake was 0.60. These correlations suggest that information collected on these traits post-weaning could be used in selection decisions to produce a correlated response in the trait in the mature animal. Feed intake and weight measured post-weaning were genetically correlated with mature body composition, with heavy animals and those with high intakes post-weaning being fatter at maturity. However, the genetic relationship of post-weaning residual feed intake with body composition at maturity was weak (0.17), indicating that selection on post-weaning residual feed intake would only have a small affect on body composition of mature animals. The genetic correlation between post-weaning and mature body composition was high (0.73), indicating that the genetic control over body composition is similar post-weaning and at maturity in mice. The corresponding environmental and phenotypic correlations between post-weaning and mature body composition were much lower (0.22 and 0.34 respectively).

Table 6.12 Phenotypic correlations of post-weaning traits with mature traits[A].

	Wt$_{21}$	Wt$_{28}$	Wt$_{35}$	Wt$_{42}$	ADG$_{PW}$	MidWt$_{PW}$	DFI$_{PW}$	RFI$_{PW}$	%FAT$_{PW}$
ADWC$_{Pre\text{-}Mat.}$	-0.13	-0.06	-0.07	-0.04	0.03	-0.06	0.02	0.07	-0.11
MidWt$_{Mat.}$	0.35	0.51	0.57	0.61	0.12	0.64	0.37	0.00	0.22
ADWC$_{Mat.}$	-0.10	-0.11	-0.09	-0.07	0.02	-0.13	-0.02	0.05	-0.02
DFI$_{Mat.}$	0.08	0.15	0.19	0.21	0.04	0.20	0.35	0.29	0.03
RFI$_{Mat.}$	0.06	0.08	0.08	0.10	0.01	0.07	0.29	0.29	-0.01
%FAT$_{Mat.}$	0.15	0.21	0.31	0.28	0.05	0.14	0.21	0.06	0.34

[A] Abbreviations for traits are given in Table 6.2.

Table 6.13 Additive genetic correlations of post-weaning traits with mature traits[A].

	Wt$_{21}$	Wt$_{28}$	Wt$_{35}$	Wt$_{42}$	ADG$_{PW}$	MidWt$_{PW}$	DFI$_{PW}$	RFI$_{PW}$	%FAT$_{PW}$
ADWC$_{Pre\text{-}Mat.}$	-0.52	-0.35	-0.31	-0.35	-0.19	-0.39	-0.05	0.36	-0.21
MidWt$_{Mat.}$	0.68	0.82	0.86	0.76	0.43	0.85	0.68	0.09	0.27
ADWC$_{Mat.}$	-0.04	-0.08	-0.15	-0.15	-0.13	-0.15	-0.10	0.02	0.31
DFI$_{Mat.}$	0.18	0.25	0.36	0.36	0.27	0.30	0.51	0.50	0.13
RFI$_{Mat.}$	0.02	0.14	0.29	0.25	0.21	0.01	0.51	0.60	-0.04
%FAT$_{Mat.}$	0.55	0.53	0.76	0.66	0.44	0.00	0.61	0.17	0.73

[A] Abbreviations for traits are given in Table 6.2.

Table 6.14 Environmental correlations of post-weaning traits with mature traits[A].

	Wt$_{21}$	Wt$_{28}$	Wt$_{35}$	Wt$_{42}$	ADG$_{PW}$	MidWt$_{PW}$	DFI$_{PW}$	RFI$_{PW}$	%FAT$_{PW}$
ADWC$_{Pre\text{-}Mat.}$	-0.03	0.01	-0.01	0.08	0.07	0.05	0.04	0.00	-0.10
MidWt$_{Mat.}$	0.00	0.42	0.44	0.52	-0.05	0.51	0.09	-0.13	0.30
ADWC$_{Mat.}$	-0.23	-0.14	-0.07	-0.04	0.06	-0.13	0.01	0.06	-0.14
DFI$_{Mat.}$	0.06	0.12	0.12	0.13	-0.03	0.15	0.29	0.23	-0.01
RFI$_{Mat.}$	0.14	0.07	0.01	0.03	-0.04	0.11	0.22	0.21	0.00
%FAT$_{Mat.}$	-0.07	0.11	0.15	0.07	-0.06	0.24	0.04	0.02	0.22

[A] Abbreviations for traits are given in Table 6.2.

6.4 Discussion

The estimates of heritability and litter environmental effects presented here were of moderate accuracy, particularly for the post-weaning traits which had more records available. Adding more data to increase the accuracy of estimates reaches the law of diminishing returns, and the extra accuracy achieved by adding more records to the post-weaning estimates was very slight. More benefit may be gained from extra records when estimating genetic correlations from multi-variate analyses where the number of variance components to be estimated increases quickly. The software used to estimate genetic parameters in this study did not provide an estimate of the sampling error of correlations for different variance components. The structure of the data analysed in this chapter was likely to yield good estimates of genetic parameters as there was a high degree of relationship between many of the mice and full-sib as well as large half-sib families were available. However with the number of records available for some traits the sampling error on covariance components may be large, and the estimates are probably informative as to whether the correlations are low, moderate or high. This was considered to be sufficient for the purposes of this experiment where the aim was to examine genetic variation in growth and feed intake of a model species and precise estimates were not required.

Variation in post-weaning test traits

Both phenotypic and genetic variation existed for growth and feed intake traits measured post-weaning, and the moderate heritabilities estimated indicate that it should be possible to obtain selection responses in these traits. In the context of selection to improve efficiency, the parameters of most interest are the genetic correlations between feed intake and growth traits as these will determine whether there is any opportunity to change the relationship between these traits. A high genetic correlation between feed intake and growth suggests that the same set of genes controls both traits and that selection for one trait will produce a strong correlated response in the other. However, a correlation significantly less than unity would indicate that although the traits are positively correlated, there is some flexibility whereby one trait can be changed independently of the other trait, although the rate of genetic progress will depend on the magnitude of the correlation as well as the heritability of the traits. The results obtained in this study suggest that in mice the genetic correlation between feed intake and growth is strong, but is not unity and hence efficiency should be able to be changed through selection.

The heritability of post-weaning residual feed intake (0.27) was similar to other estimates produced in cattle (see section 2.3.4.3) and indicates that genetic variation in efficiency exists in mice. However Kennedy *et al.* (1993) showed that residual feed intake calculated using phenotypic regression as was used here is not necessarily genetically independent of its component traits, and hence some of the genetic variation in phenotypic residual feed intake may be due to the statistical relationship of feed intake with the growth traits. Calculation of restricted residual feed intake is necessary to assess the extent of the genetic variation independent of production. In this population restricted residual feed intake was very similar to residual feed intake calculated phenotypically as the genetic correlations of phenotypic residual feed intake with the component growth traits were close to zero. The heritability of restricted residual feed intake was 0.25, indicating that genetic variation in feed intake independent of growth exists and thus it is possible to use selection to improve efficiency.

The results of the preliminary analysis in which it was found that feed intake and residual feed intake are the same trait in males and females are important. Researchers in the past (e.g. Stephens 1991) have suggested that efficiency may be determined by different factors in males and females, and hence may not be genetically the same trait. Nieuwhof *et al.* (1992) found low genetic correlations between feed intakes of growing bulls and growing heifers, although the correlation of growing bulls with lactating heifers was high. However, in that study growing bulls and lactating heifers were fed concentrates, while growing heifers were on a roughage based diet only and the low genetic correlation between growing bulls and growing heifers may have been a function of differences in diet. The results of the present study support that conclusion as when male and female growing mice were on the same diet feed intake was the same trait. This result has practical significance as it is probable that, with currently available technology, efficiency will be measured mainly on bulls (due to the high cost of measuring feed intake), but the desired selection response is to reduce feed costs of mature cows. Hence a high genetic correlation between efficiency of young males and mature females is necessary to improve efficiency using this approach.

The relationship between efficiency and body composition is important, as it is well recognised that body composition can influence feed intake and efficiency (see section 2.1.4.1). Knowledge of this relationship may help to understand the processes which are altered when efficiency is changed. In addition to its biological significance, body composition is also important in livestock species for economic reasons because it is closely associated with carcass composition and meat quality. The indirect measure of body composition used in this study gave an estimate of the percentage of body fat. Although the method used is a fairly crude prediction of gross body composition, the accuracy was sufficient to partition the variation into additive genetic and other sources of variation, and hence the genetic relationships of body composition with other traits were able to be examined.

The additive genetic relationships for body composition with feed intake and residual feed intake were low and probably not significantly different from zero. Hence selection on post-weaning residual feed intake is unlikely to produce large changes in body composition at young ages. If there is any response in body composition then the additive genetic correlation suggests that selection for efficiency (i.e. against residual feed intake) will increase the percentage body fat of the animals, a result which is suprising given that fat is energetically more expensive to deposit than protein and hence one might expect an animal which lays down fat early to be less efficient. However, maintenance requirements are lower in animals with a higher proportion of fat (and consequently a lower proportion of protein), and so the result might be due to the influence of maintenance on energetic requirements being greater than that of fat and protein deposition, even in growing animals. The relationship between body composition and energetic efficiency may differ at the phenotypic and genetic levels. Jensen *et al.* (1992) published phenotypic and genetic correlations of residual feed intake with body composition of cattle and found that while residual feed intake was positively correlated with fat percentage at a phenotypic level, the genetic correlation was negative. They also found that inclusion of a phenotypic adjustment for body composition in the model for residual feed intake strengthened the negative genetic correlation. This result agrees with the results from the mice in this study and suggests that genetically fat animals tend to be more efficient.

The variation accounted for by common environments within litters is of interest as the c^2 parameter can be considered as a measure of the influence of pre-weaning environment on the trait. The common litter environment effect was significant for all traits in the post-weaning test, including feed intake and residual feed intake. The correlations between these effects indicated that a pre-weaning environment which results in increased bodyweight (probably due to increased nutrient supply) tends to result in increased post-weaning feed intake also (probably because feed intake is closely related to weight post-weaning), while residual feed intake is decreased. This suggests that the pre-test environment may affect efficiency and therefore if animals are to be compared in some sort of central testing station a pre-adjustment phase may be important to minimise such effects, particularly if the numbers of animals from each pre-test environment are so small as to preclude any statistical adjustment to account for these effects. Biologically it is not suprising that pre-weaning environment can have some effect on efficiency as experiments by Koong *et al.* (1982, 1985) have shown large effects of previous nutrition on the energetic efficiency of mammals. Others (eg Liu and Makarechian 1993a) have shown that a pre-adjustment period is important when testing bulls for growth rate to remove herd of origin effects.

A model which included a random term for additive maternal effect was fitted for post-weaning traits but the maternal effect was negligible and the term was removed from the final model. Had this term been significant it would have been of great interest as the genetic relationship between efficiency and maternal traits could have been explored. Taylor *et al.* (1986) and others have found that across a range of cattle breeds, milk production potential is negatively associated with efficiency of maintenance which suggests that within breed selection for efficiency may produce a correlated response in maternal ability. The additive maternal effect may have been low in this population due to a lack of genetic variation in maternal ability in the mouse population studied. However this is unlikely as the two inbred lines from which the population was derived differed in maternal ability (Hughes and Pitchford 1994) and so it would be suprising if little variation existed in the composite population. A more likely explanation for the lack of maternal effects observed is that most of the litters were standardised to a relatively low number (5 or 6 pups) and hence even for poor milking dams, milk supply was unlikely to be limiting the development of the pups and so the variation in maternal effect would not be expressed under these circumstances. In this case a better method for examining the relationship between maternal ability and efficiency would be to evaluate maternal ability as a correlated response in selection lines for residual feed intake. With divergent lines it would be possible to perform a cross-fostering study which would enable maternal ability to be studied.

Variation in mature test traits

The female mice measured at maturity were not always at a stable mature weight and hence true maintenance was not achieved for all mice, although the change in weight of the mice during the test was generally small and therefore the physiological state of the mice was close to maintenance. The small changes in weight during the mature test do not invalidate the results as in most production systems animals are rarely in a maintenance state, but weight fluctuates with seasonal feed supply and with physiological demands. The residual feed intake approach adjusts the feed intake data for differences in weight change and hence provides a suitable basis for comparison of efficiency. This is similar to the approach used by Stephens (1991) who adjusted feed intake data for bodyweight but not weight change to estimate maintenance. Stephens' approach was successful in generating differences in maintenance efficiency between selection lines. Thus although not all mice in this study were literally maintaining body weight, it is probable that residual feed intake closely approximates maintenance efficiency.

The increase in the amount of phenotypic variation in feed intake and residual feed intake as mice matured observed in Chapter 5 was also observed here, while the variation in weight increased only slightly. The observed increase was due to an increase in both the additive genetic and environmental variation in feed intake and residual feed intake, as the heritabilities for each trait were similar for post-weaning and mature tests. This result differs from that of Luiting (1991) who found that the increase in phenotypic variation in residual feed intake of poultry was due to an increase in environmental variance of older birds, with the amount of additive variation remaining relatively constant.

The variation in weight at maturity is interesting as the heritability estimate is very high (0.78), suggesting that mature weight is almost entirely determined by the genetic merit of the animal. Koots *et al.* (1994a) surveyed the literature for beef cattle and also found that the heritability of mature weight in cattle is high (0.50), and tends to be higher than the heritability of weight at younger ages. Thus for both mice and cattle there appears to be an equilibrium weight which mature animals reach which is under strong genetic control. However the mechanism by which mature weight is controlled is unlikely to be the same in mice and cattle.

Results in mice show that genetic variation exists in both fat and lean mass at maturity. Bishop and Hill (1985) reported that lines selected on fatness had large differences in mature weight and fat mass but there was no difference in lean mass. Stephens (1991) found that changes in mature weight due to selection on rate of maturity were almost entirely due to an increase in the amount of fat at maturity, with no change in lean mass being observed. The high genetic correlation found in this study between percentage fat and mature weight agrees with these results. However, Bishop and Hill (1985) also showed that when mice were selected on lean mass, divergence in mature weight occurred without associated changes in body composition, suggesting that genetic variation exists in lean mass at maturity. The relative amounts of genetic variation in fat and lean mass at maturity are unlikely to be the same in cattle and mice. Selection on traits influenced by both fat and lean deposition is likely to take the path of least resistance. This path will depend on the heritability and amount of genetic variation in each trait. Although the basic mechanisms regulating mature weight might still be the same across a range of species, variation in the relative amounts of genetic variation in each component will influence which components are important in determining mature size. The difference between mice and cattle highlights the need to use caution when extrapolating results from laboratory species to livestock species. However this does not mean that results with laboratory species are of no value as they provide an opportunity to better understand the basic biology of many functions of interest in livestock species.

As in Chapter 5, the results presented here showed that phenotypic correlation between weight and feed intake at maturity was low. Together with the large amount of variation in feed intake at maturity, this meant that there was a large amount of phenotypic variation in residual feed intake. The heritability of residual feed intake was 0.24 and that of restricted residual feed intake was 0.25, suggesting that genetic variation in efficiency of mature mice also exists. This agrees with the estimate of maintenance efficiency heritability of 0.35 ± 0.18 by Stephens (1988). Stephens (1991) selected for maintenance efficiency in mice and obtained a realised heritability for maintenance efficiency of 0.18 ± 0.09. These results all suggest that there is potential to select animals to improve maintenance efficiency.

The additive genetic correlations indicate that animals selected for efficiency at maturity will not differ from inefficient animals in their mature weight or in body composition, but will have lower feed intake. These results are in close agreement with those of Stephens (1991) who found no difference in mature weight, rate of maturation and body composition in lines of mice divergently selected on maintenance efficiency, but found that high maintenance efficiency mice had lower mature feed intakes. However, the environmental correlation between residual feed intake and body composition suggests that mice which are fatter will be more efficient. This agrees with much of the literature which suggests that fat is relatively inert in energetic terms, and hence when maintenance requirement is expressed per unit bodyweight (or feed intake is adjusted for bodyweight as with residual feed intake) fat animals tend to be more efficient. The difference between the environmental and additive genetic correlations for body composition here point out the danger of assuming that knowledge gained through phenotypic studies of biological functions can be used to predict the biological consequences of selection, and highlight the value of studies where parameter estimation techniques are used to separate environmental and genetic variation and improve our understanding of the biology and genetics of traits often studied at a phenotypic level.

Relationships between post-weaning and mature traits

The relationships between post-weaning and mature traits are very important in the context of trying to improve efficiency of mature animals by selection on post-weaning traits. In Chapter 5 it was found that residual feed intake measured post-weaning was not very repeatable and the phenotypic correlation with maintenance efficiency was low. This suggested that residual feed intake was probably not going to be an appropriate criteria for selection to improve maintenance efficiency. However, the genetic parameters estimated in this chapter (Table 6.13) clearly demonstrate that post-weaning residual feed intake is genetically related to maintenance efficiency.

The genetic correlation of post-weaning residual feed intake with mature residual feed intake was moderate (0.60) and suggests that it should be possible to make genetic improvements in maintenance efficiency by selection based on a post-weaning performance test. The genetic correlations of post-weaning residual feed intake with other mature traits suggest that selection on post-weaning efficiency will produce similar biological changes in mature traits to direct selection on maintenance efficiency. Whilst there may be a small reduction in mature weight, most of the change occurring in mature animals consists of a decrease in feed intake of mature mice. In the context of animal production, a small decrease in mature weight is of little consequence if growth to the point of slaughter remains unchanged, unless a high proportion of income is obtained from sale of mature animals. This situation usually occurs only when reproductive rates are extremely low. For the traits measured in this study the main difference in correlated responses between selection on post-weaning residual feed intake and selection on mature efficiency is that post-weaning residual feed intake is likely to produce a small decrease in fat percentage whereas there is no response in body composition to selection on mature efficiency. However other differences in correlated responses in traits not studied here may exist.

Kennedy *et al.* (1993) pointed out that residual feed intake is equivalent to a selection index where the economic values are determined by the (co)variances of feed intake and the component traits. This may mean that residual feed intake is not the optimum method of selection to improve biological or economic efficiency (see Chapter 7 for a more complete discussion of this issue). However, the conclusions drawn with regards to residual feed intake in this chapter remain valid and relevant to the issue as the analysis has shown that there is genetic variation in efficiency both post-weaning and at maturity and that the genetic correlations of post-weaning growth and feed intake with mature weight and feed intake are sufficiently strong so that it is possible to formulate an index (such as residual feed intake) using post-weaning traits in order to apply appropriate selection pressure to traits of mature animals. In addition, residual feed intake is a convenient index to use when comparing efficiency of individuals and is useful for developing our understanding of the biology and genetics of growth, feed intake and related processes which influence efficiency.

Biological Considerations

The results presented in this chapter have clearly shown that processes which concern feed intake and growth post-weaning are also genetically related to the feed intake and bodyweight of mature animals which are at, or near, maintenance. Hence selection for efficiency post-weaning is likely to produce a correlated decrease in maintenance. However in animal production systems, maintenance is a rare physiological state, as animals in the breeding herd are generally either pregnant or lactating or both. In addition to this, seasonal fluctuations in feed supply mean that animals are generally either in surplus feed and are laying down fat or are in a nutrient deficit and body tissue reserves are being mobilised.

The relationship between maintenance efficiency and production efficiency is unclear. Shuey *et al.* (1993) estimated a phenotypic correlation between maintenance efficiency and production efficiency and found that it was extremely low. However their estimate of maintenance efficiency was made using calorimetric techniques on pregnant cows and hence does not represent true maintenance. While phenotypic correlations often provide a first approximation of a genetic relationship, this study has reinforced the importance of obtaining estimates of the genetic correlation before making strong conclusions, particularly when dealing with traits such as efficiency which can have large errors or temporary environmental effects associated with their measurement. Hence the study of Shuey *et al.* (1993) should not be regarded as conclusive and it is still possible or even probable that there is a strong genetic relationship between maintenance and production efficiencies. The study of Nieuwhof *et al.* (1992) suggests that feed intake and production traits are genetically related in growing bulls and lactating heifers, and hence selection for efficiency post-weaning should improve production efficiency. The present study with a model species suggests that this improvement in production efficiency is likely to be brought about by a reduction in the feed used for maintenance of the dam. This result agrees with results in poultry where it was found that variation in residual feed intake of laying hens is mainly due to variation in maintenance requirements of hens (Luiting *et al.* 1994).

There have been a number of studies which have suggested that between breed variation in maintenance efficiency is related to production potential (eg Ferrell and Jenkins 1984a; Frisch and Vercoe 1984; Taylor *et al.* 1986; Solis *et al.* 1988). As this study has shown that it is possible to select for maintenance efficiency in mice it would be of great interest to examine the effects of selection on traits representing the "production potential" of the mice. Such traits might include the milk production and reproductive rate of females. The selection lines initiated during the present study would offer an excellent model to examine these issues, providing sufficient response in efficiency is obtained. Selection response results have not been presented in this chapter as there are insufficient generations measured to make meaningful conclusions, but early results are encouraging. Although such studies have been conducted with lines selected for maintenance efficiency before (eg Stephens 1991), the selection lines initiated here differ from previous work in that the selection pressure is on post-weaning efficiency, and the outcomes in traits not considered in this chapter may differ from direct selection on maintenance efficiency. Selection on post-weaning efficiency is a better representation of the probable selection policy for livestock.

There is a need for an investigation into the underlying physiological basis to the observed variation in efficiency. A better understanding of this basis would improve the prediction of likely responses to selection and may provide a metabolic indicator of efficiency which could be used in selection to replace the need for direct measurement of feed intake. However such studies are difficult when the differences between individual animals are very small, and so selection lines for efficiency would also be a valuable research tool in this situation. It would seem that an appropriate place to start would be a full evaluation of the energy balance in high and low efficiency animals including measurement of digestive efficiency, activity levels and body composition. This may then indicate the most appropriate aspect of energy balance for investigation in greater detail.

6.5 Summary

The relationship between efficiency of growing animals and maintenance efficiency at maturity has been poorly understood in the past, and is of importance in the context of selection for efficiency in livestock based on a post-weaning efficiency test. This chapter reports the results of an experiment using mice to estimate phenotypic and genetic parameters for feed intake, growth, body composition and efficiency in mice, both post-weaning and at maturity in order to examine the biology associated with these traits in a model species.

The results of the study showed that genetic variation in efficiency exists in mice both post-weaning and at maturity. The genetic correlations between growth, feed intake and efficiency post-weaning and at maturity suggest that it is possible to select for post-weaning efficiency and produce favourable correlated gains in maintenance efficiency. The genetic parameters estimated indicate that the favourable improvement in maintenance efficiency will be brought about by a decrease in feed intake both post-weaning and at maturity, with no change in growth or post-weaning body composition, although mature animals may be slightly leaner.

Chapter 7. Selection indices utilising feed intake information

7.1 Introduction

In the previous chapters various aspects of feed intake and efficiency were examined, with the results suggesting that genetic improvement of efficiency of feed utilisation by animals may be possible. Residual feed intake has been considered as it appears to be the most appropriate measure of efficiency available, and is a convenient measure for making comparisons between individuals and for examining genetic variation in feed efficiency. This chapter now presents a consideration of how the information gained from measuring feed intake can be used in selection programs to improve the efficiency of livestock production systems.

Kennedy *et al.* (1993) showed that the trait residual feed intake itself does not add any new genetic information to that which is obtained from the individual component traits (i.e. feed intake and production traits). Residual feed intake can be considered as a selection index with index weights for feed intake and production of 1 and $-b$ respectively, where b is the regression coefficient of feed intake on production. As residual feed intake is an index it must have an implied set of economic values which are determined by the regression coefficient b, itself a function of the variance in production and the covariance of production and feed intake. However, these implied economic values do not necessarily represent the true economic value of the traits of interest to the commercial producer. Further, the correlated responses of traits in the breeding objective to selection on residual feed intake are determined by the relevant phenotypic and genetic (co)variances rather than by the value of the trait in the breeding objective. The consequence of this may be serious as correlated responses to selection on residual feed intake may not be favourable. Hence selection may act in the opposite direction to the breeding objective and biological and economic efficiency of the production system may actually decrease even though the efficiency of growing animals is improved. For example, if selection on residual feed intake of growing animals was to produce a correlated decrease in reproductive rate, the overall effect on profitability and production efficiency may be negative.

In general, selection on biological indices (of which residual feed intake is a special example in that it is linear, while most are ratios) is not well supported in the literature. Other biological indices have been proposed such as those described by Dickerson (1970) and Fowler *et al.* (1976) where the aim is to improve the ratio of total output to total feed input. This approach has been put forward as being independent of economic considerations and therefore less susceptible to fluctuations. However Simm *et al.* (1987) showed that response to selection on a biological index defined as a product or ratio is dependant on the variation present in the component traits. Although such an objective does not require derivation of economic values, the component traits do have implied economic values in a similar manner to the implied economic values on the component traits for residual feed intake. Ponzoni and Davies (1989) compared the use of biological indices with conventional economic selection indices in a pig data set and concluded that "valuable as they have been in stimulating thought and discussion, it appears that there is no justification for the use of biological indices in practical breeding programs". While residual feed intake is a convenient measure of efficiency which can be utilised to improve our understanding of the efficiency complex, use of residual feed intake as the basis for selection decisions may not be optimal for improving efficiency.

On the basis of the problems outlined above, it can be argued that the best approach to improving efficiency in livestock is to use an economic selection index with feed intake included as a trait of economic importance in the breeding objective, and feed intake and growth measurements as selection criteria in the index. The selection index calculated will then consist of selection index weights determined by the economic value of the traits in the breeding objective. These weights are likely to differ from the weights used in single trait selection on residual feed intake. The inclusion of extra traits in the index is relatively straight forward with knowledge of the genetic relationships of the extra character with feed intake and growth traits. Hence traits affecting efficiency but which are not a component of residual feed intake (such as the feed intake and reproductive rate of mature cows) may be included in the objective and influence the relative weighting placed on the criteria traits. This approach should provide a more efficient method of selection for efficiency of the production system than selection on residual feed intake, as under selection index theory the correlation between the index and the breeding objective is maximised (Hazel 1943).

Although concerns have been expressed that economic selection indices are susceptible to fluctuations in prices which change the breeding objective, Fowler *et al.* (1976) showed that the selection index is robust to wide fluctuations in economic values. Hence the use of an economic index is attractive for improving profit which is the bottom line for the commercial producer. It should be recognised that biological and economic efficiency are not necessarily synonymous. For example, in some instances it may be more profitable to increase feed inputs to achieve an increase in outputs, even though the increase in feed intake may cause a decrease in biological efficiency. This situation occurs when the increase in output has a higher monetary value than the extra input required to achieve the increase, and hence profit is increased. Often this type of improvement in economic profit can be achieved by merely rescaling the size of the production enterprise rather than by increasing the efficiency of production. Smith *et al.* (1986) discussed this situation and suggested that extra profit from genetic change which could also be obtained by rescaling the operation should not be counted in assessing the value of genetic improvement. They suggested that the ratio of income to expense or its reciprocal ratio are more appropriate measures than profit for estimating economic values. James (1982a) pointed out that when expense and income are combined as a ratio the fixed costs have an impact on the economic values, whereas fixed costs do not influence economic values when income and expense are combined as a profit function. Hence more information is required when the objective is defined as ratio rather than as profit. Ponzoni (1988) compared the different methods for defining the breeding objective using a practical example and found that the method used had negligible effect on the objective and selection index. The profit equation method, being the simplest, is probably the best breeding objective to use for most situations.

Use of conventional selection index theory to select for efficiency provides a framework for evaluating the economic gains to be made from measuring feed intake on candidates for selection. As feed is the single largest cost in almost any animal production enterprise, feed intake should be included in the breeding objective regardless of whether or not it is included as one of the traits in the selection criteria. Ponzoni and Newman (1989) showed that ignoring feed costs had significant effects on the genetic gain in traits in the breeding objective. Hence the issue should be whether or not feed intake should be included as a selection criteria in the index. The value of any criterion trait in the selection index depends upon the genetic properties of the trait (its heritability and phenotypic and genetic correlations with the traits in the breeding objective and other criteria traits in the selection index) and the difficulty and expense involved in measuring the trait.

Many of the relationships between feed intake and other traits in breeding objectives of beef cattle are unknown. Knowledge of these genetic and phenotypic parameters is required before feed intake can be included in the breeding objective. These parameters need to be determined in order to properly account for feed intake in the selection index regardless of whether or not feed intake is included as a selection criterion. The value of inclusion of a measure of post-weaning feed intake as a criterion in the selection index will depend on these parameters. In some situations there is not likely to be a great improvement in the selection index by including feed intake information in addition to liveweight information, whereas in other situations there will be a large improvement in the selection index by including feed intake as a selection criterion. It is important to know under which situations the inclusion of feed intake as a criterion in the selection index would be beneficial.

Reproductive rate and herd age structure can have a large influence on the relative contribution of growth and feed intake of the breeding herd and progeny to the efficiency of the production system. The between species comparison of Webster (1989) (see Table 2.1) demonstrates this point. Thompson and Barlow (1986) also showed that herd age structure was important in determining the relative efficiency of various production systems. Herd age structure affects the number of expressions of each trait in the breeding objective and thus the economic values of the traits. This means that selection indices calculated for different herd age structures will differ and may not select the same subset of animals. This issue is of concern as, for instance, an animal selected using an index calculated for situations where the reproductive rate is high may not be the most appropriate individual to use in situations where reproductive rates are much lower and the breeding objective is different. The correlation between indices including feed intake calculated for different production systems is of interest as it may have an impact on the application of feed intake information in selection programs.

This chapter presents the development of a simple production system model for calculation of economic values for feed intake and growth traits which are then used in a selection index. This model is used to investigate the effect of herd age structure on the resulting selection indices and to determine under which sets of phenotypic and genetic parameters the inclusion of feed intake information in the selection index is beneficial.

7.2 Methods

7.2.1 Development of the production system model and breeding objective

The development of the production system model and breeding objective followed the procedure outlined by Ponzoni and Newman (1989). The final breeding objective obtained was similar in principle to that of Ponzoni and Newman (1989), but was simplified in that only feed intake and growth traits were considered. Reproductive traits were excluded from the objective, except that the overall reproductive rate of the herd was defined in order to calculate the herd age structure. In essence this is equivalent to assuming that genetic variation in reproduction traits is negligible. While this assumption is not strictly true, the heritability of reproductive traits is generally low (Koots *et al.* 1994a) and so ignoring reproductive rate in the breeding objective is unlikely to produce large deviations from the real situation.

Specification of the breeding, production and marketing system

The first step in developing any breeding objective is to define the total economic system in which the animal is expected to perform. This will in turn determine which traits will have an impact on the profitability of the enterprise. The approach taken here was to simplify the production system as much as possible while still maintaining a representation of a real beef production enterprise in Australia. For simplicity the breeding system was defined as a pure-bred system with the breed being used in a general purpose role. This is typical of the way in which many of the British breed cattle are currently used in Australia. The increase in the use of cross-breeding in Australia means that further work in developing objectives for alternative systems with specialist maternal and terminal sire breeds will be required.

The system considered is a self-replacing grass-fed beef production unit, with all calves weaned at 200 days of age. Replacement heifers are kept and are mated at 15 months to calve at 2 years of age. All male progeny and surplus heifers are sold at 400 days of age (fixed age basis). All cows are retained in the herd until a fixed age at which they are sold as cull for age cows.

Identification of inputs and outputs

The only inputs considered in the production system were feed inputs, while the only outputs generated was the liveweight of surplus animals. In order to identify the sources of inputs and outputs five classes of animals were defined: i) breeding cows; ii) cull cows sold at a fixed age at the end of a production cycle; iii) replacement heifers kept from the progeny generated; iv) surplus heifers over and above the number of replacement heifers required; and, v) bull calves. Total feed inputs for the enterprise were calculated as the sum of animals over the five classes multiplied by the feed intake per animal in each class, to produce a figure in kg of feed. Likewise, total outputs were calculated as the sum of animals over the five classes multiplied by the liveweight of sale animals in each class to produce a figure in kg liveweight.

$$\text{Inputs} = \sum_{i=1}^{5} N_i \times \text{Feed Intake}_i$$

$$\text{Outputs} = \sum_{i=1}^{5} N_i \times \text{Liveweight}_i$$

where:

N_i = Number of animals in class i (i = breeding cows, cull cows, replacement heifers, surplus heifers and bull calves);

Feed Intake_i = average feed intake per animal in class i in one production cycle;

Liveweight_i = average liveweight per animal sold from class i in one production cycle.

It is important to note that not all classes of animals consume feed in the enterprise or produce liveweight for sale. The relevant feed intake or liveweight is set to zero for these classes. The breeding cows and replacement heifers did not produce saleable liveweight while the cull cows were considered as a by-product of the breeding herd and hence did not consume feed in the enterprise.

Biological efficiency of the production system was calculated by dividing the total output of liveweight by the total input of feed, expressed as kg liveweight per kg feed. Economic aspects of the production system were calculated by quantifying the inputs and outputs in dollar terms. The model allowed for different prices to be used for feed and liveweight for each class of animal. Thus the equations given previously were extended to:

$$\text{Expenses} = \sum_{i=1}^{5} N_i \times \text{Feed Intake}_i \times \text{price}_i$$

$$\text{Income} = \sum_{i=1}^{5} N_i \times \text{Liveweight}_i \times \text{price}_i$$

where price_i = price per kg of feed or liveweight paid for animals in class i.

For all simulations in this chapter, feed was priced at \$0.035/kg based on the current cost of standing pasture hay (\$35/tonne, South Australian Stock Journal, Nov. 2nd 1995). This value is similar to the price used by Ponzoni and Newman (1989) of \$0.03/kg. Prices received per kg liveweight varied between classes, with \$1.10/kg paid for steer progeny, \$1.00/kg for heifers and \$0.80/kg for cull cows. These values were considered to represent the approximate worth of the animals in the current market (November 1995). The lower price paid for cull cows is consistent with the discount of 0.8 applied to these animals in the feeding and growth model of Thompson and Barlow (1986).

To measure the economic performance of the production system, the income and expenses were combined in two ways. The economic ratio was calculated as the total income divided by the total expenses, giving an indication of the returns on the dollar invested. The second expression was economic profit (i.e. income - expenses). There were no fixed costs included in either expression. Determination of the breeding objective was based upon economic profit as the fixed costs can be ignored in this expression as they disappear when partial derivatives are taken for the traits. In addition, the economic profit is simpler for use in selection index calculations as the economic values are independent of the trait means, which is not the case when using the economic ratio (James 1982a).

Determination of biological traits influencing income and expense

For development of the selection index, the inputs and outputs of the production system previously identified must be expressed as a function of biological traits. Which traits are included in the breeding objective should be determined on economic grounds. All biological traits having an impact on any of the terms in the expressions developed to describe the income and expense above should be included in the breeding objective. The simplified consideration used in this study meant that this procedure was not strictly adhered to as biological traits other than feed intake and growth can impact on the profit expression but were not included. Examples of such traits may be reproductive traits which will affect the number of animals in each expression, or carcass traits such as fat depth which will influence the price received for sale animals. For any trait to be included in the breeding objective knowledge of its genetic variance and covariance with all other traits in the breeding objective and selection criteria are required. As the number of traits and characters increases, the amount of information required increases rapidly. Hence for the purpose of this study it was necessary to assume that no genetic variation for traits other than feed intake and growth existed, an assumption which is obviously incorrect in real production systems.

Choosing biological traits which influence the income was relatively straight forward, as the production system assumed that all animals were sold at a given age and their value was determined by liveweight at the time of sale. As all progeny were sold at 400 days of age the trait included was liveweight at 400 days (Wt_{400}), which is a trait used in BREEDPLAN, the genetic evaluation package used commercially in Australia. The liveweight of cull cows was the mature weight of the cows (MWt_C).

Choosing biological traits to represent the feed costs of the herd was more complicated than for liveweight as the quantity of feed consumed varies with time, maturity and production status of the animals. In order to describe feed inputs as simply and as accurately as possible the feed requirements of the herd were considered as a function of two biological traits. The first of these was the total quantity of feed consumed by a cow during a production cycle (FI_C). This intake was assumed to apply to all cows in the herd whether they had a calf during the production year or not. Yearly intake was used in preference to daily feed intake which is influenced by the physiological status of the cow (ie pregnant, lactating or both lactating and pregnant) and fluctuates widely during a production cycle. Calves were assumed not to consume any feed prior to weaning, and so their sole pre-weaning energy source of milk is included in the yearly intake of the cow.

The second intake trait used was the daily feed intake of the progeny post-weaning (DFI_{PW}), chosen as a trait which describes the feed intake of all progeny including steers, surplus heifers and replacement heifers in the period after weaning until sale or entering the cow herd. This approach was preferred to that used by Ponzoni and Newman (1989) who used separate traits to describe the feed intake of each of the above classes of animals, as these separate traits are all descriptions of what is likely to be the same trait genetically. The approach adopted in this analysis assumes that the daily feed intake of the progeny was constant from weaning to the point of sale or entering the cow herd. The total amount of feed consumed by each class of animal was calculated as the daily feed intake multiplied by the number of days from weaning until sale or entering the cow herd, which is set by the production system. Weaning was assumed to occur at 200 days of age, and hence sale progeny (steers and surplus heifers) consumed feed from 200 days of age to the point of sale at 400 days, giving a total feed intake of 200 x DFI_{PW}. Replacement heifers entered the cow herd exactly 365 days after weaning in order to keep in line with the production cycle, after which their feed intake was included with the intake of the cow herd. Hence the total feed intake of a replacement heifer was 365 x DFI_{PW}.

Derivation of the economic value of traits in the breeding objective

As pointed out by Ponzoni and Newman (1989), different traits are expressed with different frequency and at different times. These factors influence the economic value assigned to each trait. Differences in frequency of expression can be accounted for by calculating the total income and total expenses per year or production cycle. The number of expressions of each trait can be calculated based on the number of animals in each class. Differences in both frequency and time of expression of traits can be accounted for using the more sophisticated 'discounted gene flow' method. However, the approach used in this study was the "per year" approach which accounts for differences in frequency of expression only.

To describe the herd structure and calculate the frequency of expression of traits, a series of equations were developed (see Appendix D). These equations defined the number of animals in each class based on 3 parameters: i) calving rate; ii) death rate; and, iii) age at which cows are culled from the herd. Equal numbers of male and female progeny born was assumed.

$$N_{\text{Culls}} = N_{\text{Cows}}\left(\frac{2 - D(\text{Age} - 2)}{2(\text{Age} - 2)}\right)$$

$$N_{\text{R.H.}} = N_{\text{Cows}}\left(\frac{2 + D(\text{Age} - 2)}{2(\text{Age} - 2)}\right)$$

$$N_{\text{Steers}} = N_{\text{Cows}}0.5R$$

$$N_{\text{S.H.}} = N_{\text{Cows}}\left(0.5R - \frac{2 + D(\text{Age} - 2)}{2(\text{Age} - 2)}\right)$$

where :

N_{Cows} = Number of cows in the breeding herd;

N_{Culls} = Number of culled for age cows sold;

$N_{\text{R.H.}}$ = Number of replacement heifers kept;

N_{Steers} = Number of steers sold;

$N_{\text{S.H.}}$ = Number of surplus heifers sold;

R = Number of calves weaned per cow joined (calving rate);

D = Proportion of cows which die per year (death rate);

Age = Age (years) at which cows are culled from the breeding herd (age of culls).

The equations above all contain a term for the number of cows in the breeding herd. If the number of cows is fixed at a constant, then changes in the other parameters will cause a change in the number of animals in each class which will be accompanied by a change in the total amount of feed required by the enterprise, and hence the enterprise is effectively rescaled. Although this will have no effect on the economic values relative to each other, the absolute values of the economic values will change and the trends will be more difficult to observe. An alternative to this scenario was adopted where the size of the breeding herd is adjusted as the parameters change, so that the total feed inputs to the production system remain unchanged, although the relative amounts going to each class of animal could still vary. This was achieved by dividing the equations describing the number of animals in each class by the number of cows in the breeding herd and calculating the total amount of feed consumed per breeding cow. The feed intake trait means assumed were 10 kg/day for post-weaning daily feed intake and 4500 kg/year for feed intake of cows, with the latter value taken from Ponzoni and Newman (1989). A total amount of feed available to the enterprise was a fixed constant at 6,706,250 kg of feed, based on a 1000 cow herd with a calving rate of 1.0, a death rate of 0 and age of culls at 10 years. From the total amount of feed available and the feed intake per breeding cow, the appropriate number of breeding cows for the parameter set under consideration was calculated. This number was then used in the equations given above to calculate the number of animals in each class.

$$\begin{aligned}\text{Feed per cow} &= \frac{\sum_{i=1}^{5} \mathrm{N}_i \times \text{Feed Intake}_i}{\mathrm{N}_{\text{Cows}}} \\ &= \overline{\mathrm{FI}}_{\mathrm{C}} + \frac{2 + \mathrm{D(Age} - 2)}{2(\mathrm{Age} - 2)}(365\overline{\mathrm{DFI}_{\mathrm{PW}}}) + 0.5\mathrm{R}(200\overline{\mathrm{DFI}_{\mathrm{PW}}}) \\ &\quad + (0.5\mathrm{R} - \frac{2 + \mathrm{D(Age} - 2)}{2(\mathrm{Age} - 2)})(200\overline{\mathrm{DFI}_{\mathrm{PW}}})\end{aligned}$$

$$\mathrm{N}_{\text{Cows}} = \frac{6{,}706{,}250}{\text{Feed per cow}}$$

With expressions developed for the number of animals in each class, biological traits which affect income and expenses identified and prices set for the relevant costs and income, all information required for determining the profit equation on which the selection index is based was available. The final profit equation is shown below.

$$\begin{aligned}P = {} & N_{\text{Culls}} \times \$0.80 \times MWt_C + N_{\text{Steers}} \times \$1.10 \times Wt_{400} + N_{\text{S.H.}} \times \$1.00 \times Wt_{400} \\ & - N_{\text{Cows}} \times \$0.035 \times FI_C - N_{\text{R.H.}} \times \$0.035 \times 365 \times DFI_{PW} \\ & - N_{\text{Steers}} \times \$0.035 \times 200 \times DFI_{PW} - N_{\text{S.H.}} \times \$0.035 \times 200 \times DFI_{PW}\end{aligned}$$

The economic value of each trait in the breeding objective was calculated as the partial derivative of profit (P) with respect to that trait. The resulting expressions for the economic values of the four traits are shown below.

$$\frac{dP}{dWt_{400}} = N_{\text{Steers}} \times \$1.10 + N_{\text{S.H.}} \times \$1.00$$

$$\frac{dP}{dMWt_C} = N_{\text{Culls}} \times \$0.80$$

$$\frac{dP}{dDFI_{PW}} = -N_{\text{R.H.}} \times 365 \times \$0.035 - N_{\text{Steers}} \times 200 \times \$0.035 - N_{\text{S.H.}} \times 200 \times \$0.035$$

$$\frac{dP}{dFI_C} = -N_{\text{Cows}} \times \$0.035$$

7.2.2 Choice of selection criteria

While the choice of traits for inclusion in the breeding objective is based purely on economic grounds, the choice of traits for selection criteria takes into consideration the genetic properties of the traits, correlations of the traits with other traits in the objective and selection index and the ease and cost of measurement of the traits. The characters chosen as selection criteria were those able to be measured post-weaning upon which selection decisions might be based if feed intake information was available. Although the traits in the selection criteria are not necessarily the same as the traits in the objective, in this case the traits chosen as selection criteria were weight at 400 days (WT_{400}) and post-weaning daily feed intake (DFI_{PW}).

In order to assess the value of measuring feed intake for inclusion in the selection criteria two indices were calculated. The first index included both 400-day weight and post-weaning daily feed intake and is hereafter referred to as index 1. The second index included only 400-day weight and is hereafter referred to as index 2. Both indices were constructed with information available from the same sources, which were kept constant throughout the simulations. The information included records on 400-day weight and post-weaning daily feed intake measured on the individual, on the sire and on 20 paternal half-sibs.

7.2.3 Parameters

7.2.3.1 Simulation 1 - Effect of production system parameters on the selection index

To investigate the effect of the production system parameters determining herd structure, the relevant parameters were varied and selection indices calculated and compared for each parameter set. The production system model was used to calculate the economic and biological efficiency of the system as well as the economic values of the traits in the breeding objective.

The genetic and phenotypic parameters used in this simulation were held constant and are given in Tables 7.1 and 7.2. The mean and phenotypic standard deviation for feed intake of cows were obtained from Ponzoni and Newman (1989). Genetic parameters involving the two growth traits and the heritability of the feed intake traits were obtained from Koots *et al.*(1994a,b). Data on genetic parameters of post-weaning and mature feed intake of beef cattle are scarce in the literature. The only study with appropriate parameters is that conducted in the Netherlands using dairy cattle, and papers by Korver *et al.* (1991), van Arendonk *et al.* (1991) and Nieuwhof *et al.* (1992) were consulted to obtain estimates of feed intake of growing dairy heifers and the correlation with feed intake during first lactation. However, the heritabilities and genetic correlations involving both feed intake and growth traits obtained in this study were higher than those which might be expected for beef cattle, and when the resulting matrices including parameters for growth traits were tested against the criteria of Foulley and Ollivier (1986) they were found to be non-permissible. Hence the parameters used in the simulations were modified from those obtained from the Netherlands experiment, although an attempt was made to maintain the correlations between traits as close as possible to literature estimates.

Parameters determining herd structure were chosen for a base population, with a calving rate of 0.85, death rate of 0.03 and age of culls of 10 years. For simulations each of the three parameters was varied individually while the other parameters were held constant. A fourth comparison was made between the most efficient and least efficient production system with all three parameters at the extreme end of the values used in the previous simulations.

Table 7.1 Mean, phenotypic standard deviation and heritabilities for the traits in the breeding objective used in simulation 1.

Trait	Units	Mean	s.d. (phenotypic)	Heritability
WT_{400}	kg (liveweight)	400	30	0.3
MWt_C	kg (liveweight)	600	50	0.5
DFI_{PW}	kg (feed)	10	1.5	0.5
FI_C	kg (feed)	4500	740	0.3

Table 7.2 Phenotypic and genetic correlations between traits in the breeding objective used in simulation 1. Phenotypic correlations are shown on the upper diagonal, genetic correlations are on the lower diagonal.

	WT_{400}	MWt_C	DFI_{PW}	FI_C
WT_{400}		0.70	0.60	0.30
MWt_C	0.70		0.40	0.40
DFI_{PW}	0.70	0.30		0.30
FI_C	0.50	0.50	0.50	

7.2.3.2 Simulation 2 - Effect of genetic parameters on the selection index

The second simulation was conducted in order to determine the value of including feed intake as a character in the selection index for different sets of genetic parameters. The breeding objective was held constant while the genetic parameters involving the feed intake traits were varied. For each set of parameters, selection indices 1 (including feed intake) and 2 (without feed intake information) were calculated. The production system parameters used in calculating the breeding objective were the set of base parameters used in the first simulation. Genetic parameters were chosen to represent the possible range of parameters which might be encountered in real populations. As parameters involving growth traits only were not of interest in this context, the heritabilities of weight at 400 days (Wt_{400}) and mature cow weight (MWt_C) and the genetic correlation between these traits were set at the values given in Table 7.1 and Table 7.2. In order to reduce the total number of parameter combinations, the relationships between the genetic correlations of growth traits (400-day weight and mature cow weight) with feed intake traits (feed intake of cows (FI_C) and daily feed intake post-weaning (DFI_{PW})) were assumed to be fixed relative to the genetic correlation between 400-day weight and daily feed intake post-weaning. The relationships were:

$$\begin{aligned} r_{g_{WT_{400},FI_C}} &= r_{g_{wt_{400},DFI_{PW}}} - 0.2 \\ r_{g_{MWT_C,FI_C}} &= r_{g_{wt_{400},DFI_{PW}}} - 0.2 \\ r_{g_{MWT_C,DFI_{PW}}} &= r_{g_{wt_{400},DFI_{PW}}} - 0.4 \end{aligned}$$

The varied parameters and the values chosen are given below:

$$\begin{aligned} h^2_{DFI_{PW}} &= 0.2,\ 0.5,\ 0.8; \\ h^2_{FI_C} &= 0.1,\ 0.3,\ 0.5; \\ r_{g_{DFI_{PW},FI_C}} &= 0.2,\ 0.5,\ 0.8; \\ r_{g_{DFI_{PW},WT_{400}}} &= 0.5,\ 0.7,\ 0.9; \\ r_{p_{DFI_{PW},WT_{400}}} &= 0.6,\ 0.8. \end{aligned}$$

A sample of the genetic parameter sets used in the simulations were tested for permissibility against the criteria of Foulley and Ollivier (1986). Matrices for the most extreme parameter sets were tested, as well as a carefully selected sample of other sets. In all, approximately 35 of the 162 parameter sets were tested, and a reasonably high degree of confidence in the permissibility of the matrices not tested was assumed. Permissibility of matrices for each parameter set was not checked due to the heavy demands on time which this process required.

7.2.4 Calculation of indices

Selection indices were calculated using the program of Kunzi (1976) which utilises SELIND (Cunningham and Mahon 1977) as a sub-routine. The formulae used in these programs are given by Ponzoni (1992). The selection index weights were derived by solving the equation:

$$b = P^{-1}Gv$$

where: $b = b_1 \ldots b_n$ is a vector of index coefficients;

P = a $n \times n$ matrix of phenotypic (co)variances among the n criteria in the index;

G = a $n \times m$ matrix of genetic covariances between the n criteria in the selection index and the m traits in the breeding objective;

$v = v_1 \ldots v_m$ is a vector of economic values for m traits in the breeding objective.

The variance of the index is given by:

$$\sigma_I^2 = b'Pb$$

The variance of the aggregate genotype (T) is:

$$\sigma_T^2 = v'Cv$$

where C = a *m x m* matrix of genetic variances and covariances among the *m* traits in the breeding objective.

The correlation between the selection index (I) and the aggregate genotype (T) (i.e. the accuracy of the selection index) is given by:

$$r_{I,T} = \frac{\sigma_I}{\sigma_T}$$

The genetic gain in the i^{th} trait after one generation of selection with selection intensity equal to one is calculated as:

$$\Delta g_i = \frac{b'G_i}{\sigma_I}$$

where G_i is the column of G corresponding to the i^{th} trait.

For calculation of correlations between indices and between breeding objectives, the formulae given by James (1982b) were used.

$$r_{I_1,I_2} = \frac{b_1'Pb_2}{\sqrt{(b_1'Pb_1).(b_2'Pb_2)}}$$

$$r_{T_1,T_2} = \frac{v_1'Cv_2}{\sqrt{(v_1'Cv_1).(v_2'Cv_2)}}$$

Where the breeding objective is the same for two indices (e.g. for comparison of index 1 with index 2), the correlation between the indices is reduced to:

$$r_{I_1,I_2} = \frac{\sigma_{I_1}}{\sigma_{I_2}}$$

7.3 Results

7.3.1 Simulation 1 - Effect of production system parameters on the selection index

Variation in production system parameters, and particularly calving rate, had a large effect on the efficiency of the production system and on the economic value of traits in the breeding objective (results shown in Table 7.3, Table 7.5, Table 7.7 and Table 7.9). Absolute values of biological efficiency were very low for all systems considered, varying from 2.6 % in the least efficient system to 6.4 % in the most efficient system (see Table 7.9). In economic terms this represented a difference of \$225,000 in profit (excluding fixed costs) between the best (\$171,000) and worst (\$-54,000) production systems considered. The index with only 400-day weight information (index 2) is equivalent to single trait selection on 400-day weight, and was poorly correlated with the breeding objective, with correlations varying from 0.00 to 0.17. The correlations of index 1 with the breeding objective were higher than that for selection on weight only, ranging from 0.37 to 0.46. The correlations between the indices utilising different information were low, ranging from 0.00 to 0.43, indicating that, for the genetic parameters assumed, a different sub-set of animals would be selected by including feed intake information in the index.

Genetic gains in traits included in the breeding objective are given for index 1 in the relevant tables. Genetic gains in post-weaning daily feed intake and feed intake of cows where index 1 was used were negative for all breeding objectives, although the magnitude of the reduction in feed intake traits varied considerably. However, the growth traits of 400-day weight and mature cow weight had positive genetic gains under some breeding objectives and negative gains under others.

The magnitude of genetic gains in index 2 were not affected by the breeding objective as this index only had included information on one trait, but the direction of the gains were altered by the objective and are given in the appropriate Tables. The magnitude of predicted gains for index 2 when selection was in a positive direction were: Wt_{400} 9.961 kg (liveweight); MWt_C 15.003 kg (liveweight); DFI_{PW} 0.450 kg (feed); and FI_C 122.853 kg (feed). The direction of gains for index 2 were positive for most situations considered. The exceptions to this occurred when calving rate was very low (see Table 7.3).

Table 7.3 Effect of calving rate on biological and economic efficiency and selection indices.

	Calving Rate					
	0.95	0.85	0.75	0.65	0.55	0.45
Biological efficiency	0.059	0.054	0.050	0.045	0.039	0.034
Economic ratio	1.71	1.57	1.43	1.28	1.12	0.94
Profit ($)	165,573	134,224	100,863	65,289	27,275	-13,440
Economic values for traits in the breeding objective						
Wt_{400} ($)	867.23	784.71	696.89	603.24	503.17	395.99
MWt_C ($)	89.00	91.77	94.71	97.85	101.21	104.80
DFI_{PW} ($)	-7543.14	-7047.77	-6520.59	-5958.45	-5357.75	-4714.38
FI_C ($)	-35.40	-36.50	-37.67	-38.92	-40.25	-41.68
Selection Indices						
Accuracy of index 1	0.405	0.395	0.388	0.383	0.383	0.387
Accuracy of index 2	0.145	0.101	0.053	0.001	0.053	0.108
Correlation between indices	0.359	0.255	0.136	0.002	0.138	0.279
Genetic gain by selection on index 1[a]						
Wt_{400} (kg)	0.999	-0.145	-1.425	-2.800	-4.199	-5.534
MWt_C (kg)	7.398	5.891	4.116	2.104	-0.064	-2.269
DFI_{PW} (kg)	-0.430	-0.499	-0.569	-0.636	-0.694	-0.739
FI_C (kg)	-41.023	-57.076	-74.253	-91.752	-108.436	-123.164
Direction of genetic gain by selection on index 2[b]	+	+	+	+	-	-

[a] genetic gain after one generation of selection with selection intensity equal to one.

[b] Magnitude of genetic gains for index 2 are given in the text, and are the same for all situations.

Table 7.4 Correlations between breeding objectives and selection indices utilising post-weaning weight and feed intake information for production systems differing in calving rate. Correlations between objectives are given on the upper diagonal, correlations between indices are on the lower diagonal.

Calving Rate	0.95	0.85	0.75	0.65	0.55	0.45
0.95		0.997	0.986	0.967	0.939	0.901
0.85	0.994		0.996	0.985	0.964	0.933
0.75	0.973	0.992		0.996	0.983	0.960
0.65	0.933	0.967	0.991		0.996	0.982
0.55	0.873	0.921	0.962	0.990		0.995
0.45	0.793	0.855	0.912	0.959	0.990	

Table 7.5 Effect of age at which cows are culled on biological and economic efficiency and selection indices.

	Age of culls				
	5	7	10	12	15
Biological efficiency	0.058	0.056	0.054	0.054	0.054
Economic ratio	1.56	1.57	1.57	1.57	1.57
Profit ($)	132,002	133.397	134,224	134,507	134,771
Economic values for traits in the breeding objective					
Wt_{400} ($)	538.66	693.16	784.71	816.01	845.27
MWt_{C} ($)	252.09	151.42	91.77	71.37	52.30
DFI_{PW} ($)	-7881.12	-7357.85	-7047.77	-6941.74	-6842.64
FI_{C} ($)	-34.65	-35.81	-36.50	-36.73	-36.95
Selection Indices					
Accuracy of index 1	0.459	0.423	0.395	0.384	0.374
Accuracy of index 2	0.084	0.095	0.101	0.102	0.104
Correlation between indices	0.183	0.225	0.255	0.267	0.278
Genetic gain by selection on index 1[a]					
Wt_{400} (kg)	-0.920	-0.470	-0.145	-0.020	0.102
MWt_{C} (kg)	4.827	5.449	5.891	6.059	6.222
DFI_{PW} (kg)	-0.542	-0.517	-0.499	-0.491	-0.484
FI_{C} (kg)	-67.578	-61.514	-57.076	-55.357	-53.672
Direction of genetic gain by selection on index 2[b]	+	+	+	+	+

[a] genetic gain after one generation of selection with selection intensity equal to one.

[b] Magnitude of genetic gains for index 2 are given in the text, and are the same for all situations.

Table 7.6 Correlations between breeding objectives and selection indices utilising post-weaning weight and feed intake information for production systems differing in age at which cows are culled. Correlations between objectives are given on the upper diagonal, correlations between indices are on the lower diagonal.

Age of culls	5	7	10	12	15
5		0.984	0.959	0.948	0.936
7	0.999		0.994	0.989	0.983
10	0.997	1.000		0.999	0.997
12	0.996	0.999	1.000		0.999
15	0.995	0.998	1.000	1.000	

Table 7.7 Effect of death rate on biological and economic efficiency and selection indices.

	Death rate			
	0.01	0.03	0.05	0.10
Biological efficiency	0.056	0.054	0.053	0.049
Economic ratio	1.62	1.57	1.53	1.42
Profit ($)	144,373	134,224	124,127	99,108
Economic values for traits in the breeding objective				
Wt_{400} ($)	797.18	784.71	772.30	741.55
MWt_C ($)	100.37	91.77	83.21	62.01
DFI_{PW} ($)	-7005.52	-7047.77	-7089.80	-7193.94
FI_C ($)	-36.59	-36.50	-36.40	-36.17
Selection Indices				
Accuracy of index 1	0.395	0.395	0.396	0.399
Accuracy of index 2	0.117	0.101	0.084	0.042
Correlation between indices	0.297	0.255	0.213	0.106
Genetic gain by selection on index 1[a]				
Wt_{400} (kg)	0.309	-0.145	-0.599	-1.731
MWt_C (kg)	6.498	5.891	5.272	3.678
DFI_{PW} (kg)	-0.472	-0.499	-0.524	-0.584
FI_C (kg)	-50.783	-57.076	-63.263	-78.238
Direction of genetic gain by selection on index 2[b]	+	+	+	+

[a] genetic gain after one generation of selection with selection intensity equal to one.

[b] Magnitude of genetic gains for index 2 are given in the text, and are the same for all situations.

Table 7.8 Correlations between breeding objectives and selection indices utilising post-weaning weight and feed intake information for production systems differing in death rate. Correlations between objectives are given on the upper diagonal, correlations between indices are on the lower diagonal.

Death rate	0.01	0.03	0.05	0.10
0.01		1.000	0.998	0.991
0.03	0.999		1.000	0.994
0.05	0.996	0.999		0.997
0.10	0.981	0.988	0.994	

Table 7.9 Comparison of high and low efficiency production systems on biological and economic efficiency and selection indices.

	Hi	Lo
Biological efficiency	0.064	0.026
Economic ratio	1.73	0.77
Profit ($)	171,291	-54,009
Economic values for traits in the breeding objective		
Wt_{400} ($)	635.29	413.15
MWt_C ($)	253.15	25.75
DFI_{PW} ($)	-8292.28	-4642.23
FI_C ($)	-33.73	-41.84
Selection Indices		
Accuracy of index 1	0.460	0.384
Accuracy of index 2	0.139	0.166
Correlation between indices	0.301	0.431
Genetic gain by selection on index 1[a]		
Wt_{400} (kg)	0.361	-6.911
MWt_C (kg)	6.566	-4.717
DFI_{PW} (kg)	-0.469	-0.771
FI_C (kg)	-50.059	-136.757
Direction of genetic gain by selection on index 2[b]	+	-

[a] genetic gain after one generation of selection with selection intensity equal to one.

[b] Magnitude of genetic gains for index 2 are given in the text, and are the same for all situations

Although changes in production system parameters produced changes in the economic values of the traits in the breeding objective, the correlations between breeding objectives presented in Tables 7.4, 7.6 and 7.8 were generally high. For the most extreme situations considered (the high vs low efficiency systems in Table 7.9) the correlation between breeding objectives was 0.75, while the correlation between indices was 0.73. For all other comparisons the correlation between objectives was greater than 0.90. Correlations between indices were generally high also. The age of cull cows and death rate parameters had little effect on the indices and hence the correlations were very high (Table 7.5 and Table 7.7). Calving rate had a larger effect on the indices (Table 7.3), but correlations between indices were still over 0.90 when calving rate differed by as much as 0.30.

7.3.2 Simulation 2 - Effect of genetic parameters on the selection index

When the (co)variance matrices used in the simulation were tested for permissibility a subset were found to be non-permissible. The non-permissible parameter sets occurred when the genetic correlation between post-weaning daily feed intake and 400-day weight was 0.9 and the genetic correlation between post-weaning daily feed intake and feed intake of cows was 0.2. Results for this subset of parameters are not reported. The (co)variance matrices were permissible for all other parameter sets tested.

The correlation between index 1 and 2 was used as an indication of the value of utilising feed intake information in the index. If the correlation between the indices is high, then the same selection decisions are made regardless of the extra information and there is little point in measuring feed intake. The opposite is true when the correlation is low, and hence feed intake information is useful. The correlations between index 1 and 2 were calculated for each set of parameters used and are presented in Table 7.10.

Where the genetic correlation between post-weaning daily feed intake and 400-day weight was 0.5 or 0.7 it is possible to pick out some general trends. As the heritabilities of post-weaning daily feed intake and the feed intake of cows increased, the correlation between index 1 and 2 decreased, and so post-weaning daily feed intake added more information to the index. An increase in the genetic correlation between post-weaning daily feed intake and feed intake of cows also caused a decrease in the correlation between the indices, as post-weaning daily feed intake contributed more information on another trait in the breeding objective. An increase in the phenotypic correlation between post-weaning daily feed intake and 400-day weight produced a decrease in the correlation between the indices.

The effects of changes in the genetic correlation between post-weaning daily feed intake and 400-day weight were more complex as it depended on the values of the other parameters. When the heritability of post-weaning daily feed intake and feed intake of cows were low the correlation between index 1 and 2 increased as the genetic correlation between post-weaning daily feed intake and 400-day weight increased. However, when the heritabilities of post-weaning daily feed intake and feed intake of cows were high the correlation decreased as the genetic correlation between post-weaning daily feed intake and 400-day weight increased. The heritability values at which an increase or a decrease in the correlation occurred were not fixed, but depended on the genetic correlation between post-weaning daily feed intake and feed intake of cows. The phenotypic correlation between post-weaning daily feed intake and 400-day weight also had a small effect. When the genetic correlation between post-weaning daily feed intake and feed intake of cows was high, the correlation tended to decrease even for relatively low heritabilities. These results suggest that even when there is a strong genetic relationship between post-weaning feed intake and growth, measurement of feed intake may still add valuable information under some circumstances.

Although the trends outlined above were generally true there were exceptions to the trends under certain circumstances. For example, when the genetic correlation between post-weaning daily feed intake and 400-day weight was 0.7, the genetic correlation between post-weaning daily feed intake and feed intake of cows was 0.2 and the heritability of post-weaning daily feed intake was 0.2, the correlation between index 1 and 2 increased as the heritability of feed intake of cows increased, whereas in other situations it decreased. These results suggest that the value of the extra information gained by including feed intake as a character in the index needs to be assessed for each individual set of genetic parameters.

The trends outlined above applied when the genetic correlation between post-weaning daily feed intake and 400-day weight was 0.5 or 0.7, but when the genetic correlation rose to 0.9 the trends in the correlation between index 1 and 2 began to behave more erratically. For example, when the heritability of post-weaning daily feed intake was 0.2 or 0.5, an increase in the heritability of feed intake of cows caused the correlation between index 1 and 2 to decrease and then increase. Examination of the genetic response to selection in each trait (results not presented) indicated that this was a consequence of the changing balance between feed intake and growth. When the heritability of feed intake of cows was 0.1, feed intake had little influence on the index and so index 1 applied positive selection pressure on 400-day weight. In this situation index 2 was also able to place positive selection pressure on weight and so similar results were achieved. When the heritability of feed intake of cows was 0.3, any increase in weight was balanced by an increase in feed intake and so the variance of index 1 was very low. As index 2 did not include measurements on post-weaning daily feed intake there was no balance achieved between weight and feed intake and so index 2 continued to apply selection pressure on weight, producing a lower correlation between indices than those observed for other heritabilities of feed intake of cows. However, when the heritability of feed intake of cows was set to 0.5, feed intake had a very large influence on the index. In this case strong negative selection pressure was placed on feed intake, resulting in a negative genetic gain in the weight traits. In this situation a similar outcome to selection on index 1 was able to be achieved by applying negative selection pressure on 400-day weight using index 2, and hence the correlation between index 1 and 2 was greater than it was when the heritability of feed intake of cows was 0.3.

Another interesting pattern to the correlations between index 1 and 2 was observed when the heritability of post-weaning daily feed intake increased, with the correlation increasing and then decreasing under some circumstances. This observation can be explained using similar reasoning to that given in the previous paragraph as it is a result of the changing balance between feed intake and growth in the index. These situations only occurred when the genetic correlation between post-weaning daily feed intake and 400-day weight was high (0.9). Under these circumstances a change in 400-day weight produced a strong correlated response in post-weaning daily feed intake and vice versa, and hence when strong selection pressure was placed on either trait by index 1, similar results were achieved with selection only on 400-day weight by index 2.

Table 7.10 Effect of genetic parameters on the correlation between the selection index calculated using 400-day weight only and the selection index calculated using 400-day weight and DFI_{PW}. Cells are shaded according to the magnitude of the correlation.

			$r_{p_{DFI_{PW},Wt_{400}}} = 0.60$			$r_{p_{DFI_{PW},Wt_{400}}} = 0.80$		
			$h^2_{DFI_{PW}}$			$h^2_{DFI_{PW}}$		
$r_{g_{DFI_{PW},Wt_{400}}}$	$r_{g_{DFI_{PW},FI_C}}$	$h^2_{FI_C}$	0.2	0.5	0.8	0.2	0.5	0.8
0.5	0.2	0.1	0.830	0.669	0.497	0.665	0.497	0.342
		0.3	0.773	0.558	0.377	0.608	0.407	0.258
		0.5	0.718	0.468	0.292	0.558	0.339	0.200
	0.5	0.1	0.731	0.544	0.391	0.569	0.396	0.268
		0.3	0.588	0.380	0.252	0.449	0.275	0.173
		0.5	0.482	0.283	0.178	0.367	0.205	0.123
	0.8	0.1	0.641	0.452	0.320	0.493	0.327	0.219
		0.3	0.459	0.283	0.188	0.350	0.206	0.130
		0.5	0.351	0.200	0.127	0.269	0.146	0.088
0.7	0.2	0.1	0.96	0.86	0.61	0.85	0.72	0.46
		0.3	0.98	0.68	0.21	0.88	0.54	0.15
		0.5	1.00	0.16	0.18	0.93	0.13	0.14
	0.5	0.1	0.84	0.61	0.38	0.69	0.48	0.28
		0.3	0.60	0.26	0.08	0.47	0.20	0.06
		0.5	0.33	0.03	0.06	0.26	0.03	0.05
	0.8	0.1	0.695	0.449	0.270	0.549	0.343	0.198
		0.3	0.379	0.152	0.052	0.294	0.117	0.039
		0.5	0.175	0.019	0.037	0.138	0.015	0.028
0.9	0.5	0.1	0.995	0.967	0.369	0.989	0.960	0.283
		0.3	0.564	0.889	0.684	0.526	0.924	0.654
		0.5	0.907	0.930	0.764	0.775	0.965	0.756
	0.8	0.1	0.867	0.486	0.098	0.723	0.377	0.075
		0.3	0.118	0.221	0.279	0.092	0.184	0.230
		0.5	0.383	0.399	0.370	0.335	0.349	0.314

7.4 Discussion

The production system model presented in this study shows the importance of herd-age structure in determining biological and economic efficiency and confirms previous results (eg Thompson and Barlow 1986; Webster 1989). The most important parameter in determining herd-age structure is the reproductive rate of the breeding herd. This parameter is responsible for much of the difference in production system efficiency between species. Although the amount of within species variation in reproductive rate is generally low compared to the between species variation, the range considered in the production system model probably represents the extremes of cattle production in Australia, from the high calving rates obtained in the best of environments in southern Australia to the very low calving rates obtained in the harsh environment cattle are run under in the tropical areas of northern Australia.

Reproductive rate had a large effect on biological and economic efficiency (Table 7.3), and produced large differences in the economic values of some traits in the breeding objective, particularly traits of the progeny, but the breeding objectives were still highly correlated even between relatively extreme production systems. As pointed out by Ponzoni (1988), the correlations among selection indices are of greater practical interest than correlations between objectives, as selection decisions are based on the index, not the objective. The correlations between indices were moderate to high, even for situations with extreme differences in reproductive rate and herd-age structure. These results agree with the results of Fowler *et al.* (1976) who showed that selection indices are relatively robust to changes in economic values of the traits. Smith (1983) also showed that unless the direction of selection for a trait is altered, changes in economic values have little effect on the efficiency of index selection.

It is unlikely that there would be much transfer of genetic material between extreme production systems in Australia as the cattle used in these situations are very different. For production systems where genetic material is likely to be exchanged (eg for production systems differing in calving rate by up to 0.30) the correlations between indices were generally greater than 0.90, indicating that the same index could be used in a wide range of situations without compromising the efficiency of selection.

Although the indices were highly correlated, herd age structure did effect the way in which the index achieved the economic gains. In general, for systems where a greater number of progeny were sold, the economic value of weight at slaughter (400-day weight) was higher and growth traits received more emphasis in the index. On the other hand, for production systems where the cost of maintaining the breeding herd was relatively higher a greater emphasis would be placed on decreasing feed costs, sometimes at the expense of a correlated reduction in growth traits. Indices were more accurate in situations where there was a greater proportion of progeny in the production system, a reflection of the fact that all characters in the selection index were measured on the progeny.

The correlations between indices calculated with and without post-weaning feed intake included as a character in the index suggest that measurement of feed intake is likely to add useful information for most sets of genetic parameters. The magnitude of correlation required in order for measurement of feed intake to be economically beneficial will depend on other factors such as the cost of measurement and the genetic influence of the selected individuals in commercial beef herds. Without this knowledge it is difficult to identify a cut off point for the correlations between indices below which measurement of feed intake is beneficial. As well as depending on the genetic parameters of the population, the value of measuring feed intake will be determined by the economic values of the traits in the objective, which in turn are influenced by the role of the breed in the production system. For example, where a breed is used to supply terminal sires to commercial herds, the economic value of feed intake of mature cows will be close to zero as very few of the progeny are kept as breeding cows. Hence decisions on whether to include feed intake as a character in the selection index will be specific to each breed with different genetic parameter sets and roles in the beef industry.

Regardless of whether or not feed intake is to be included as a selection criterion it is important that estimates of the relevant genetic parameters are obtained so that feed intake can be included in the breeding objective as an important cost in beef production. The parameters required include not only those between feed intake and growth traits, but with all traits which are either of economic significance or are potential traits for inclusion as criteria in the selection index. The best estimates of the few of these parameters which have been studied to date are mainly on cattle breeds not used in Australia. Thus it is important for the beef industry in Australia that estimates of these parameters are obtained for Australian genotypes under Australian conditions.

The model production system considered in this chapter was greatly simplified in order to examine one aspect of using feed intake information in selection indices. There are many issues still to be explored in order to optimise the use of such information and this is likely to be a fertile area of research. Future work could include further development of the breeding objective by extending the production system model to encompass a wider range of situations, such as different turn-off ages for progeny and specialised roles for breeds (eg maternal, terminal, etc).

More work is also required on defining feed costs accurately. An increasing proportion of cattle in Australia are going though a grain-fed finishing phase. While the breeding herd consumes low energy forage which is relatively low cost, under this system the finishing animals consume high cost grain-based rations. This is likely to have some impact on the economic values assigned to feed intake, and the value of feed intake as a criterion in the selection index. The breeding objective should be extended to include the grain-fed finishing phase with its extra associated costs and income, and the impact of this phase on selection decisions could then be assessed.

Another important aspect of feed costs which has been largely ignored in the past and has not been covered in this chapter is the seasonal supply of feed. Fluctuations in feed supply throughout a production cycle mean that at some points feed supply is limiting while at other points feed is in surplus. This is a function both of fluctuations in pasture growth and in demands of the production system, and so the times when feed is limiting may not necessarily coincide with the time at which pasture growth is lowest. This variation in feed supply impacts on the economic value assigned to feed, and so ideally the price assigned to feed in the breeding objective should vary during a production cycle also. The price for feed used in this chapter was the value of standing pasture hay which obviously is during a time of surplus feed. The average price of feed during a production cycle may be higher than this. Morris *et al.* (1994) discussed the problems associated with variation in pasture supply in the context of improving biological and economic efficiency and concluded that "more sophisticated models were required which differentially value feed throughout the year". However modelling this variation and including this information in a breeding objective is likely to be difficult and may create unmanageable complexities in the selection index. If it is assumed that within a production system there is little genetic variation in the pattern of feed demand (although quantity of feed demanded is still important) the use of an average cost of feed across a production cycle is likely to be sufficient for practical purposes.

The simulations in this chapter showed that in some situations a selection index which includes feed intake in the objective may produce negative gains in growth traits. Although this may improve profit, the adoption of such an index may be resisted. A reduction in growth potential may not be desirable for marketing reasons, among others. In this situation it may be desirable to use a restricted index, where growth traits are held constant while feed intake is decreased, or where feed intake is held constant while growth is increased. Such an index has been used successfully by Eisen (1977) to improve efficiency of post-weaning gain in mice. However, the index used by Eisen (1977) is similar to the special case of selection on residual feed intake considered by Kennedy *et al.* (1993) and did not allow for restriction of other traits in the breeding objective not used as criteria in the selection index, such as feed intake of mature animals. The advantage of a restricted index in the context of improving production efficiency is that it will avoid genetic change that can be achieved simply by rescaling the production system as the feed inputs will either remain unchanged or decrease, depending on whether feed intake or growth is restricted. Thus the problems with rescaling effects when the profit equation is used to define the breeding objective may be overcome using a restricted index. However, use of a restricted index requires good knowledge of the relevant genetic parameters, otherwise the restriction will be ineffective. Practical difficulties in obtaining accurate estimates of genetic parameters for traits such as feed intake which are expensive and difficult to measure may preclude the use of a restricted index.

As feed intake is currently an expensive and difficult trait to measure it is likely that it will only be measured on elite animals. This means that some sort of two-stage selection will likely occur, with animals selected using information available before being placed on test for measurement of feed intake. This information is likely to include traits such as pre-weaning growth measured on the individual and siblings as well as other information (which may include post-weaning feed intake) collected on non-contemporary relatives. After the feed intake test a further round of selection would use the extra information generated during the period the animal is on test. The framework for multi-stage selection using selection index theory has been laid out by Cunningham (1975). However the practical implications of such a scheme where feed intake measurements are included are unknown and should be investigated, particularly in terms of the cost-effectiveness of selection.

7.5 Summary

Use of a conventional selection index is likely to be a superior means of improving efficiency to selection on residual feed intake as additional traits not measured can be included in the breeding objective. Using a conventional index which included only feed intake and growth traits it was shown that even for production systems with large differences in efficiency and economic values of traits, the indices calculated were highly correlated and hence selection decisions made under one production system are likely to be appropriate for a reasonably wide range of situations. Comparison of indices with and without feed intake included in the selection index indicated that for most genetic parameter sets considered the measurement of feed intake was likely to add useful information and selection decisions would differ from those made without information on feed intake. There is a need for estimation of parameters for feed intake and other traits in Australian genotypes under Australian conditions. There is still a good deal of investigation required into optimal ways of using information on feed intake in selection decisions. This appears to be a fertile area for further research.

Chapter 8. Summary

8.1 Synthesis

The hypotheses addressed in this thesis are whether genetic variation in the efficiency of feed utilisation by animals exists, and if so, how can this variation be utilised in selection programs for beef cattle? To investigate genetic variation in lifetime efficiency of beef cattle under production systems is a large undertaking as a multitude of biological aspects which affect efficiency exist, and the overall efficiency is a summation of many of these aspects and their interactions with one another. Hence it is useful to attempt to break the efficiency complex down into a small number of traits for consideration. A search of the literature indicates that a number of researchers have attempted to do this in the past, and one general recommendation arising from this approach is that for species with relatively low reproductive rates (e.g. sheep and cattle) large gains in efficiency can be made by reducing the feed intake of the breeding herd without changing the growth rate of progeny. In order to achieve this, improvement of maintenance efficiency has been identified as an appropriate biological objective (Thompson and Barlow 1986; Webster 1989).

In Chapter 2 a number of studies were reviewed which suggested that genetic variation in the efficiency of maintenance exists in cattle, and thus it may be possible to improve maintenance efficiency through selection. However it is not feasible to measure and select directly on maintenance efficiency in cattle used for commercial purposes, and therefore an appropriate selection criteria measured on cattle post-weaning is required to improve efficiency. Selection on a post-weaning measure of efficiency in order to improve lifetime production efficiency assumes that the post-weaning measure of efficiency represents variation in the intrinsic efficiency of animals and that this intrinsic efficiency is genetically determined and is related to the lifetime efficiency of the animal.

A number of methods of expressing efficiency were reviewed in Chapter 2 and it was concluded that residual feed intake was the measure most likely to reflect variation in the intrinsic efficiency of cattle. The literature contains reports suggesting that residual feed intake of growing cattle is at least moderately heritable. Hence this thesis concentrated on residual feed intake and explored issues concerning the potential of a post-weaning measure of efficiency to improve lifetime efficiency.

The potential of a post-weaning measure of efficiency to improve lifetime efficiency in cattle is dependant on the correlation of post-weaning efficiency with efficiency at maturity, but there are no data sets in existence which enable this relationship to be examined in beef cattle. In the absence of such knowledge the repeatability of efficiency post-weaning can provide useful information as to the upper limit of the phenotypic correlations between efficiency at different stages of maturity. The data set analysed in Chapter 3 suggested that residual feed intake has only low repeatability, and the phenotypic correlations between measurements of residual feed intake decreased as the interval between the measurements increased. These initial results suggested that efficiency post-weaning was unlikely to be related to efficiency at maturity, at least phenotypically.

Similar analyses of a more reliable cattle data set in Chapter 4 indicated that residual feed intake was moderate to highly repeatable when the amount of measurement error was reduced, but there was still a tendency for correlations between measurements to decrease as the intervening period increased. This evidence supported the conclusions made earlier that post-weaning efficiency is a poor phenotypic predictor of efficiency at maturity. The decrease in phenotypic correlations could be a result of decreases either in the underlying genetic correlations or the environmental correlations. Results from the second cattle data set suggested that the observed decrease in phenotypic correlations was due to a decrease in the environmental correlations and not the genetic correlations, and so while post-weaning residual feed intake is phenotypically unrelated to mature efficiency, it may be genetically correlated. This suggests that selection for efficiency using a post-weaning test may be possible.

Results with mice in Chapters 5 and 6 supported the hypotheses formed from analyses of cattle data. In Chapter 5 residual feed intake was compared with an alternative way of examining lifetime efficiency by using curves to describe growth and feeding. The results confirmed that the phenotypic correlation between post-weaning efficiency and efficiency at maturity was low. However it was found that as the mice matured the correlation between residual feed intake and maintenance efficiency rose.

The poor phenotypic correlation of post-weaning efficiency with maintenance efficiency suggests one of two scenarios. The low correlation may mean that the concept of an animal possessing a genetically determined intrinsic efficiency throughout its lifetime is false. In genetic terminology this means that efficiency post-weaning is genetically unrelated to mature efficiency as a different subset of genes determine efficiency at different ages (i.e. the genetic correlation is zero). Alternatively, the low phenotypic correlation may be a result of different environmental effects influencing efficiency post-weaning and at maturity, although there may still be a strong genetic relationship between the two traits. Under this second scenario there is still potential for a post-weaning measure of efficiency to be used as a selection criteria for improving lifetime efficiency.

Estimates of genetic parameters for efficiency of mice in Chapter 6 suggested that the real situation lies somewhere between the two scenarios envisaged in the previous paragraph. The genetic correlation between post-weaning and maintenance efficiency was 0.60, and so the genetic relationship between post-weaning and mature efficiency was strong. This suggests that animals possess an intrinsic efficiency under genetic control which operates across different stages of maturity. Therefore selection on post-weaning efficiency is likely to improve maintenance efficiency at maturity and, more generally, lifetime efficiency. However the genetic correlation was not unity and hence genetic variation in efficiency also exists which is specific to a particular age or physiological state, so that some of the genetic variation in efficiency of growing animals is independent of efficiency of maintenance at maturity.

Conceptually this result might be explained by the fact that some basic physiological processes are common to both the growing animal and the mature animal at maintenance. For example, nutrient uptake is an important function at all stages of maturity and so an animal more efficient at absorption of nutrients would be at an advantage both when growing and at maintenance. Where a process is specific to particular physiological state, such as the conversion of nutrients to milk in the udder of a lactating animal, one would not expect genetic variation in this process to influence the efficiency of the animal when in an entirely different physiological state and the process is not functioning. Such reasoning would suggest that genetic variation in the partial efficiencies of energy utilisation for different functions exists. The literature concerning variation in these partial efficiencies was recently reviewed by Veerkamp and Emmans (1995) who did not find any strong evidence that such genetic variation exists. However the measurement of partial efficiencies is difficult and it could be argued that division of energy requirements into a series of distinct partial efficiencies is artificial, and hence it is not suprising that such evidence does not exist.

The genetic correlation between efficiency of mice post-weaning and at maturity is significant as it is the only evidence that efficiency in growing animals is related to efficiency in mature animals at or near maintenance, and suggests that the intrinsic efficiency of animals is expressed across a range of physiological states from production to maintenance. Previous studies have compared animals either in a state of production (growing vs lactating; Nieuwhof *et al.* 1992) or in a state of maintenance (Taylor *et al.* 1981) and found that there is a relationship between efficiency of animals in these states which is under genetic control. The relationship between efficiency of production and maintenance is important as it suggests that livestock selected for post-weaning efficiency are likely to be superior for efficiency across a wide range of situations, from high production in times of high nutrient availability to maintenance of bodyweight during periods of low nutrient availability. This is important as comparison between breeds have found that there is a large interaction between genotype and nutritional environment on biological efficiency (Jenkins and Ferrell 1994). However the genotype by environment interaction on biological efficiency are largely a result of differences in reproductive rate, which has not been investigated in this thesis.

It is tempting to speculate as to the possible correlated responses which would occur as a result of selection for post-weaning efficiency. The genetic parameter estimates in Chapter 6 indicated that there would be very little change in growth, mature size and body composition, but that the major change would be a reduction in feed intake both post-weaning and at maturity. However, knowledge of the correlated response to selection in other traits such as milk production and activity levels would be of both scientific and practical significance. Of major importance, but not dealt with in this thesis, is the relationships between efficiency, reproductive rate and production potential. The evidence concerning these relationships is scarce and hence no firm conclusions can be made. It is possible that the relationship between efficiency and reproductive rate is antagonistic. Nielsen (1995) reported a difference in reproduction of mice selected for heat loss at approximately 10 weeks of age, with high heat loss mice (presumably inefficient) having higher ovulation rates and litter sizes than control and low heat loss lines. Hocking *et al.* (1985) found that lines of hens which produced more eggs also had higher maintenance requirements. However both these studies compare the relationship of reproductive rate with maintenance efficiency, and the outcome where selection is on post-weaning efficiency may be different. The relationships between efficiency and many of these traits are best assessed as correlated responses to selection rather than using a genetic parameter estimation approach. Selection line experiments both in model species and in cattle should be established to improve the understanding of both the genetics and the physiology of efficiency.

The importance of reproductive rate in determining production system efficiency means that the selection index approach discussed in Chapter 7 is a better method for selecting for efficiency, as all biological traits which affect efficiency can be accounted for by including them in the breeding objective. While this method changes the focus from a biological objective to a bio-economic objective, it provides a well established framework whereby selection decisions may be optimised and other traits of economic importance can be included with knowledge of the appropriate parameters. The simulations performed in Chapter 7 showed that under a majority of situations there was a considerable improvement in selection decisions made by including measurements of post-weaning feed intake in the selection index. Hence the measurement of feed intake on elite animals would appear to be worthwhile for the beef industry.

The work in Chapter 7 also highlighted the need for reliable estimates of genetic relationships between feed intake and other traits included in the breeding objective, regardless of whether feed intake is to be included as a character in the selection index or not. As a minimum requirement for the industry in Australia it would seem necessary to estimate parameters separately for British breeds, European Breeds and *Bos indicus* type cattle. There is also a need to examine strategies to optimise ways in which feed intake information can be utilised in selection decisions for application in industry herds.

A major limitation to the application of selection for efficiency in industry herds is the lack of technology for measuring feed intake of individual animals at pasture with sufficient accuracy. Currently the only reliable means of obtaining feed intake information is to use a specialised facility to measure feed intake in a central test station. Although it has been shown in this thesis that it is possible to reduce the length of efficiency test to ten weeks, representing considerable savings in the cost of testing, measurement of feed intake in such stations is still expensive, inconvenient and is only likely to be performed on elite animals.

The existence of an accurate method for measuring feed intake at pasture would allow on-farm testing of animals in contemporary groups and considerably more animals could be tested if the technology was cheap enough. With more animals tested it would be possible to make some sacrifices in the accuracy of the feed intake data, as the reduction in heritability would be offset by a greater amount of information on related animals and an increase in the selection intensity applied to feed intake.

8.2 Conclusions

The aim of this thesis was to determine whether genetic variation in the efficiency of feed utilisation by animals exists, and how this variation can be utilised. Clear evidence has been presented from cattle and mice to indicate that genetic variation in post-weaning efficiency exists, and that variation in maintenance efficiency at maturity also exists. While there does not appear to be a strong relationship between post-weaning efficiency and maintenance efficiency at maturity at a phenotypic level, results from mice have shown that the genetic correlation between the two traits is moderate, and hence selection on post-weaning efficiency is likely to produce a correlated improvement in mature efficiency. These results with a laboratory species suggest that selection based on post-weaning efficiency may lead to a favourable correlated response in efficiency of maintenance in livestock species.

Appendix A. Publications

Journal Publications:

Archer, J.A. and Pitchford, W.S. (1996) Phenotypic variation in residual feed intake of mice at different ages and its relationship with efficiency of growth, maintenance and body composition. *Animal Science* **63(1):**149-157.

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Note:

Archer *et al.* (1994) and Archer and Parnell (1995) report the work which is presented in Chapter 3 of this thesis.

Archer *et al.* (1997a,c) report results from Chapter 4 of this thesis.

Archer and Pitchford (1995, 1996) are based on the results presented in Chapter 5 of this thesis.

Archer *et al.* (1997b), Pitchford *et al.* (1997) and Hughes *et al.* (1997) present results from Chapter 6 of this thesis.

Appendix B. Derivation of formula for repeatability

The formula used to calculate repeatability in Chapters 3 and 4 can be derived as follows. Becker (1984) gives the expected mean squares from the repeated measures analysis as:

$$MS_B = \sigma_E^2 + n.\sigma_W^2$$

$$MS_W = \sigma_E^2$$

where:

MS_B = Mean squares between individuals;
MS_W = mean squares between measurements, within individuals;
σ_{E}^2 = variance attributed to temporary environmental effects and measurement error;
σ_W^2 = variance attributed to genetic variance plus permanent environmental variance;
n = number of measurements per individual (equal number for each individual);

Combining these equations we obtain:

$$\sigma_W^2 = \frac{MS_B - \sigma_E^2}{n}$$

$$= \frac{MS_B - MS_W}{n}$$

Substituting into the expression for repeatability (Becker 1984):

$$\text{Repeatability (R)} = \frac{\hat{\sigma}_W^2}{\hat{\sigma}_W^2 + \hat{\sigma}_E^2}$$

$$= \frac{\dfrac{MS_B - MS_W}{n}}{\dfrac{MS_B - MS_W}{n} + MS_W}$$

$$= \frac{\dfrac{MS_B - MS_W}{n}}{\dfrac{MS_B + (n-1)\,MS_W}{n}}$$

$$= \frac{MS_B - MS_W}{MS_B + (n-1)\,MS_W}$$

Appendix C. Measurement of body composition

Body composition of the mice described in Chapter 6 was measured using a Model SA-2 Small Research Animal Body Composition Analyser (EM-SCAN Inc., Illinois USA). The analyser measures the change in an electrical field created by the subject. As body fat and fat-free mass have significantly different electrical conductivity properties it is possible to predict fat-free mass from the change in the electrical field. However position of the subject is critical and so a standard position must be adopted for reliable results.

The technique used followed that of Nielsen (personal communication). The mouse was placed in a supine position with the tail extended and head facing the core of the machine. The "usual widest part of the body" between the lower rib and hind leg was positioned on the scribe mark on the animal carrier plate. Readings were taken in fixed mode, and a minimum of 5 readings were used with a maximum coefficient of variation of 6 %. If a coefficient of variation greater than 6 % was obtained, the extreme high and low readings were deleted pairwise until the above conditions were satisfied. The EM reading and body mass (BM) was used to predict fat-free mass (FFM) according to the equation given by Nelson and Nielsen (1994). The equation used was:

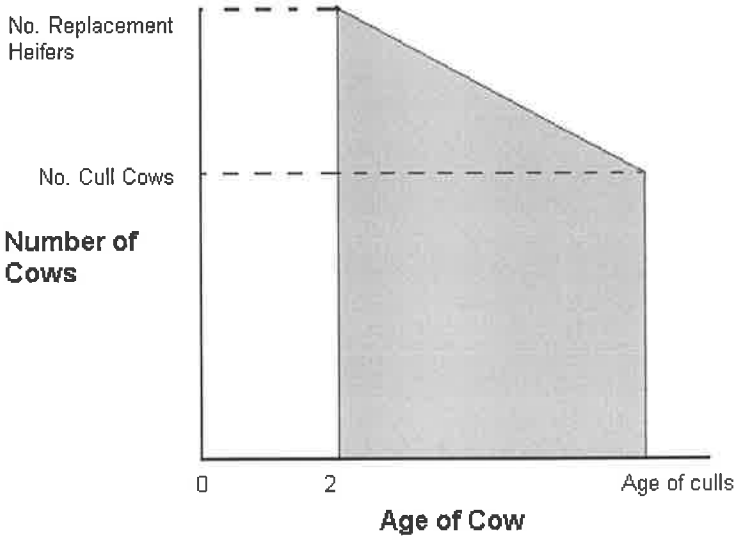
$$\mathrm{FFM} = -1.727 + 1.5640 \times \mathrm{EM}^{0.5} + 0.6247 \times \mathrm{BM}$$

Percentage body fat was calculated using the predicted fat-free mass and was used in the final analysis.

When mice were not required again, mice were humanely euthanised by asphyxiation using carbon dioxide before analysis of body composition. Where mice were still required (eg females and sires at the post-weaning test) they were anaesthetised using 0.3 ml of Avertin injected intra-peritoneally.

Appendix D. Derivation of equations describing herd age structure.

A similar herd age structure to that used by Ponzoni and Newman (1989) was assumed, where the number of cows dying in each age class is a constant. The herd age structure can be represented graphically, as shown below.



The number of different age classes is given by (Age-2) (see page 153 for explanation of abbreviations). The total number of deaths per year is given by the number of cows (N_{cows}) multiplied by the death rate (D). For the herd to maintain a constant size, the number of deaths per year must also be equal to the number of replacement heifers ($N_{R.H.}$) minus the number of cull cows sold (N_{culls}). This gives equation 1.

$$(1) \qquad N_{R.H.} - N_{Culls} = N_{Cows}.D$$

The total number of cows (N_{cows}) is equal to the shaded area under the line. An equation to describe this area can be developed.

$$(2) \qquad N_{Cows} = N_{Culls}.(Age-2) + \frac{1}{2}(N_{R.H.} - N_{Culls}).(Age-2)$$

Substituting in equation (1) we have:

$$(3) \qquad N_{Cows} = N_{Culls}.(Age-2) + \frac{1}{2}(N_{Cows}.D).(Age-2)$$

Solving for N_{culls}:

$$(4) \qquad N_{Culls} = N_{Cows}\left(\frac{2-D.(Age-2)}{2(Age-2)}\right)$$

To find an expression for $N_{R.H.}$ we substitute equation (4) into equation (1) and solve for $N_{R.H.}$:

$$\begin{aligned} N_{R.H.} &= N_{Cows}.D + N_{Culls} \\ &= N_{Cows}.D + N_{Cows}\left(\frac{2-D.(Age-2)}{2(Age-2)}\right) \\ &= N_{Cows}\left(\frac{2+D.(Age-2)}{2(Age-2)}\right) \end{aligned}$$

Assuming that equal numbers of male and female calves are born, the number of steers (N_{Steers}) is a function of the total number of cows (N_{Cows}) and the reproductive rate (R).

$$N_{Steers} = 0.5N_{Cows}.R$$

The number of surplus heifers ($N_{S.H.}$) is equal to the total number of heifers born minus the number of heifers kept as replacements ($N_{R.H.}$):

$$\begin{aligned} N_{S.H.} &= 0.5N_{Cows}.R - N_{Cows}\left(\frac{2+D.(Age-2)}{2(Age-2)}\right) \\ &= N_{Cows}\left(0.5R - \frac{2+D.(Age-2)}{2(Age-2)}\right) \end{aligned}$$

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