GENETIC RESPONSE TO SELECTION FOR RATE AND EFFICIENCY OF LEAN GAIN IN BEEF CATTLE

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Thesis presented for the degree of Doctor of Philosophy
in the Faculty of Science, University of Edinburgh
August, 1988

To God's glory

TABLE OF CONTENTS

DECLARATION

I declare that this thesis is my own composition and reports analysis of data done by me. The data were collected by members of staff of the AFRC Animal Breeding Research Organisation (now Institute of Animal Physiology and Genetics Research).

Abstract

A selection experiment with Hereford cattle to study the efficiency of lean production was established by the Animal Breeding Research Organisation (now Institute of Animal Physiology and Genetics Research). There were two replicated selection lines, one selected for lean growth rate (LGR) from birth to 400 days and the other for lean food conversion ratio (LFCR) from 200 to 400 days of age. Bulls were selected on their performance on a complete diet of dried grass and barley fed ad libitum for 7 years. A control line and an open line bred by frozen semen from foundation bulls and superior progeny tested Hereford bulls respectively were also maintained.

Responses in the selection lines were evaluated by 3 methods : deviation from control line, prediction of progeny breeding value and Restricted Maximum Likelihood (REML).

Generation interval was about 2.4 years in both selected lines. Cumulative selection differentials were 59g/day for LGR and -3.2kg feed/kg lean gain for LFCR in their respective lines. Average sire selection differential (primary) per generation were 1.3 and -1.4 standard deviation units for LGR and LFCR respectively. A high percentage of the maximum potential selection differential was achieved in both lines.

The estimates of direct annual genetic change using deviations from control were 5.0±1.6g/day for LGR and -0.13±0.08kg feed/kg lean gain for LFCR. Corresponding estimates from REML were similar but more precise. The correlated response for LFCR in the LGR line was higher than the direct response for LFCR. Significant correlated responses occurred in growth rate, food conversion ratio (FCR) in

the LGR line and in lean percent for both lines. Selection in both lines was not accompanied by adverse correlated responses in reproductive traits.

Realised heritabilities were 0.53±0.14 for LGR and 0.38±0.13 for LFCR using the control. Corresponding estimates from REML were 0.47±0.11 and 0.29±0.16. Genetic correlations between selected traits and other economic traits were estimated.

In a crossbred trial involving 5 bulls from the four lines mated at random to Holstein/Friesian cows, about 66% of the expected response from the purebred performance was observed in the crossbreds for LGR. A non-significant negative response was observed for LFCR, consistent with predictions from the purebred.

Relative to the initial differences between the open and control lines, significant genetic trends were observed in the open line for LGR, LFCR, FCR and growth rate although standard errors of estimates were high.

In conclusion, the observed response for LGR was consistent with the predicted theoretical possible rate of genetic change for growth traits in beef cattle. The importance of design and effective selection on rates of response achieved in practice was discussed. The use of alternative selection criteria to improve efficiency of lean production was examined.

ACKNOWLEDGEMENTS

I would like to thank Professors W.G. Hill, C. Smith and Mr. R. Thompson for supervising this project.

I am greatly indebted to Mr. Thompson for guiding and stimulating this research, and for the valuable skills which I learnt from him.

I am grateful to Professor Hill for his encouragement, invaluable discussions and general support.

Professor Smith initiated and supervised the research project. I appreciate the opportunity he gave to me to analyse the data and his help at the initial stages of the work.

I wish to express my gratitude to the late Professor R.B. Land, Station Head of the IAPGR (ERS), for allowing me access to the facilities of the Institute. My thanks also go to other members of staff of the Institute for their hospitality and assistance, particularly Dr. N. Cameron for his kindness and useful discussions, Dr. R. Findlay and Mr. D. Nicholson in computing matters.

Acknowledgements are also due to Mr. D.J. Drury, Mr. C. Coutts and other members of the Cold Norton Farm for managing the experimental animals and collecting the data.

I acknowledge with appreciation the financial support of the Commonwealth Scholarship Commission and British Council throughout the course of this study.

Mrs. R. Johnston patiently and expertly typed the thesis and her efforts are fully appreciated.

The encouragement and support from colleagues and friends have been very valuable. The families of Drs. S. Hutchison and D. Harrison have made my stay in Edinburgh pleasurable.

Finally I am deeply grateful to my parents and my brother for support and encouragement throughout the whole period of my study in Edinburgh.

CHAPTER I

INTRODUCTION

Selection constitutes one of the main methods utilised by breeders to change livestock populations; consequently traits of economic importance have been the main objectives in most selection experiments. In beef cattle, majority of selection experiments have centred on growth rate, the selection criteria commonly being weaning and yearling weight. This is due to the high association of growth rate with economy of gain (Irgang, Dillard, Tess and Robison, 1985a) and growth rate is also easy to measure. However, several workers have recently expressed doubt about improving bio-economic efficiency of beef cattle by increasing growth rate, especially in breeds that function as maternal breeds. This is because increased growth rate may be accompanied by increased mature body size, fatness and reduced fertility (Scholtz and Roux, 1984). These effects are important in beef cattle because of the low reproductive rate so that the costs of rearing and maintaining adult breeders are spread over few young (Dickerson, 1982).

Moreover, the most dominant trend in consumers' demand over the past few years has been for leaner meat (Bailey, 1986). This is due probably to the implication of the saturated fat in causing coronary heart diseases. Today's typical beef carcass contains about 22% of fat but the continued pressure for leanness implies that producers must aim for fat contents of about 18% (Fisher and Winstanley, 1986). Estimates of changes in carcass composition for cattle and pigs over the past decade in Britain showed a marked contrast between the fatness of pigs which has fallen dramatically and the fatness of cattle which has changed relatively very little (Kempster and Solly, 1988). A major reduction in fatness could be effected easily by restricted feeding or by earlier slaughtering at

lighter weights. However there is an optimum slaughter point for the current beef breed populations and production system at which the overall cost of producing and distributing lean meat to the point of consumption is minimised (Kempster and Solly, 1988). Therefore the above strategies may not be the best since reduction in fatness may be achieved at the expense of overall efficiency with which lean meat is produced. Jones and Kay (1986) mentioned that reduction in slaughter weight would lead to penalties due to loss of conformation and reduced economic return to the farmer.

Dickerson (1982) and Barlow (1984) have suggested that the greatest scope for improving efficiency in cattle (other than through reproduction) is using faster growing lean terminal sire breeds. This is particularly important in countries like Britain and Ireland where up to 35 to 45 percent of the dairy herd may be crossed with beef breed sires for the production of crossbred calves. Similarly, for the biological efficiency of production of lean tissue, Fowler, Bichard and Pease (1976) proposed the improvement of lean tissue food conversion as a selection objective in pig breeding. It was suggested that the most suitable means of achieving this way by increasing lean tissue growth rate.

Genetic improvement in beef cattle through selection is limited because of the high cost of keeping large herds, the long generation interval and by the problems of assessing carcass traits (such as leanness) in live animals. There are yet no experimental results on the effects of direct selection for lean content in beef cattle. However, positive responses for lean content have been observed in other species, in rats (Gosey, 1976; Notter, Dickerson and DeShazer, 1976) and in pigs (Ollivier, 1980). Webster (1976)

indicated that in animals fed ad libitum, protein deposition appears to have rigidly defined upper limits which are set by the intrinsic capacity of the individual for the synthesis of milk protein or lean body mass. These limits could only be modified by genetic selection or more directly by physiological interference. Improvement of the efficiency of lean meat production is therefore likely to be a long-time selection objective in beef cattle.

This thesis is concerned with the evaluation of response in two lines of Hereford cattle selected respectively for lean growth rate (LGR) and lean food conversion ratio (LFCR) from the base year of 1978-79 to 1986. In 1977, a 200-cow pedigree Hereford was established by the then Animal Breeding Research Organisation now Institute of Animal Physiology and Genetics Research to provide information on selection for efficiency of lean meat production. Two selection lines were available, one selected for LGR from birth to 400 days and the other for LFCR from 200 to 400 days of age. Bulls were selected on their own performance on a pelleted dried grass and barley diet, fed ad libitum. In addition, there was a control and an open line bred by frozen semen from foundation bulls and superior Hereford bulls in artificial insemination centres respectively.

Initially, selection experiments in beef cattle are reviewed with respect to design, analysis and responses achieved. This is followed by a description of the expeirmental materials, selection criteria and procedure. The analytical part of the thesis consists of six chapters:

1. measurement of selection pressure applied.

2. direct and correlated responses for lean growth rate and lean food conversion ratio in the selected and open lines
3. evaluation of correlated responses and genetic parameters for secondary traits measured in recorded bulls
4. correlated responses in body weight and measurements at various ages in all calves and reproductive performance in female calves
5. evaluation of direct and correlated responses to selection for LGR and LFCR in crossbred progeny sired by bulls from selected and control lines and
5. an alternative algorithm for incorporating the relationship matrix into Mixed Model equations for estimation for (co)variance components using Restricted Maximum Likelihood (REML). Finally a general discussion of the results is presented with the efficacy of selection for LGR and LFCR in improving lean meat production examined.

CHAPTER 2

SELECTION EXPERIMENTS IN BEEF CATTLE. A REVIEW OF DESIGN, ANALYSIS AND RESPONSES

2.1 Introduction

Compared with laboratory species, relatively few cattle selection experiments have been undertaken due to the high costs and the long generation interval. Most early studies were prompted by the effectiveness of selection experiments in laboratory animals and other larger species, such as the pig, which checked the theoretical predictions of artificial selection. Many early selection experiments in beef cattle were limited to measuring phenotypic time trends which could not be partitioned into the respective genetic and environmental components owing to lack of controls or proper design, and so had limitations. This is why Barlow (1978) observed that "the omission of control populations from most of the available experiments and the tendency towards multi-trait selection has resulted in genetic trends and realised paramters having to be recovered from the data, using varying techniques to measure environmental trends".

Most reviews on selection experiments in beef cattle were concerned mainly with growth rate or weight for age (Barlow, 1978; Koch, Gregory and Cundiff, 1982; and Baker and Morris, 1984) and were therefore limited in scope. The review of Barlow (1978) was restricted to preweaning growth rate while Koch *et al*. (1982) mainly summarised the results of North American selection experiments on growth rate.

In this review selection experiments in beef cattle are examined in the light of current principles of design with a view of assessing their value, and in highlighting the developments that have occurred in the design of beef selection experiments over the years.

Secondly, the results of selection experiments on growth

rate and other traits are briefly summarised.

2.2 The design and analysis of beef selection experiment

2.2.1 Population size

In a review of selection experiments in beef cattle, Dalton and Baker (1979) concluded that one of the major limitations associated with all early work on cattle prior to the 1970 was small population size. For example, Hoornbeek and Bogart (1966) selected in an Angus line consisting of about two sires and 20 females and three Hereford lines each consisting of one sire and 15 females on the basis of an index for preweaning gain, feed test gain, feed per unit of gain and conformation scores. Although selection differentials were positive, phenotypic trends were negative for all traits except score in the Hereford lines, but positive for all traits in the Angus line. The genetic trends were not estimated. In another case, Nelms and Stratton (1967) carried out selection for unadjusted weight at the end of a 268 day feed test in a small line of about 30 Hereford cows with response evaluated on 302 calves born during the selection period of 12 years. The design of the experiment did not permit the estimation of genetic trend. Similarly, Chevraux and Bailey (1977) carried out selection in a line of Hereford cattle consisting of one or two sires and about 25 to 30 cows for post weaning growth rate from 1956 to 1977 and phenotypic response was evaluated on 390 calves born during the selection period of 19 years.

Population size is important in artificial selection in two respects. Firstly, from the work of Robertson (1960), selection in small populations increases the chance of loss of desirable alleles

and hence leads to a lower limit to selection. Secondly, in small populations, genetic drift is an important source of variation among selected lines, producing not only variation in mean responses (Hill, 1971) but also variation in within line additive genetic variance (Bulmer, 1976 and Avery and Hill 1977). Thus estimates of parameters from these early experiments with small sizes should have large standard errors. However, most of the reports did not give standard errors for the parameter estimates.

Hill (1980) showed how the variance of response can be reduced by increasing the total size of the selection experiment. Using the expression for expected drift variance, Nicholas (1980) estimated the minimum size required to obtain a specified coefficient of variation of response to achieve a specified proportion of the expected response to selection. Recent selection experiments in beef cattle have been done with larger population size. For instance, Koch, Gregory and Cundiff (1974a) selected for weaning weight, yearling weight and an index consisting of yearling weight and muscle score in 3 lines each consisting of 150 cows and 6 sires. Similarly, Pacer, Razook, Trovo, Bonilha, Figueiredo, Nascimento, Pacola, Candido, Campos and Machado (1986) reported response for yearling weight in 2 lines of Nelore and Guzera cattle each consisting of 120 cows and 6 sires.

2.2.2 Levels of inbreeding

Closely associated with the problem of small population size in early experiments was that of high levels of inbreeding. Many of these trials were concerned with the effectiveness of selection in lines which were already inbred (Armstrong, Stonaker, Sutherland and

Riddle, 1965; Hoornbeek and Bogart, 1966; Nwakolor, Brinks, Richardson, 1976) but in some cases selection and inbreeding occurred concurrently (Brinks, Clark and Kieffer, 1965; Nelms and Stratton, 1967). In the inbred line, the average inbreeding coefficient ranged from 19% (Hoornbeek and Bogart, 1966) to 33% (Armstrong et al., 1965 and Nwakalor et al. 1976). Working with populations which were not initially inbred, Brinks et al. (1965) and Nelms and Stratton (1967) reported average inbreeding coefficients of 12 and 5% respectively for dams and 16 and 11% respectively for calves.

The expected response from selection is likely to be reduced by inbreeding as a result of a proportionate decline in the additive genetic variance of the traits. In addition traits associated with fitness may be directly depressed by moderate levels of inbreeding.

Hill (1980) discussed ways of eliminating effects of inbreeding. Firstly, the use of lines with large population size in short duration experiments; secondly, the maintenance of a genetic control population with the same increment of inbreeding as the selected populations; thirdly, the maintenance of replicate lines which are crossed at the end of the experiment to estimate response, and fourthly, minimising inbreeding by maximum avoidance of mating between closely related individuals.

In recent selection experiments in beef cattle the level of inbreeding has been effectively lowered by better design and increased population size. For example, the average inbreeding coefficients reported by Buchanan, Nielsen, Koch and Cundiff (1982a) and Irgang et al. (1985a) were 0.03 and 2.0 percent respectively for dams and 0.05 and 3.5 percent for calves in the lines selected for weaning weight.

2.2.3 Genetic change and realised heritabilities

Generally, selection experiments are concerned with the estimation of selection response (genetic change), realised heritability and their precision. The estimates of response should be unbiased by environmental fluctuations. Techniques used for evaluating genetic trends in beef cattle include maintaining a random bred control population, repeat mating schemes, intra-year comparison of sire or dam birth-year progeny groups that differ in generations of selection or in birth year and semen storage with subsequent evaluation on a common tested herd (Smith, 1962; Dickerson, 1969; Koch et al., 1982). Few divergent (high and low) selection experiments have been carried out in beef cattle (Seifert, 1975a,b; Barlow, 1980). Estimates of genetic change can be achieved by contemporary comparison of such two divergent selection lines. Mixed model methodology (Henderson, 1973) as a means separating genetic trends from environmental trends has also been attempted by Sharma, Wilms, Hardin and Berg (1985).

Most early beef selection experiments relied on repeat matings for the estimation of genetic change (Hoornbeek and Bogart, 1966; Armstrong et al. 1965; Benson, Brinks, Knapp and Panhish 1972; Nwakalor, et al. 1976). In some cases these repeat matings were not planned but were found and used in an attempt to separate the genetic and environment changes (Flower, Brinks, Urick and Willson, 1964; Brinks et al. 1965). Consequently, the number of repeat matings were small and it was not possible to estimate genetic change for some years or traits due to inadequate number of repeat matings. Response was taken as zero in those years with no repeat matings, it is therefore likely that these estimates of genetic

change were biased. Also the sampling errors from the small number of repeat matings should be large. Hill (1972a) discussed the use of repeat matings in the estimation of genetic change. The possible sources of sampling error are drift variance, error of measurement and genotype by environment interaction. If a repeat mating design is established in the population, the drift variance can be eliminated and the interaction variance is minimised, but there is a substantial contribution of the measurement error variance to the sampling error. The method has the particular advantage that few or no facilities are devoted to estimating the change. However, to some extent, some loss of genetic response will be associated with structuring the herd to permit repeat mating comparisons.

Bailey, Harvey, Hunter and Torrell (1971) and Chevraux and Bailey (1977) evaluated performance of progeny from different dam birth-year groups in estimating genetic change. Koch et al. (1982) found that estimates of genetic change from intra-year comparison of sire or dam birth year progeny groups are subject to large random errors because the number per group and the spans of generation or birth year are usually small. Also where comparison involves dams differing in age, genetic change is confounded with age of dam effects and the validity of the differences is highly dependent on accurate estimates of age of dam correction factors. The data of Chevraux and Bailey (1977) were associated with limited number of records in the younger dam age subclass and small variation in generation coefficients within years.

Stanforth and Frahm (1975) used semen from foundation and advanced generation sires on a common tester to estimate genetic trend. The use of semen storage for the estimation of response could

be very efficient since there is no accumulation of drift variance in the control. However, only the additive component of change is estimated without bias (Hill, 1972a).

The first beef selection experiment to feature a control line was that of Newman, Rahnefeld, and Fredeen (1973) in Canada on Shorthorn cattle. Their data demonstrated the usefulness of controls or other comparable methods of correcting for environment changes; without the control the effectiveness of selection would have been overestimated since more than half of the increase obtained in yearling weight (about 60%) resulted from environmental changes. More recently, Barlow (1980), Frahm, Nichols and Buchanan (1985a) and Irgang et al. (1985a) also used control populations in their experiments. In the case of Frahm et al. (1985a), the original design did not include an unselected control line. An Angus line which had previously undergone one generation of selection for yearling weight was used to start the control line. The adequacy of this Angus population as a control line for the selected Hereford lines rested on the absence of breed by environment interactions. Frahm et al. (1985a) indicated that analysis of data from early years of the study before selection showed that breed by year interactions were generally non significant on the traits measured.

In experiments with control populations, response is measured as a deviation of the selected line from the control. The variance of response is the sum of the variances of the means of both selected and control lines, and the control might be set up to minimise its variance. This variance involves both variation of the selection differential (about zero) and the drift variance. By ensuring a selection differential of zero or nearly zero, the drift

variance can be reduced. Hill (1972a) showed how to construct a control such that the selection differentials are zero and the drift variance reduced. It essentially involves choosing breeding individuals such that their mean performance for some particular trait is close to the mean performance of all recorded individuals in that generation. In some of the selection experiments, some unintentional selection had been reported in the control lines (Newman et al., 1973; Irgang et al., 1985a). Frahm et al. (1985a) observed slight increases in their control line which was attributed to a small amount of selection that occurred during the early years in the population before conversion to a control line. Such directional change through natural or unintentional selection in the control would increase the variance of response (Hill, 1972a).

A well designed control population in beef cattle selection is that used by Irgang et al. (1985a). Attempts were made to minimise genetic change from selection and genetic drift by random selection of replacement bulls within sire families and maintenance of low inbreeding levels by mating least-related individuals (see Hill, 1980).

If several selection lines and a control have been maintained contemporaneously, these animals could be used in the analysis of any trait, explaining the response or correlated response in terms of cumulative selection differentials, genetic regressions and environmental effects. This could lead to more precise environmental estimates and hence of estimates of response than just when each selected line is compared with the control. The above methodology is essentially the multiple regression procedure of Richardson, Kojima and Lucas (1968), which has been widely used in

evaluating selection experiments in species with discrete generations (Leymaster, Swiger and Harvey, 1979; Quijandra, Zaldivar and Robinson, 1983). Recently the technique has been used in estimating response in beef cattle by Frahm et al. (1985b) and Irgang et al. (1985b) and they indicated that it resulted in a more precise estimate of response compared with estimates from deviation of selected lines from the control. This was attributed to the fact that the method uses all available information to estimate simultaneously environmental effects and selection responses. In addition correlations between genetic responses in selected lines due to substraction of a common control are avoided (Irgang et al., 1985b). The procedure assumes, however, that the error variance structure in each generation is independent but this is not so. Selection experiments are stochastic processes and performance in a given generation is dependent on the genetic samples retained in previous generations (see Hill, 1972b).

More recently the use of mixed model methodology (Henderson, 1973) for the separation of genetic and environmental trends has been used in the analysis of selection experiments. Sharma et al. (1985) estimated genetic trends in a beef synthetic and a Hereford control line using the mixed model method. The method yielded estimates of sampling variances which were smaller than those from repeat matings or control population analysis.

The use of mixed model analysis as a means of separating genetic trends from environmental trends was first suggested by Henderson, Kempthorne, Searle and Van Krosigk (1959) in dairy cattle subject to culling. Blair and Pollak (1984) used this technique to evaluate response using an assumed estimate of heritability to

predict genetic worth. The estimate of realised heritability was obtained by the regression of predicted yearly genetic means on cumulative selection differential. However Thompson (1986) has shown that the predicted yearly genetic means depends on the assumed value of heritability and not on the value of heritability in the population; in one example the estimated heritability was approximately three-quarters the assumed value. Hence the regression estimate is not an unbiased estimate of the population heritability. Utilising a different approach, Sorensen and Kennedy (1984) have shown that mixed model analysis could be used to estimate genetic trends even after several cycles of selection if certain conditions are met:

(1) the genetic and non-genetic variances, or their ratios, of the trait before selection are known
(2) selection is a linear function of the records and
(3) the relationship matrix (A), is complete, that is, all animals involved in the selection decision regardless of whether they contribute offspring are used to derive A.

The use of A allows relationships between individuals to be used and increases the accuracy of predictions of breeding values. The relationship matrix also circumvents the possible problems resulting from the reduction of genetic variance generated by gametic disequilibrium that builds up as a consequence of selection (Sorensen and Kennedy, 1984).

2.2.4 Precision of estimates of response

The precision of estimated response to selection is a function of the design of the selection experiment. Hill (1980) has reviewed the appropriate features for the design of selection experiments.

In most published early experiments in beef cattle, estimates of genetic changes and realised heritabilities were given without standard errors (Flower et al., 1954; Brinks et al., 1965; Koch et al., 1974b). So the reliability of their estimates of response and the value of such experiments are greatly reduced. However, Newman et al. (1973) estimated variance of genetic response from the variance of the weighted regression of cumulative response on cumulative selection. Chevraux and Bailey (1977) estimated response by linear regression of trait on dam birth year group and the variance of the regression coefficient (also variance of response) was estimated by maximum likelihood. Frahm et al. (1985b) estimated variance of response from the variance of the regression of cumulated response on cumulative selection differential. Hill (1972b) has shown that the variance of the simple regression of cumulative response on cumulative selection differential is biased downwards because observations are assumed to have equal variance and to be uncorrelated, when in reality the variance of the population mean increased due to genetic drift as selection effects accumulate. Recently Atkins (1985) confirmed these observations from the analysis of a sheep selection experiment. Most analysis of selection experiments have neglected this component of the sampling variance. Irgang et al. (1985b) however reported standard errors of realised heritabilities for weaning weight and postweaning gain which included

the drift variance. Hill (1972b) and Sorensen and Kennedy (1983) have given formulae for estimating the drift variance.

However, Johnson (1977) has indicated that the usual expression for drift variance is only asymptotically true for overlapping generations. He has developed a more exact formula for this drift variance and shown the true drift in the early years of an experiment to be much larger than the apparent drift from the approximate formula. Using the approach of Johnson (1977) and Hill (1972b) to estimate drift variance, Atkins (1985) found that the inclusion of the more appropriate formula of Johnson (1977) for overlapping generations had only a small influence on the variance of the regression in his experiment with five generations of selection.

2.2.5 Replication

Only few beef cattle selection experiments have included replication in their design (Newman et al., 1973; Irgang et al., 1985b). Actually, the latter workers did not include replication in their initial plan but because selection was practised only in bulls and sire families were confounded with years and repeated every third year, the data were grouped into three replicates within each line to evaluate empirical variation in selection response. The variance among replicates represents the sum of genetic drift and random error. Except in the case of weaning weight for bull calves, the variance of response from the variance among replicates tended to be smaller than the variance from estimates of genetic drift and random error measurement obtained by approximate formulae.

The theoretical variance of response to selection represents variance between conceptual replicated lines. Thus, the obvious

advantage of replication is that variance among lines can be estimated directly and independently of parameter estimates from the experiment (Hill, 1980). Unreplicated selection experiments are therefore confronted with a problem, in that they do not provide an estimate of the true variance of response. Although it is possible to estimate the variance of response using formulae of Hill (1980) it is only approximate and apply to populations with discrete generations. Moreover, while an estimate of drift variance can be made for directly selected traits the drift variance of correlated traits cannot be estimated in this way (Hill, 1980). Thus the need for adequate replication is emphasised in selection experiments in species with overlapping generations.

However, the problem with the variance from replicates is that it requires a high degree of replication before it can be reliable. For instance, with r replicates, this variance will be estimated with r-1 degree of freedom, that is 1 or 2 df for r = 2 or 3 respectively. Such an estimate of between line variance while unbiased, is not reliable. With limited facilities in beef cattle, a very high degree of replication may not be possible for as individual lines rapidly become inbred. The best compromise as Hill (1980) suggested may be is to compute the total size of the experiment on the basis of the ratio of coefficient of variation of response of the mean of the replicates and then divide these facilities into as many replicates as inbreeding and practical considerations allow. Moreover, Muir (1986) has shown a precise method for estimating the variance about response even with limited replication. The method is based on a Satterwaite approximate which combines variance components estimated more precisely by other

sources of variation in the analysis of variance. Using variance components estimated by this procedure, Muir (1986) markedly improved the precision of the estimates of realised heritability.

2.3 Results of beef selection experiment

The primary aim of the beef industry is the efficient production of meat. This is greatly dependent on traits related to growth. Emphasis on growth has narrowed the experience of selection in beef cattle compared with other species of farm livestock. Most selection experiments were directly concerned with improvement of growth rate and share similar features. A review of these experiments is given and a summary is presented in Table 2.1. Subsequently, experiments with alternative selection criteria or objectives are examined.

2.3.1 Selection experiments on growth traits

In order to have an understanding of what has been achieved, the experiments are discussed in several subsections:

(i) Generations of selection and generation interval

The generations of selection are usually determined by the formula of Brinks, Clark and Rice (1961):

$$GC = (GC_s + GC_d)/2 + 1$$

where GC is the generation coefficient of the calf and GC_s and GC_d are generation coefficients of the sire and dam respectively. Foundation animals are assigned a GC of zero. The GC of an animal

after selection is the average number of Mendelian segregations in its pedigree and measures one more than the number of generations of selection. The number of generations of selection for published beef cattle experiments is given in Table 2.1. The average over all experiments is 2.89 generations, with a range of 1.8 (Koch et al., 1974a; Irgang et al., 1985a) to 3.87 (Aaron, Frahm and Buchanan, 1986a). The range of generation coefficients among calves within a year or line is about 1.7 generations (Koch et al., 1974a; Chevraux and Bailey, 1977; Frahm et al., 1985a). In short-term selection, response should be proportional to the generations of selection assuming linearity of response.

Generation interval is the average age of the parents at the birth of their selected offspring. The generation intervals in the selection experiments reviewed are shown in Table 2.1. The overall average was 4.36 years. The average age for sires ranges from 2 years (Baker, Carter and Hunter, 1980) to 4.3 years (Koch et al., 1982) and the average for dams from 4.0 to 6.6 years (Bailey et al., 1971; Baker et al., 1980). Most of these results were from natural mating herds and selection was on the basis of individual performance. The generation interval reported by Aaron et al. (1986a) when selection was based on combined individual and progeny performance in weaning weight was 5.6 years compared to 4.1 years obtained in a similar line selected for the same trait using individual performance alone.

Koch et al. (1982) concluded that reducing average sire age from 3 to 2 years will improve annual selection differentials only marginally because of compensatory loss of selection intensity. However preliminary results of the experiment of Baker et al. (1980)

TABLE 2.1

Summary of results from selection experiments on growth traits

Author(s)	Period	N	GI	GS	% F Calf	% F Dam	Selection Criteria	Selection Differential** Mid-parent	% realised through Sires	% realised through Dams	% of potential maximum Sires	% of potential maximum Dams	Annual Genetic change*** Rate	Annual Genetic change*** % of mean	h^2_R	Method for estimating genetic change
Flower et. al. (1964)	1954-59	392	4		18		WW + PG	0.15 0.25	81 100	18			2.1	1.14	0.77	Repeat matings
Brinks et. al. (1965)	1934-59	1594	4.9		16	12	WW + WS + PG	0.13 0.10 0.22	85 80 100	15 20			0.6 0.1	0.29 0.18	0.23* 0.15*	Repeat matings
Nelms and Stratton (1967)	12 years	302	4.3		11	5	YW	0.19								
Bailey et. al. (1971)	1955-69	1488	4.7				PG PG FE FE YS	0.22 0.13 0.17 0.20 0.20					1.5 2.2 0.2 0.2 -0.1	1.64 2.40 0.17 0.17 -0.11	0.57 1.00 0.60 0.44 0	Regression on dam's birth year
Chapman et. al. (1972)	1963-69	765	4.3				PG WW YS	0.29 0.22 -	83 85 -	17 15 -					0.84 0.33 0.22	Deviation from herd of average performance
Newman et. al. (1973)	1960-69	3577	3.2				YW	0.33	69	31			3.1	0.77	0.45	Control population
Gaskins (1974)	1947-69	1135	-				WW + WS + W/A						0.7 -0.0 0.0			Regression on dam birth year

TABLE 2.1 (continued)

Summary of results from selection experiments on growth traits

Author(s)	Period	N	GI	GS	% F Calf	% F Dam	Selection Criteria	Selection Differential** Mid-parent	% realised through Sires	% realised through Dams	% of potential maximum Sires	% of potential maximum Dams	Annual Genetic change*** Rate	Annual Genetic change*** % of mean	h^2_R	Method for estimating genetic change
Koch et. al. (1974 a,b)	1960-70	2956		20 18 19			WW YW YW+MS	0.19 0.21 0.18	79 88 84	21 12 16	77 94 97	52 50 71	1.1 3.1 2.3	0.53 0.74 -	0.27* 0.28*	Various regression methods
Nwakolar et. al. (1976)	1946-71	3408			33	21	WW + FE+PG + YG						1.9[c]			Repeat matings
Chevraux & Bailey (1977)	1955-74	390	4.7	3.2			PG	0.22	83	17	92	60	4.3	3.65	0.35	Regression on dam birth year and generation coefficient
Martin & Alenda (1982)	21 years	2576	4.0				YW						4.1			Modified procedure of Smith (1962)
Buchanan et. al. (1982)	1963-77	2125 2098 2135	4.3 4.4 4.4	 3.7	0.0	0.0	WW YW YW+MS	0.23 0.24 0.21	79 84 81	21 16 19	86 95 93	66 62 74				
Frahm et. al. (1985a, b)	1964-78	627 605	4.7 4.7	3.2 3.2			WW YW	0.21 0.23	70 76	30 24	88 100	70 67	1.0 1.0	0.55 0.32	0.24 0.18	Control populations and multiple regression
Irgang et. al. (1985a b)	1970-81	2467	3.8 3.9	2.00 1.9	4	2	WW PG	0.19 0.14			82 89		0.8 0.5	0.51 0.43	0.25 0.18	Control population and multiple regression

TABLE 2.1 (continued)

Summary of results from selection experiments on growth traits

Author(s)	Period	N	GI	GS	%F Calf	%F Dam	Selection Criteria	Selection Differential** Mid-parent	% realised through Sires	% realised through Dams	% of potential maximum Sires	% of potential maximum Dams	Annual Genetic change*** Rate	Annual Genetic change*** % of mean	h^2_R	Method for estimating genetic change
Nicoll & Johnson (1986)	1976-85	458	3.8	2.1			YI	0.28			86					
Aaron et. al. (1986a, b)	1964-79	2249	4.1 5.6 4.7	3.9 2.7 3.7			WW IWW YW	0.23 0.21	67 76	33 24	94 100	81 64	1.5 2.1 3.5	0.72 1.04 1.06	0.30 0.35	Same method as used by Frahm et. al. (1985)
Nwakolar et. al. (1986)	1946-73	4833	4.1	5.5	36	26	WW + PG + FE + YG	0.33 0.69[m] 0.10[m]	77	23			0.6[C] 0.0[I]			Regression of offspring deviations on generation number
Pacer et. al. (1986)	1980-84		4.8				YW YW	0.24 0.15	75 78	25 22			3.2 1.8	1.17 0.69	0.22*	Control population

N = Number of calves
I = Inbred line calves
m = Males only
C = Corrected for inbreeding effects
GS = Generations of selection
G.I = General Interval
%F = Percentage average inbreeding coefficient
IWW = Weaning weight (selection on the basis of individual and progeny performance
FE = Feed efficiency - kg gain/100 kg TDN (Bailey et al., 1971) units (Nwakalor et al., 1986a,b)

WS = Weaning score
W/A = Weight per day of age
MS = Musle score
YS = Yearling score
YG = Yearly grade
YI = Yearling index composed of adjusted weaning and yearling weight, cow fertility and maternal weaning weight
* = Values were estimated
** = Selection differential in standard units per year
*** = Genetic change in kg/year for growth traits

showed that mating of bulls selected on the basis of yearling weight (average age of sire 2 years) doubled with the rate of response compared to a scheme whereby bulls were selected on 18 months weight (average age of sire 3 years) with the same selection pressure applied. They did not indicate what proportion of the difference in response could be attributable to reduction of generation interval or to the difference in genetic variance between yearling and 18 months weights. Koch et al. (1982) mention that the average age of dams could be significantly reduced by use of multiple ovulation and embryo transfer.

(ii) Selection differential

Mid-parent selection differentials, converted to standard deviation units and expressed on an annual basis to allow comparisons of selection intensities for different traits and between experiments, are given in Table 2.1. In most experiments about 0.20 standard deviation of selection per year had been reported for single trait selection on the basis of individual performance, about 2 percent of the mean for traits with a coefficient of variation of 10%. Sire selection accounted for about 70-85% of the total selection intensity achieved (Chevraux and Bailey, 1977; Buchanan et al., 1982a; Frahm et al., 1985a; Aaron et al., 1986a).

The comparison of actual and maximum potential selection differential provides an evaluation of the effectiveness of selection that actually occurred relative to the maximum potential, that is, if the highest ranking individuals were used as replacements. In 23 experiments studied about 80% of the maximum selection differential for sires and dams was achieved. This was about 90 to 100 percent

in sires and 50 to 74 percent in dams. Inability to achieve the maximum possible selection differential has been attributed to unsoundness, colour markings, death before production of any offspring and failure of heifer to conceive.

Some of the effects of natural selection on artificial selection can be assessed by the ratio of the actual selection differential in parents leaving progeny to that expected from individuals chosen for breeding (Falconer, 1981). Irgang et al. (1985a) selecting for weaning and post weaning gain, did not observe any effects of natural selection.

Selection for growth at one stage of life either in a form of single trait or index is usually accompanied by positive secondary selection differentials for growth at other stage of life (Table 2.2). From the reports of Koch et al. (1974a), Buchanan et al. (1982a), Frahm et al. (1985a) and Aaron et al. (1986a) the secondary selection differential obtained for weaning weight in lines selected for yearling weight was about 76% of the selection differential obtained by direct selection for weaning weight. On the other hand, the secondary selection differential for yearling weight in line selected for weaning weight was about 80% of the selection differential for yearling weight from direct selection. These figures could be attributed to the strong genetic correlation between weaning and yearling weights. Frahm et al. (1985b) reported a realised genetic correlation of 0.69 between weaning and yearling weights. The secondary selection differential obtained by Irgang et al. (1985a) for post weaning weight in the post weaning gain line was only 37 percent of the selection differential for weaning weight by direct selection. The realised genetic correlation for weaning and

post weaning gain was 0.63±0.16. The secondary annual selection differentials for birth weight resulting from selection on either weaning or yearling weights were of about the same magnitude (0.10 standard deviation). Selecting on the basis of a yearling index composed of adjusted weaning and yearling weight, cow fertility, and maternal weaning weight, Nicoll and Johnson (1986) reported that secondary selection differential accumulated at the annual rate of 0.17 and 0.25 standard deviation per year respectively for cow fertility and cow maternal weaning weight; which they claim to be probably the first estimates for these two traits in beef cattle.

(iii) Genetic Change and Realised Heritability

A summary of the various techniques used to evaluate genetic trends in beef cattle is given in section 2.2. Here, the various methods used by different workers and estimates of realised heritability (h^2_R) obtained are presented in Table 2.1.

Koch et al. (1982), from a review of selection experiments in beef cattle, concluded that the unweighted averages for h^2_R were in agreement with heritability (h^2) estimates from paternal half-sibs or offspring-sire regression. The average values of h^2_R they presented, and those from the summary of literature values reported by Woldehawariat, Talamantes, Petty and Cartwright (1977) were respectively: birth weight 0.46 and 0.45, weaning weight 0.21 and 0.26, postweaning gain 0.36 and 0.34, final weight 0.36 and 0.46 and gain efficiency 0.23 and 0.38. Most subsequent reports in the literature have been in agreement with these values. Frahm et al. (1985b) and Aaron et al. (1986b) respectively obtained pooled h^2_R estimates of 0.24±0.04 and 0.30±0.03 for weaning weight and 0.14±0.05

and 0.34±0.03 for yearling weight. Irgang et al. (1985b) found a h^2_R of 0.25±0.11 and 0.18±0.09 for weaning weight and post weaning gain respectively by deviation from a control group. They however obtained a very low estimate of 0.05±0.05 for weaning weight using multiple regression procedures.

The average rate of genetic change computed from reports in the literature (see Table 2.1) were 2.65, 1.15 and 2.21kg per year respectively for yearling weight, weaning weight and postweaning gain. The estimates were obtained from 9, 10 and 3 experiments respectively, where the traits were either selected on their own or in an index. Bailey et al. (1971) reported a rate of 0.17kg gain/100kg total digestible energy (TDN) per year for efficiency of gain. Following the example of Smith (1984) the annual genetic changes achieved by various workers were expressed as a percentage of the mean performance (Table 2.1). The average rate of genetic change averaged 0.63, 0.80 and 2.03% per year for weaning weight, yearling weight and postweaning gain respectively. Smith (1984) has indicated that the possible rate of genetic change in growth rate expressed as a percentage of the mean is 1.4% per year. Thus the achieved responses are somewhat lower than the possible responses in weaning and yearling weight, but higher for postweaning gain. The rates of genetic change from selection experiments are higher than those that have been realised in industry (see Smith, 1984).

(iv) Correlated responses

There is a positive correlation between growth at one stage of life and growth or body size at other stages. The estimates of genetic correlation among birth weight (BW), preweaning gain (WG) and

TABLE 2.2.

Summary of correlated responses to selection on growth traits in beef cattle

Author(s)	Selection criteria	Secondary selection differential*								Correlated responses**									Realised genetic correlations	
		BW	WW	WG	PG	YW	MS	FE	YS	BW	WW	WG	PG	YW	MS	FE	YS	FAT		
Flower et. al. (1969)	WW+PG	0.09				0.13				0.44										
Brinks et. al. (1965)	WW+WS+PG	0.08				0.16				0.18						0.20	-0.13			
Bailey et. al. (1971)	PG							0.20	0.03							0.42			PG,FE	0.98*
	PG							0.09									0.05		PG,YS	-1.08*
	FE				0.14				0.04				1.12							
	FE				0.17								0.92							
	YS				0.05			0.04					1.23	0.11						
Frahm and Lalande (1974)	PG									0.05	0.48									
Anderson et. al. (1974)	YW									0.03	0.71									
Koch et. al. (1974)	WW	0.08		0.19	0.09	0.18	0.04			0.18		4.30	4.76	2.61	0.02				WW,YW	0.34*
	YW	0.08	0.14	0.13	0.18		0.10			0.22	0.77	2.76	7.82		0.01					
	YW+MS	0.08	0.11	0.10	0.15					0.22	0.68	2.54	7.48							
Chevraux and Bailey (1977)	PG			0.06							3.47									

TABLE 2.2. (continued)

Summary of correlated responses to selection on growth traits in beef cattle

Author(s)	Selection criteria	Secondary selection differential*								Correlated responses**									Realised genetic correlations	
		BW	WW	WG	PG	YW.	MS	FE	YS	BW	WW	WG	PG	YW	MS	FE	YS	FAT		
Martin and Alenda (1982)	YW										0.14		14.0							
Buchanan et. al. (1982)	WW	0.13		0.22	0.08	0.20	0.15													
	YW	0.11	0.17	0.16	0.20		0.10													
	YW+MS	0.12	0.17	0.15	0.18															
Frahm et al. (1985)	WW	0.09		0.20	0.06	0.17				0.27		3.83	-1.6	1.51	0.55				WW,YW	0.69
	YW	0.11	0.85	0.17	0.17					0.24	0.91	3.38	0.80							
Irgang et. al. (1985)	WW									-0.0		3.52		0.97	0.23			0.17	WW,PG	0.63
	PG									0.10		5.60		1.97	0.02			0.16		
Aaron et. al. (1986)	WW	0.10		0.23	0.03	0.16				0.24		5.91	4.43	2.10					WW,YW	0.79
	IWW	-	-	-	-	-						8.71	9.70	3.50						
	YW	0.10	0.16	0.15	0.18					0.45	1.52	5.21	12.34							

* = Secondary selection differentials in standard units per year

** = Correlated responses in kg/year for BW, WW, YW, grams per day per year for WG, PG mm per year for fat, feed/gain/year for FE (Irgang et al., 1986c) and kg gain/100kg TDN (Bailey et al., 1971)

*** = Realised genetic correlations estimated from data

See Table 2.1 for explanation of symbols for traits

postweaning gain (PG) reported by Koch et al. (1982) from the literature were BW and WG, 0.34 to 0.36, BW and PG, 0.34 to 0.51, WG and PG, 0.16 to 0.22. Brinks et al. (1965) reported genetic correlations of 0.65, 0.55 and 0.79 between mature weight and weight at birth, weaning weight and 18 month weight. Thus selection for body weight at any age usually results in correlated responses in body weight at all other ages. A summary of correlated responses resulting from selection on growth rate is presented in Table 2.2 and is discussed below.

a) Birth weight, calving difficulty and calf mortality

One of the major criticisms of selection for growth rate is the associated problem of increased birth weight and in some cases an increased incidence of calving problems and calf mortality (Barlow, 1978). It seems however that much criticism, especially concerning calving difficulty and calf mortality, has been based on reviews of correlations between growth rate and incidence of dystocia and not on empirical evidence from selection experiments. With the exceptions of Frisch (1981) and Bailey and Lawson (1986), positive correlated responses were reported by most other workers for BW. The average rates of correlated response in BW from single trait selection experiments for weaning weight and yearling weight respectively were 0.17 and 0.21 (about 0.38 and 0.47% of the mean resectively). Thus the correlated response for BW resulting from direct selection for yearling weight is slightly higher than from selecting for weaning weight. Buchanan et al. (1982b) reported genetic correlations of 0.56 and 0.63 between BW and weaning weight and yearling weight.

In a trial to evaluate the effect of selection for growth

rate on calving difficulty and calf mortality, Koch et al. (1982) found that birth weights, calving difficulty and calf mortality increased significantly in offspring of 2-year old heifers in a line of Hereford selected for growth rate. In older cows, there was little difference in calving difficulty (Baker and Morris, 1984). However in the divergent lines of Angus cattle selected for growth rate in the Trangie Agricultural Research Station, Australia, there had not been any adverse effects on fertility or any calving problems in either heifers or cows in spite of 20 percent different in growth rate between the high and low lines (Baker and Morris, 1984). The high line was just as fertile as the control line and had fewer calving problems in heifers than the control. The ratio of birth weight and pelvic area has been identical in the 3 lines. Similar reproductive performance has been reported for the selection experiment for yearling or 18-months weight at Waikite, New Zealand (Baker et al., 1980).

Frisch (1981), selecting a line of Hereford x Shorthorn cattle for higher growth rate under conditions of moderate to high environmental stress, reported that birth weight has declined in the selected line relative to the control while live weight at all other ages has increased significantly in the selected line. At the same time, calf mortality has been lower, with heifer calving rate higher in the selected line than in the control. These results were attributed to the effects of stress conditions of the tropical climate. More recently, Bailey and Lawson (1986) reported a significant decline in BW in a line of Hereford selected for increased postweaning gain for 12 years and no change in BW in an Angus line selected on the same criterion. Interestingly,

Luesakul-Reodecha, Martin and Nelson (1986) obtained a significant trend of -0.4 for dystocia score in an Angus line selected for yearling weight for 19 years. These trends seem to disagree with the commonly held opinion that selection for growth is accompanied by increased birth weight and dystocia. Recently, Kress, Nelvins, Anderson, Doornbos and Linton (1987) demonstrated how increases in BW can be restricted while selecting for increased body weight by means of an index. Using an index with a negative and positive weights on BW and yearling weight respectively, they reported an annual genetic change of -0.2kg/yr for BW and a positive trend of 2.8kg/yr for yearling weight in Hereford cattle.

b) Other growth traits:

The correlated response in weaning weight obtained from direct selection for yearling weight by Koch et al. (1974b) and Frahm et al. (1985b) was on average about 81% of the direct response for weaning weight. The correlated response reported by Aaron et al. (1986b) for weaning weight from direct selection for yearling weight was greater than the response from direct selection (1.52 vs. 1.45 kg/year). On the other hand, the corresponding correlated response for yearling weight as a result of selection for weaning weight was about 67% of the direct response for yearling weight. It seems therefore that selection for yearling weight had resulted in more improvement in weaning weight than the reverse. The above results were from single trait selection experiments. Selecting for weaning weight on the basis of combined individual and progeny performance, Aaron et al. (1986b) reported that the correlated response for yearling weight was equal to the response from direct selection on

individual performance.

The average annual correlated response for preweaning daily gain from reports in the literature were 4.30 and 3.63g/day respectively from selection for weaning weight and yearling weight. Corresponding annual estimates for post weaning growth rate were 4.30 and 9.23g/day.

There are not many reports on feed efficiency. Koch et al. (1982) reported that bulls from lines selected for growth rate had a significantly higher feed efficiency on test. The correlated responses in the weaning weight line and yearling weight line were 0.39 and 0.57 kg per Mcal of metabolisable energy (ME) respectively. Irgang et al. (1985c) did not observe any significant correlated response for feed efficiency from selection for weaning weight or post weaning gain.

Another criticism against selection on growth rate is that it is usually accompanied by increased mature cow size. Baker and Morris (1984) mentioned that evidence from experiments on correlated responses in cow weight is somewhat fragmentary. The only result they mentioned indicated that selection for early growth led to increased cow size. Luesakul-Reodecha et al. (1986) reported a positive but non significant trends of 0.35 and 4.12kg/year for 205-day and 54-month weight in Angus line selected for 365-day weight. However, Morris and Wilton (1978) in a review of the association between cow size and biological efficiency of reproduction, concluded that where all postweaning food requirements were added to the cow herd food costs, herd efficiency was little affected by cow size unless reproduction performance has also changed.

c) Carcass traits

The genetic correlation estimates from the literature predict that selection for increased weight should result in reduced fatness at constant weight (Koch et al., 1982). However, much experimental evidence seems to indicate no significant correlated response in carcass traits from selection for growth rate. Gallagher (1964) reported no significant differences between carcass traits for progeny of bulls selected for fast or slow growth. The only consistent and significant correlated response in carcass traits in the selection experiment for yearling weight in the Shorthorn reported by Anderson, Fredeen and Weiss (1974), was a higher percentage of bone and a lower lean to bone ratio. Almost similar results were reported by Martin and Alenda (1982) for Angus cattle. The data of Koch et al. (1982) indicated a correlated response of -0.19, -0.03 and 0.23 mm per year in fat thickness at 281 kg body weight respectively from selection on weaning weight, yearling weight and on an index combining yearling weight and muscle scope. But, Irgang et al. (1985c) reported significant correlated responses of 0.13±0.04 and 0.16±0.4mm fat depth per year in lines selected for weaning weight and post weaning gain respectively.

Perhaps the level of feeding during the finishing phase may affect these correlated responses (Baker and Morris, 1984). For example, mice selected for high 6-weeks weight on a low plane of nutrition had a lower fat percentage at that age than mice selected on the same basis with adequate nutrition, when both lines were placed on the same nutritional plane (Falconer, 1960).

d) Milk yield in beef cattle.

From literature estimates of the genetic correlation between direct and maternal effects for weaning weight (r_g = -0.43), Barlow (1978) concluded that selection for weaning weight would reduce milk yield. However, as pointed out by Baker (1980) and discussed by Baker and Morris (1984), most of the estimates summarised by Barlow (1978) were from dam-offspring relationships and they could be seriously biased by negative environmental covariance caused for example by levels of feeding for heifers. Baker (1980) mentioned that high levels of feeding either pre-weaning (mainly from milk production of the dam) or post-weaning (particularly high energy levels) reduce the amount of secretary tissue in the udder of daughters and their milk production, hence affect the weaning weight of their calves. In the absence of such negative environmental covariance arising from dam-offspring relationships, the genetic correlation betweem direct and maternal effects for weaning weight is lower, ranging from -0.05 to -0.28.

Frahm et al. (1985b) reported that milk production was not significantly different between progeny sired by bulls selected either for weaning weight or yearling weight. However, butter fat percentage was 0.4 higher for progeny of bulls selected for yearling weight. Aaron et al. (1986b) also obtained a similar result but in addition the daily milk production of progeny sired by bulls selected for weaning weight was significantly higher than the control. This indicates that selection for weaning weight may not necessarily lead to a reduction in milk production as Barlow (1978) mentioned; the result is more consistent with the explanations of Baker (1980). Lawson (1978) indicated that selection on postweaning gain on a high

plane (HP) or low plane (LP) of nutrition resulted in a significantly higher solid-not-fat and protein in the milk content of animals on LP relative to the HP in Hereford cattle. Also Angus cows from a line selected for postweaning gain on a roughage diet exceeded those selected for the same criterion on a concentrate diet in milk yield, fat %, solids-not-fat % and protein % by 5.1%, 7.6%, 7.8% and 12.5% respectively (Bailey and Lawson, 1986). The last two results illustrate the effects of high plane of nutrition in prepubertal heifers of reducing mammary development as Baker (1980) indicated.

2.3.2 Other selection experiments

Other selection experiments not primarily concerned with growth may be grouped by their objectives:

(i) Comparison of alternative selection schemes or methods

Carter (1971) investigated the effectiveness of sire selection on the basis of either corrected weaning weight, corrected final weight or postweaning gain, by evaluating the performance of their progeny in a test herd for a period of 10 years. The regression of the performance of progeny on the performance of sires indicated that selection on either weaning weight or yearling weight should result in appreciable genetic gains. On the other hand, sire's post-weaning gain was a poor indicator of progeny performance for any criteria.

Baker et al. (1980) compared the effectiveness of selection in Angus cattle on 13-month liveweight (AS1) followed by first mating of selected animals at 14 months of age, with selection on 18-month liveweight (AS2), with first mating as 2 year olds. A yearly mated

TABLE 2.3

Direct and correlated genetic responses to selection on either 13-month or 18-month body weight in cattle (kg/yr) (Baker et al., 1980)

Line	Birth weight	Weaning weight	13-month weight	18-month weight
HS1	0.08 ± 0.04	0.88 ± 0.4	1.65 ± 0.56(D)	3.10 ± 1.39
AS1	0.25 ± 0.05	0.98 ± 0.38	2.56 ± 0.55(D)	2.71 ± 1.01
AS2	0.04 ± 0.06	0.34 ± 0.32	1.22 ± 0.65	1.48 ± 0.96(D)

D - direct response

HS1 - Hereford line selected on 13-month liveweight

AS1 - Angus line selected on 13-month liveweight

AS2 - Angus line selected on 18-month liveweight

Hereford herd selected on 13-month weight (HS1) and a control line of Angus with mating as 2 year olds (AC0) were also kept. Relative to the control line, AS1 and HS1 improved in both 13-month and 18-month weights at about twice the rate at which AS2 improved. A summary of the preliminary results are presented in Table 2.3. The advantage of the selection scheme in AS1 and HS1 relative to that in AS2 is that it allows heifers to be mated at 2 years rather than the traditional 3 years in Australia and this can result in increased calf production and permit early identification of less productive females. This coupled with selection and mating of yearling bulls should increase annual genetic progress through reduction of generation interval.

(ii) Response in synthetics and purebreds

Berg (1984) carried out selection on 2 synthetic cattle populations and a purebred Hereford line to identify any superiority in response of the synthetic lines over the pure Hereford line due to a broader genetic base. One of the synthetic lines was developed by crossing Charolais, Angus and Galloway (SY1) while the second consisted of 60% of large dairy breeds (Holstein, Brown Swiss, Simmental) with 40% of beef breeds (SD). The selection criteria were preweaning and postweaning gain at one year of age in the synthetic lines while industrial bulls selected on the basis of superior performance or progeny test were used by artificial insemination in the Hereford herd each year. A summary of results is present in Table 2.4. There were higher trends for the synthetic lines in cow productivity, birth weight and 365-day weight. However, industrial bulls used in the Hereford line were not

TABLE 2.4

Comparative performance of Hereford cattle and two synthetic lines selected for growth rate (1962-1982)

Trait	HE[1]	Cattle Populations SY	SD
Calf crop %	78	83	82
Phenotypic trend (1962-1982)			
Birth weight (kg/yr)	0.17	0.25	0.34
365-day weight (kg/yr in males)	2.02	4.36	5.18
Average performance (1977-1980)			
Feed efficiency (kg feed/gain)	5.17	5.37	5.76
Average daily gain (kg/day)	1.34	1.57	1.46
Dressing %	58.5	60.4	58.9
Fat cover (cm)	1.38	1.11	0.88
Loin eye area (sq cm)	75.6	89.6	86.9

HE[1] = Hereford
SY = Synthetic line composed of Charolais, Angus and Galloway
SD = 60% dairy breeds and 40% beef cattle breeds

subjected to the same amount of selection pressure nor selected on the same criteria as those used in synthetic lines. These differences could have affected the results.

An experiment with similar objective has been initiated at Wokalup, Western Australia, in 1979 to compare the performance of purebred Hereford cattle to a synthetic (Wokalup Multibreed) line (Anonymous, 1985).

Similarly, Sharma et al. (1985) compared genetic response in a purebred Hereford and a multibreed synthetic line which were treated in the same way. The main selection criterion was weight for age in bulls at one year of age. Genetic trends were estimated by deviation from a control population and the best linear unbiased predictor (BLUP) using MIVQUE (minimum variance quadratic unbiased estimates) variance components estimated from the population. The summary of the results are presented in Table 2.5. Briefly, the mean selection differential was higher in the synthetics, which was attributed to the larger genetic base and greater variation in the synthetic line. Sire variance components were higher in synthetics than in Hereford and non-genetic sources of variation seem to be more important in the Hereford. The estimated genetic trends were similar for preweaning traits but slightly higher for postweaning traits in the synthetic population.

(iii) Selection for disease or parasite resistance

A few selection studies concerned disease resistance in beef cattle. Wharton, Utech and Turner (1970) reported heritability estimates of 39 and 49 percent for tick resistance respectively from dam-calf and full-sib correlations in the Australian Illawara

TABLE 2.5

Estimated genetic response per year to selection in purebred Hereford and a synthetic population (1966-1978) (Sharma et al., 1983)

Trait		Mean	MSD	Annual genetic change estimated by: Control population	Annual genetic change estimated by: BLUP
Birth weight (kg/yr)	HE	33.1	0.3	0.06±0.21	0.08±0.06
	SY	35.1	0.8	0.29±0.22	0.07±0.06
Preweaning daily gain (g/day)	HE	874	29.4	9.6±5.4	4.2±1.20
	SY	1077	33.2	7.5±4.9	4.8±2.30
Weaning weight (kg/yr)	HE	194	5.3	1.80±0.03	1.10±0.21
	SY	233	7.2	1.64±0.92	0.86±0.43
+Postweaning daily gain (g/day)	HE	1297	33.9	13.72±44	17.93±11
	SY	1399	46.7	48.12±49	31.25±11
+Yearling weight (kg/yr)	HE	418	12.2	5.81±9.39	8.21±6.00
	SY	471	13.8	11.31±12.17	6.78±2.15
++18-month weight (kg/yr)	HE	376	0.3	7.54±4.93	-6.10±2.10
	SY	408	0.2	7.52±4.36	-11.90±2.50

HE = Hereford line
SY = Synthetic line (composed of 35.7, 34.7, 21.7, 4.5 and 3.4% respectively of Angus, Charolais, Galloway Brown Swiss and others.
MSD = Mean selection differential

\+ Males only
++ Females only

Shorthorn cattle and proposed that selection for tick resistance might be effective. Utech, Seifert and Wharton (1978) carried out divergent selection for tick resistance in a population of the Australian Shorthorn. All the cattle acquired their resistance by exposure to field infestation. Selection was based on the number of semi-engorged female ticks on animals grazing together in naturally infested pastures for a period of at least 3 weeks and also on the number of female ticks maturing after artificial infestation with a known number of larvae to determine resistance level. The line selected for high resistance carried significantly fewer ticks than the low line at all times on exposure to naturally or artificially infested pastures.

A similar divergent selection experiment for high and low resistance lines to helminths, in particular Cooperia and Haemonchus has also been initiated in Australia (Anonymous, 1985).

d) Effectiveness of selection for twinning

Heritability estimates for twinning, reviewed by Maijala and Syvajarvi (1977) were about 3 percent, with repeatability of 6 percent. With such low values, most workers have dismissed selection for twinning as impracticable and undesirable (see Morris, 1984). Land and Hill (1975) have shown the importance of having a high initial herd average. They demonstrated theoretically that selection with the assistance of superovulation and embryo transfer should achieve genetic progress of 0.42% and 1.10% per year for initial herd twinning frequencies of 2% and 16% respectively.

Mechling and Carter (1964) reported selection for twinning over 30 years in Aberdeen Angus but concluded that little real

progress had been achieved. In a recent review, Morris (1984) reported a series of selection experiments on twinning in Australia, USA, France and Germany. The frequency of twinning for daughters from second or later calvings reported were

Australia	8 percent from 76 calvings (controls 0.6 percent)
USA	6.8 percent from 176 calvings (including first calving) and
France	11 percent from 89 calvings

In the German experiment, comparison of twin-born and control (single-born) females showed a difference of 0.94 percent in twinning.

(iv) Genotype x environment (gxe) interaction

When gxe interactions are important, response from selection in one environment is not likely to be fully transferred to other environments. Under such situations, genes governing performance in one environment are not all the same as those governing performance in another environment and it might be necessary that selection of stocks should be done under the specific environment in which progeny of stocks will be reared (Falconer, 1981).

A series of beef selection experiments aimed at identifying important line by location interactions have been reported by Butts, Koger, Pahnish, Burns and Warwick (1971), Koger, Burns, Pahnish and Butts (1979), Burns, Koger, Butts, Pahnish and Blackwell (1979) and Pahnish, Urick, Burns, Butts, Koger and Blackwell (1985) in Hereford cattle. Butts et al. (1971) investigated gxe in 2 herds of Hereford

cattle, each consisting of 2 lines, one herd at Miles City, Montana and one at Brooksville, Florida. A 7 year period of selection was followed by reciprocal exchange of animals. The primary selection criterion was an index with equal emphasis on preweaning and postweaning growth in bulls. They observed significant line by location interactions in birth weight, weaning weight, yearling weight and in pregnancy and weaning percentages.

Koger et al. (1979) and Burns et al. (1979) evaluated gxe in reproductive traits, birth weight, and weaning weight in 4 lines of cattle which were partly a continuation of the work by Butts et al. (1971). In addition to 2 lines which were developed independently in Montana and Florida (unrelated lines), they had another pair of lines which were developed from the same base population in Montana, before undergoing subsequent selection in the two different locations (related lines). There are significant line by location interactions in preweaning rate, weaning rate, birth weight, and daily gain in the unrelated and related lines. However, line by location interaction was not significant for survival rate in all lines. Pahnish et al. (1985) examined line x location interactions for postweaning traits in the same populations. Significant line by location interactions were observed in the unrelated line for post weaning daily gain, end of test weight and conformation score. The same result was obtained for the related lines. Investigations to understand the mechanism underlying these interactions identified differences in thyroid function of these animals which could not however be related to the results. There were no differences in milk production. However the degree of gxe was not quantified in terms of genetic correlation between the same traits in the different

locations.

Frisch (1981) investigated factors underlying gxe interaction in growth rate under tropical conditions by studying correlated responses to selection for growth under stressful tropical conditions. A line of cattle selected for growth rate from 1970-1975 and a control line with significant differences in liveweight, were exposed to several different levels of stress: plane of nutrition, high ambient temperature, infection with bovine infectious keratoconjunctivitus (BIK) or gastro-intestinal helminths (GIH). The selected line was shown to be more heat tolerant, to have lower maintenance requirement, greater resistance to infection with BIK and GIH and, consequently, always had higher growth rate in the presence of these stress factors. However, they did not have superior growth rate at low levels of these stress factors. Thus reversal of rank between selected and control lines for growth rate under conditions of high and low level of stress could be attributed to differences in resistance to environmental stress and not in growth potential.

The results of Pacer et al. (1986) seem to indicate some degree of interaction between line and plane of nutrition. While the Angus line selected for postweaning growth on a concentrate diet was significantly different from foundation animals in postweaning gain, weight per-day-of-age and final weight, a similar line selected on a roughage diet did not differ significantly in any of the above traits.

2.4 Discussion and conclusions

Most early selection experiments suffered from inadequate

designs in terms of small population size, high levels of inbreeding and inadequate means of measuring genetic trend. Many reports were without estimates of error variance and in the others the drift variance was not included.

More recent experiments have shown improvement in design with larger population size and lower inbreeding rates. In addition, control populations or divergent lines have been maintained to measure the genetic trends.

The positive genetic trends reported for growth traits indicate that direct selection for the improvement of growth traits is effective. Correlated responses in other growth traits from direct selection on yearling weight were generally larger than those from weaning weight selection. Thus if the main objective is to increase weight in sire lines, selection on yearling weight is preferable. Experimental evidence seem to disagree with the commonly held opinion that selection for growth is necessarily accompanied by increased birth weight and dystocia.

The rate of genetic change so far achieved in growth traits is somewhat lower than the possible rate indicated by Smith (1984). The lower rates of genetic change achieved in practice in beef cattle have been attributed by Smith (1986) to:

1) concern about other traits of uncertain economic importance
2) conservatism of breeders
3) selection and generation turnover rates which are not optimal.

Land and Hill (1975), Smith (1984) and Land (1985) have discussed the possible ways by which the present rate of selection

response could be improved. One of the major limitations to genetic improvement in beef cattle is the low female reproductive rate which has restricted selection intensity among females. If the reproductive rate of female cattle could be increased, it would be theoretically possible to double the selection intensity applied to the population as a whole and hence double the rate of genetic change (Land, 1985). For traits which can be measured in both sexes before reproductive age, the rate of genetic change could be increased by 1.6 times, by using multiple ovulation and embryo transfer (MOET) compared with normal reproduction (Land and Hill, 1975).

Two other routes to faster improvement may be the use of major genes and indirect selection on physiological traits. An example of a major gene currently being exploited in breeding programmes in cattle is the double muscling gene which results in a higher yield of lean meat. Hanset and Michaux (1985) reported about 30% higher total muscle weight in veal calves of Belgian White and Blue cattle homozygous for the double muscling gene compared with normal homozygotes. It is, however, associated with calving difficulties.

Selection on physiological traits or biochemical factors, indicating or controlling performance, may allow indirect selection for commercial traits. This could offer a great scope for reducing the generation interval as animals could be selected early in life and may also be useful in selecting young males for sex-limiting traits. Presently, no such technique is available in beef cattle. However, the high and low growth rate lines of the Trangie Agricultural Research Station, Australia present a great opportunity to examine the biochemical and physiological components of response

to selection for growth rate.

The reports in the literature show that improvement of growth traits still continues to be the main selection objective in beef cattle experiments with very little emphasis on other traits.

The increasing demand for lean meat also implies that selection objectives in beef cattle should be broadened to include efficiency of lean production. Apart from the consumer's view, it had been suggested that the greatest scope for improving bio-economic efficiency in beef cattle other than through reproduction, is by use of faster growing lean terminal sires (Dickerson, 1982 and Barlow, 1984). Selection for efficiency of lean production in live animals is possible by ultrasonic measurement of fat depth or area. Simm (1983) reported a correlation coefficient of about 0.70 between lean content estimated from ultrasonic measurements and carcass evaluation.

CHAPTER 3

DESCRIPTION OF EXPERIMENTAL METHODS

3.1 Introduction

In 1977 the then Animal Breeding Research Organisation (ABRO), now Institute of Animal Physiology and Genetics Research (IAPGR) established a 200 cow research herd of purebred registered Hereford cattle at its experimental farm at Cold Norton, Staffordshire, aimed at providing information on selection for efficiency of lean meat production. The Hereford breed was chosen because it was then the dominant beef breed in the United Kingdom. The cows were purebred and registered to make the results relevant and applicable to cattle breeders.

3.2 Objectives

The mean goal of the project was to test and select for efficient production of lean meat. This biological selection objective is closely related to commercial goals and parallels the current trend in beef cattle production with demands for higher growth rates and lower fat cover. There were two selection lines each of about 75 cows selected respectively for lean growth rate (LGR) and lean food conversion ratio (LFCR). In addition, there was a genetic control line (CTL) and an open line (OPL) which was bred by artificial insemination from selected progeny tested Hereford bulls.

In addition to the main selection programme, a continuing series of complementary research trials were carried out. These included,

(i) comparison of sources of stock; which was aimed at testing differences among

(a) females from performance tested herds, weight recorded herds and non-recorded herds, and

(b) males from Milk Marketing Board (MMB) progeny tests, Meat and Livestock Commission (MLC) performance tests, MLC progeny tests, unrecorded bulls and Canadian Hereford bulls

(ii) examination of the value of ultrasonics for estimation of carcass composition in live animals.

(iii) assessment of the effects of pre-test environments on performance test results. Bulls were weaned at 3 ages (birth, 84 and 168 days) to measure pre-test effects.

However this thesis is mainly concerned with the evaluation of response in the selection programme. Most of the results of the complementary research trials have been reported by Simm (1983) and Aragon (1985).

3.3 Herd establishment and experimental design

The foundation cows were purchased from 62 pedigree herds throughout the United Kingdom so as to get a broad cross section of the breed. Approximately one third of the females came from herds which were performance tested, one third from other MLC weight recording herds and the remaining one third from non-recording herds.

During 1977-1978, the females were bred largely by artificial insemination (AI) from some 48 bulls standing in AI

stations and private herds. After the two initial year period, the herd was closed and cows randomly alloted to the two selection lines (LGR and LFCR lines). Beginning with the 1978 calf crop, all bulls were ranked in 1979 and 1980 for LGR and LFCR and the best 6 for each trait were selected and used for mating by natural service in their respective lines. Each of the selected lines consisted of three replicates, with about 25 cows and 2 bulls per replicate.

The control line consisted of about 35-40 cows derived from cows not in-calf or returning to oestrus in the foundation years. These were bred by frozen semen taken from a fixed panel of some 25 bulls born in the project during 1978-1979. These were representatives of the original breeding stocks and so set a fixed genetic base or control from which to measure genetic trends in selected lines. The bulls on the semen panel were mated to each others daughters in a rotational order to minimise inbreeding in the control line. The control was also made up of three replicates, each of about 12 cows.

The open line consisted of about 30 cows which were bred by AI from selected progeny tested Hereford bulls. The objective of this line was to demonstrate how a breeder could use test results effectively and to measure the genetic gains achieved.

3.4 Herd management

3.4.1 Feeding

Cows and heifers grazed on pasture when possible and were housed and fed indoors in winter (November to mid-March). The ration consisted of hay and barley. The levels of stocking and winter feeding were such as to avoid overfatness. Bulls were

usually performance tested and their feeding regime is described later.

3.4.2 Mating

Mating in the selection lines was restricted to three oestrus periods in July and August for calving in April and May mainly out of doors. Cows of good reproductive performance were usually kept 4 to 5 years for breeding. Cows not in-calf or returning to oestrus were used in the foundation years to build up the control and open lines. Most of these were culled after calving or weaning but some were retained for a further year. Heifers produced in all lines were saved as replacements and were mated at 13-14 months of age to calve first at two years of age.

3.4.3 Calf management

Calves were born from April to May each year. Within 24 hours of birth, all calves were tagged and tattooed for identification and birth weight recorded. Calving difficulty scores were assigned to each calf at birth following the scoring system used at Clay Centre, Nebraska, United States of America on a scale of one (no difficulty) to five (caesarean birth). The full description of score scales is given in chapter seven (Table 7.11), where calving difficulty is analysed. Heifer calves were allowed to run with their dams on pasture and received no creep feed. Cows whose calves were weaned early (see below) were milked through the milking parlour. Such cows were dried off when daily milk yield was less than 3kg per day. Heifer calves were weaned at 168 days of age from 1978 to 1983 and thereafter either at 98 to 126 days of

age.

The first six bull calf crops (1978-1983) from the selected lines were weaned at one of three ages: at birth (after getting colostrum), at 84 and 168 days. This was designed to evaluate the effect of pre-test treatment on performance test results. The analysis of this aspect of the experiment has been reported by Simm (1983). The bull calves weaned at birth were housed in groups and fed milk and milk replacement at least twice daily on a scale up to 10 per cent of their liveweight. The temperature of the calf house was kept low (under $55^{o}F$) and calves were offered dry feed from birth ad libitum, to get them started on a pelleted feed. Calves were completely weaned from milk and milk replacement at 10 weeks of age and trained to use the Calan Broadbent feed gates.

The other two groups of bulls calves weaned at 84 and 168 days were creep-fed and put directly onto the test ration and trained to use the electronic gates. The performance test for LFCR commenced at 200 $\pm$ 4 days and normally continues until 400 $\pm$ 4 days of age. The test ration was a complete grass/barley pelleted diet, offered ad libitum. Nutrition information on the diet is given in Table 3.1.

After 1983, all bull calves were weaned at about 84 days of age and had a similar postweaning management to those weaned at that age prior to 1983.

3.5 Selection criteria and procedure

Bulls were selected on the basis of performance test up to 400 $\pm$ 4 days of age for LGR and on a 200-400 $\pm$ 4 days test for LFCR in their respective lines. The bulls were scanned by ultrasonics

TABLE 3.1

Nutritional information on the dried grass/barley complete diet

Dry matter (DM) (g/kg)	910.1
Crude protein (g/kg DM)	154.7
Fibre (g/kg DM)	155.7
Digestibility of organic matter in DM (in vitro) (g/kg)	745.5
Metabolisable energy (derived) (mJ/kg DM)	11.7

Based on 14 samples (Simm, 1983)

towards the end of test on two occasions usually in April and May at three sites: the 10th, 13th rib and 3rd lumbar vertebrae. The scanning was carried out by personnel from the MLC and repeatability across sites and occasions varied from 0.5 to 0.81. Bulls not selected for breeding in the first four years of the experiment were slaughtered and dissected by the MLC and the Institute of Food Research (FRI), Bristol at about 400 days of age. Using the scanning results and the dissectible carcass lean on these bulls, lean percent was predicted as:

$$L = \bar{L} + b_{L.F}[(F-(W-\bar{W})b_{F.W}) - \bar{F})$$

where

L	=	predicted lean percent
$\bar{L}$	=	mean of dissectible carcass lean percent at 400 days (about 60%)
$b_{L.F}$	=	regression coefficient of lean percent on fat area
$b_{F.W}$	=	regression coefficient of fat area on body weight at scanning
F	=	fat area (cm^2) as determined by the scanogram
$\bar{F}$	=	yearly mean for fat area (cm^2)
W	=	body weight of animal at scanning (kg)
$\bar{W}$	=	yearling mean for body weight (kg)

Lean percent (LEAN) predicted from the individual bull fat areas were averaged over the six measurements.

Lean growth rate and lean food conversion ratio were estimated respectively as:

LGR = GRT up to 400 days x LEAN x killing out percent.

where

$$\text{GRT} = \text{growth rate} = \frac{\text{final weight at 400 days - birth weight}}{\text{400 days}}$$

LFCR = FCR/(LEAN x killing out percent)

where

$$\text{FCR} = \text{food conversion ratio} = \frac{\text{food intake on test (200-400 days)}}{\text{final weight day (400 days) - initial weight (200 days)}}$$

A constant killing out percent of 57.7 estimated from the bulls slaughtered in the initial years of the experiment was used in estimating LGR and LFCR. The estimated LGR and LFCR were then adjusted for the effects of date of birth, dam's age and weaning type within years using the LSML76 program (Harvey, 1977). In addition, LFCR was adjusted for differences in initial weight at the beginning of test.

Selection was then based on the adjusted LGR and LFCR in their respective lines. The bulls were ranked by their standardised deviation within their test groups and those with the

largest favourable deviation were selected within sire families and replicates. Attempts were made to select one male progeny from each of the two sires in each replicate, however with only four to eight bulls per replicate, it was sometimes necessary to select two male progeny (half sibs) from the same sire if there was no alternative bull or no other with good performance record. This occurred about one-third of the time and occasionally the spare bull chosen from the other sire was used to avoid close inbreeding. Selected bulls were used for mating only for one year in most cases.

3.6 Performance records

In addition to LGR and LFCR, performance data such as birth weight, growth rate, lean percent, food intake (FEED) and food conversion ratio on test were also measured in recorded bulls. All calves born in the project were recorded for body weight at about one month intervals in early life or two months at older ages up to about 13 months of age for males and 48 months of age for females. Body measurements taken over the same age periods on both male and female calves were: head length, first rib width, hook width, wither height, body length and rump height at at about two months intervals. Scrotal circumference was measured also in male calves and reproductive performance of all heifers recorded. The reproductive traits analysed in this thesis included conception rate, age at first calving, calving date, calving difficulty score, calf mortality and calving interval.

3.7 Statistical analyses

The statistical analyses of the data was centred on two

main issues : namely, estimation of selection pressure applied and estimation of realised direct and correlated responses in the selected populations. The details of the various statistical techniques utilised are given in the appropriate chapters but the general procedures followed are briefly outlined below.

3.7.1 Estimation of cumulative selection differential

Cumulative selection differential was estimated by the method of Pattie (1965) (the incorrect method, James (1986)) and that of Newman et al. (1973) (the correct method). Using the incorrect method, the individual cumulative selection differential of bulls was computed as the sum of the individual bull's deviation from its contemporary group and the average of the total selection differential accumulating through its parents. The correct method differs in that the individual bull's deviation was added to the average cumulative selection differential of all parents of the contemporary group.

3.7.3 Estimation of direct and correlated responses

Responses to selection were evaluated by three methods:

(i) Deviation of selected lines from control

Direct response to selection for LGR and LFCR in their respective lines were calculated as the deviation of the mean phenotypic performance of each selection line from the mean performance of the control. The same procedure was used to estimate correlated responses in secondary traits measured in recorded bulls in each selection line. The variance-covariance matrix of response

that accounted for drift variance was estimated approximately by means of the relationship matrix. Realised heritability was then obtained for each selected trait as a generalised least-squares solution of the regression of response on cumulative selection differential.

(ii) Prediction of progeny breeding value.

The method is concerned with prediction of breeding values of progeny from their own performance and that of their parents, with account being taken of the changes in the regression coefficient in each generation of selection. The heritability that minimises the sums of squares of deviations between predicted and observed progeny value is an estimate of realised heritability (Juga and Thompson, 1988). The method utilises both ancestral and contemporary information and is therefore a combination of the correct and incorrect methods for estimating cumulative selection differential. Estimates of realised heritabilities were calculated for LGR and LFCR using this technique.

(iii) REML to estimate (co)variance components and estimate genetic trend

Estimates of variance components, heritabilities and genetic change for selected traits were obtained by univariate REML analysis of each trait in their respective lines only or with the control, fitting an individual animal model. Correlated responses for secondary traits in each selection line were estimated by multivariate REML analysis. To account for selection bias (see Thompson and Meyer, 1986), such multivariate analysis involves the

selected trait and secondary trait of interest using only the selected line or with the control. Correlated responses estimated from all three lines, that is, both selected lines plus the control usually involved multivariate analysis on both selected traits and the secondary trait of interest.

CHAPTER 4

MEASUREMENT OF SELECTION APPLIED

4.1 Introduction

This chapter examines the amount of selection pressure applied in the selected lines. General information about the population in terms of means and standard deviation of traits, inbreeding and generation interval within lines is presented. The various methods of estimating cumulative selection differential with overlapping generations are examined.

4.2 Materials and methods

4.2.1 Management of animals

The management of animals, the structure of the selected lines and the selection procedure have been given in chapter three.

4.2.2 Statistical analysis

(i) Generations of selection, generation interval and inbreeding coefficient

Generations of selection (GS) in both lines were obtained from generation coefficients which were calculated by the procedures developed by Brinks et al. (1961). The generation coefficient (GC) of an individual is the average number of Mendelian segregations in its pedigree back to ancestors in the foundation population and measures one more than the number of generations of selection, therefore, GS were obtained by subtracting one from the GC. Sires (s) and dams (d) utilised in the foundation population were given a GC of zero:

$$GC_s = GC_d = 0,$$

for selected bulls (b):

$$GC_b = 1 + 0.5\ (GC_s + GC_d)$$

For heifers (h) utilised in the breeding herd, since they were unselected:

$$GC_h = 0.5\ (GC_s + GC_d)$$

Generation interval was calculated as the average age of parents when their progeny were born. Inbreeding coefficients of dams and calves were calculated directly from pedigree information from the base year of 1978. The GS, generation interval and inbreeding coefficients were all calculated within replicates and summarised per line.

(ii) Selection differential

(a) Adjustment for fixed environmental effects

Least squares analysis of variance within years was carried out on each trait using the LSML76 program (Harvey, 1977) to adjust data for fixed effects. The fixed effects fitted were:

1 weaning type; at birth, 12 weeks and 24 weeks of age (see Chapter three),

2 dam age; the age of dam at the time of her progeny's birth, which could be 2, 3, 4 to 6 or more than 6 years of age and

3 birth date: which was fitted as a covariate.

All traits were adjusted for the above factors irrespective of significance of the effects. In addition LFCR, FCR and FEED were adjusted for initial weight at the beginning of test. In the first four years of the experiment, the dam age adjustment factors used were those derived from the analyses of each respective year's data. However in subsequent years, the dam age adjustment factors used were pooled estimates from the first four years of the experiment when the dams used consisted mainly of foundation cows. It was assumed that, because younger dams used in later years were progeny of selected bulls, adjustment for dam age may wrongly introduce a bias in selection response, since dam age is confounded with cumulative selection differential in females. The pooled dam age adjustment factors are shown in Table 4.1. The adjusted data were used in the calculation of selection differentials.

(b) Cumulative selection differential

The cumulative selection differential (CSD) measures the total amount of selection pressure applied up to a particular time. When compared with the total direct response for a particular trait, CSD can be used to evaluate the effectiveness of selection. In species with discrete generations, CSD can be calculated by simply adding selection differentials of successive generations. However, where there is considerable overlap in generations, a procedure which combines information across years is required, since the parents of any progeny crop will have different numbers of generations of selection behind them.

Cumulative selection differentials for LGR and LFCR were estimated in both lines by two commonly used methods when

TABLE 4.1

Pooled additive correction factors for age of dam used to adjust traits

	Traits						
Age of dam (yrs)	BWT	LP	FEED	GRT	LGR	FCR	LFCR
2	3.3	-0.5	2.0	15.0	2.3	3.0	1.0
3	0	3.8	-7.5	3.25	4.8	-6.0	-1.25
4-6	-2.3	2.8	20.8	-17.5	-2.8	7.0	0
7 and above	-1.5	-5.0	-15.0	-0.8	-1.0	-1.8	0

generations are overlapping:

1) The technique used by Pattie (1965) and described by Turner and Young (1969); and

2) The method of Newman et al. (1973).

A contemporary group is defined as a group of calves of the same sex, born in the same year and line. Using Pattie's method, an individual selection differential (ISD) was calculated as the deviation of the individual's performance from its contemporary group. An individual cumulative selection differential (ICSD) was calculated as the sum of the ISD and the average of the cumulative selection differential of its parents, the selection differentials for parents of calves in the foundation herd being set to zero. Thus for selected bulls,

$$ICSD = ISD + 0.5\ (ICSD_s + ICSD_d)$$

and for heifers,

$$ICSD = 0.5(ICSD_s + ICSD_d)$$

where

$ICSD_s$ = individual cumulative selection differential of sire

$ICSD_d$ = individual cumulative selection differential of dam

The cumulative selection differential for each calf birth

year-line-sex subclass was calculated as the mean of the CSD of all calves of one sex born in the same line and year.

The method of Newman et al. (1973) is similar to that of Pattie's except for estimating ICSD. The ICSD was calculated as the sum of the ISD and the mean accumulated selection differential (MAS) for the contemporary group, the MAS for the contemporary group being calculated as half of the weighted average CSD of all sires plus the average CSD of all dams which produced the contemporary group. The ICSD of an individual can be thought of as the average prior selection practised for the contemporary group plus the additional selection practised on the individual. Thus for selected bulls,

$$ICSD = ISD + 0.5\ (\overline{ICSD}_{ss} + \overline{ICSD}_{dd})$$

and for heifers,

$$ICSD = 0.5\ (\overline{ICSD}_{ss} + \overline{ICSD}_{dd})$$

where

$\overline{ICSD}_{ss}$ = weighted average ICSD for all sires of the contemporary group

$\overline{ICSD}_{dd}$ = weighted average of the ICSD for all dams of the contemporary group

The same procedures were utilized to calculate cumulative selection differentials for BW, LEAN, feed intake (FEED), growth rate (GRT) and food conversion ratio (FCR) (secondary cumulative selection differentials) resulting from the direct selection of LGR and LFCR in their respective lines.

James (1986) showed that Pattie's method was biased upwards and tends to underestimate realized heritability. Atkins (1985) had earlier reported that the method of Pattie (1965) overestimated CSD by about 15 to 20 percent in lines of sheep divergently selected on an index of cannon bone length at 8 weeks of age adjusted for body weight. James (1986) showed that the ICSD estimated by the method of Pattie (1965) is essentially the sum of the individual's deviation and all of its parental deviations weighted by their genetic contribution to the individual. He argued that better parents in any generation will tend to have above average progeny and so will have more progeny than the average of those selected. Thus, their genetic contribution to the grand-progeny generation will be greater than to the progeny generation and so higher deviations will receive progressively more weight for some generations. The result will be an upwards bias in cumulative selection differential. James therefore considered the method of Newman et al. (1973) to be the correct method (CM) and that of Pattie's as incorrect (ICM) under situations where generations are overlapping.

However, Juga and Thompson (1988) argued that both the correct and incorrect methods are compromises of a more general scheme or method. Although the correct result takes account of the genetic worth of the contemporaries that contribute to the selection

differential, it ignores individual parental values and it may not always be very clear how to group individuals with overlapping generations. The incorrect method on the other hand uses parental values but does not take account of the genetic worth of contemporaries. Juga and Thompson (1988) therefore proposed a general method which uses direct ancestoral information and resulting changes in regression coefficients each generation due to selection to predict breeding value of progeny which can be used to estimate realised heritability in populations with overlapping generations. The general method tends to the CM as heritability approaches one and to the ICM as heritability goes to zero. Since the general method is essentially concerned with estimating realised heritability, a detailed account of the method is given in chapter five which deals with evaluation of selection response.

(c) Actual and maximum potential selection differentials

Actual (effective) selection differential (EFSD) per generation was calculated as the weighted average of the ISD of selected bulls, the weight given to each sire being his proportionate contribution to the individuals that were measured in the next generation. Expected (unweighted) selection differential (EXSD) was calculated by simple averaging of the ISD of selected bulls. The weighting of the selection differential partly accounts for the effects of natural selection; therefore a comparison of EFSD and EXSD may be used to discover whether natural selection is operative (Falconer, 1981). Annual selection differential (ASD) was calculated by dividing the weighted average of the ISD of selected bulls by their respective age at the birth of their

progeny.

Maximum potential selection differential (MPSD) was calculated by averaging the ISD of bulls (the same as were actually selected) with the largest value for the primary criteria in each line. Comparing the EXSD and MPSD provides an estimate of the proportion of the possible selection that was applied towards the primary trait in each line. The EFSD, EXSD, ASD and MPSD were all estimated within replicates and summarised per line.

4.3 Results

4.3.1 General

Over the seven years of selection, a total of 175, 150, 77 and 46 progeny were measured in the LGR, LFCR, CTL and OPL lines respectively. A classification of the number of male calves by year and line is shown in Table 4.2. Line means pooled across years and standard deviations calculated from sums of squares pooled across all line-year subclasses are presented in Table 4.3.

4.3.2 Generations of selection, generation interval and inbreeding coefficients

The generation turnovers represented in the 1986 calves were 1.51 and 1.50 respectively in the LGR line and LFCR lines (Table 4.4). Thus the generations of selection were the same in both selected lines. Similarly, generation interval was the same in both selected lines, 2.4 years; and showed very little variation from year to year during the duration of selection. Over the whole period of selection, the average age of sires was 2.01 years in the LGR line and 2.07 years in the LFCR line while corresponding average

TABLE 4.2

Classification of number of recorded male animals recorded by year and line

Calf birth Year	Lines			
	LGRL	LFCRL	CTL	OPL
1980	40	28	-	-
1981	20	26	9	2
1982	19	31	12	1
1983	32	22	8	6
1984	22	18	17	7
1985	19	7	13	10
1986	23	18	18	20

TABLE 4.3

Line means and pooled within line and year standard deviations for traits

Trait	Line mean				Standard deviation
	LGRL	LFCRL	CTL	OPL	
BW (kg)	33.67	33.69	32.71	32.79	3.19
LEAN (%)	60.09	60.35	59.76	60.24	2.30
FEED (kg)	1326	1350	1361	1262	122
GRT (g/day)	9540	907.9	887.5	976.6	78.5
LGR (g/day)	329.6	314.6	304.6	335.1	30.2
FCR (kg feed/kg gain)	5.98	6.01	6.38	5.47	0.60
LFCR (kg feed/kg lean gain)	17.03	17.22	18.39	15.54	1.74

TABLE 4.4

Generation interval, generations of selection and inbreeding per year

	LGRL					LFCRL				
Year	No. of Sires	L	GS	FD %	FC %	No. of sires	L	GS	FD %	FC %
1980	5	2.02	0.50	0.0	0.0	5	2.08	0.50	0.0	0.0
1981	5	2.06	0.50	0.0	0.0	6	2.23	0.48	0.0	0.0
1982	6	2.52	0.80	0.0	0.88	8	2.59	0.75	0.0	0.34
1983	6	2.61	0.87	0.0	1.98	6	2.40	0.85	0.0	1.24
1984	6	2.66	1.13	0.20	2.66	6	2.63	1.09	0.30	1.55
1985	6	2.73	1.26	0.75	4.04	6	2.47	1.25	0.83	3.32
1986	8	2.44	1.51	1.83	2.58	6	2.51	1.50	1.53	3.58

L = generation interval in years
GS = generations of selection
FD = dam inbreeding coefficient
FC = calf inbreeding coefficient

ages of dams were 2.86 and 2.76 years respectively.

Inbreeding coefficients of dams were about the same in both lines but inbreeding coefficients of calves were slightly higher in the LFCR line compared with LGR line (2.58% versus 3.58%) in the final year of selection (Table 4.4). The average inbreeding coefficient of calves was unusually high in the LGR line in 1985 (4.04%); this was due to the fact that the selected bulls and some of the dams used for mating in one of the replicates this year were paternal half sibs.

4.3.3 Selection differential

(i) Cumulative selection differential

The CSD for LGR and LFCR classified by year and line are presented in Tables 4.5 and 4.6; and are illustrated in Figures 4.1 and 4.2. In the LGR line, cumulative selection differentials for LGR were 58.8g/day (1.97 standard deviation units (SDU)) and 56.9g/day (1.90 SDU) by the correct and incorrect methods respectively, and corresponding estimates for LFCR in the LFCR line were -3.17kg feed/kg lean gain (-1.82 SDU) and -3.3kg feed/kg lean gain (-1.86 SDU). There was not much difference between estimates of CSD by the correct and incorrect methods but the estimates tend to be slightly lower for the incorrect (Figures 4.3 and 4.4). Similarly, estimates of primary CSD for LGR and LFCR obtained on a line basis, that is, ignoring replicates, did not differ much from estimates for each trait obtained as a weighted average of CSD calculated within replicates (Tables 4.5; 4.6 and Figures 4.5 and 4.6). This indicates that selection within replicates did not drastically affect the total amount of selection applied.

TABLE 4.5

Primary and secondary cumulative selection differentials for lean growth rate (g/day)

Calf birth Year	LGR line				LFCR line				CTL line
	Pooled[a]		Line basis[b]		Pooled		Line basis		Pooled
	CM	ICM	CM	ICM	CM	ICM	CM	ICM	CM
1980	19.13	19.13	19.13	19.13	20.00	20.00	20.00	20.00	-
1981	28.68	28.68	28.63	28.63	9.25	9.25	9.25	9.25	1.20
1982	42.27	42.46	45.87	46.45	12.62	13.46	13.05	13.63	9.60
1983	36.25	35.97	35.65	35.23	29.06	31.16	29.66	31.19	7.51
1984	48.52	46.72	48.06	46.91	17.17	17.74	16.02	17.38	4.97
1985	53.14	51.74	53.63	53.39	35.01	36.57	31.91	35.91	4.62
1986	59.51	57.56	61.17	60.83	35.20	37.99	36.21	40.14	14.94

[a] weighted average of 3 replicates
[b] estimate ignoring replicates
CM = correct method
ICM = incorrect method

TABLE 4.6

Primary and secondary cumulative selection differentials for lean food conversion ratio (kg feed/kg lean gain)

	LGR line				LFCR line				CTL line
Calf birth Year	Pooled[a]		Line basis[b]		Pooled		Line basis		Pooled
	CM	ICM	CM	ICM	CM	ICM	CM	ICM	CM
1980	0.16	0.16	0.16	0.16	-1.30	1.30	1.30	-1.30	-
1981	-0.35	-0.38	-0.35	-0.35	-1.46	-1.46	-1.46	-1.46	0.17
1982	-1.76	-1.74	-1.69	-1.90	-2.11	-2.02	-2.13	-2.06	0.13
1983	-0.46	-040	-0.48	-0.39	-2.69	-2.69	-2.62	-2.52	-0.42
1984	-2.18	-2.19	-2.15	-.225	-2.39	-2.22	-2.43	-2.25	-0.28
1985	-1.33	-1.27	-1.39	-1.32	-2.51	-2.43	-2.53	-2.43	-0.10
1986	-1.18	-1.89	-1.18	-1.90	-3.16	-3.22	-3.17	-3.24	-0.47

a,b : see Table 4.6 for definition of symbols
CM = correct method
ICM = incorrect method

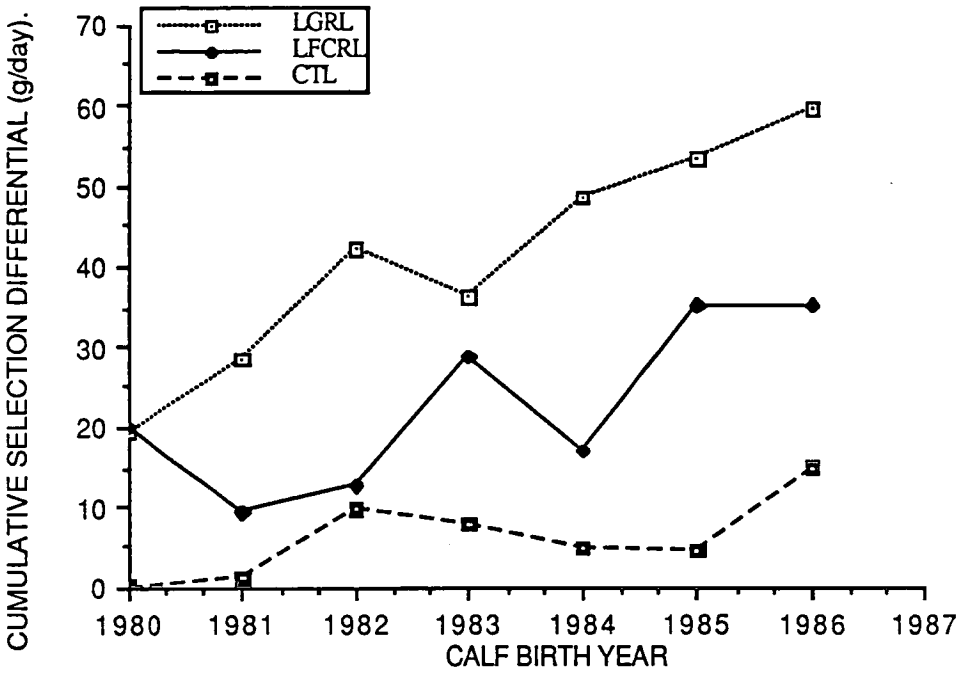

Fig. 4.1 Cumulative selection differentials (CM) for LGR by year and line.

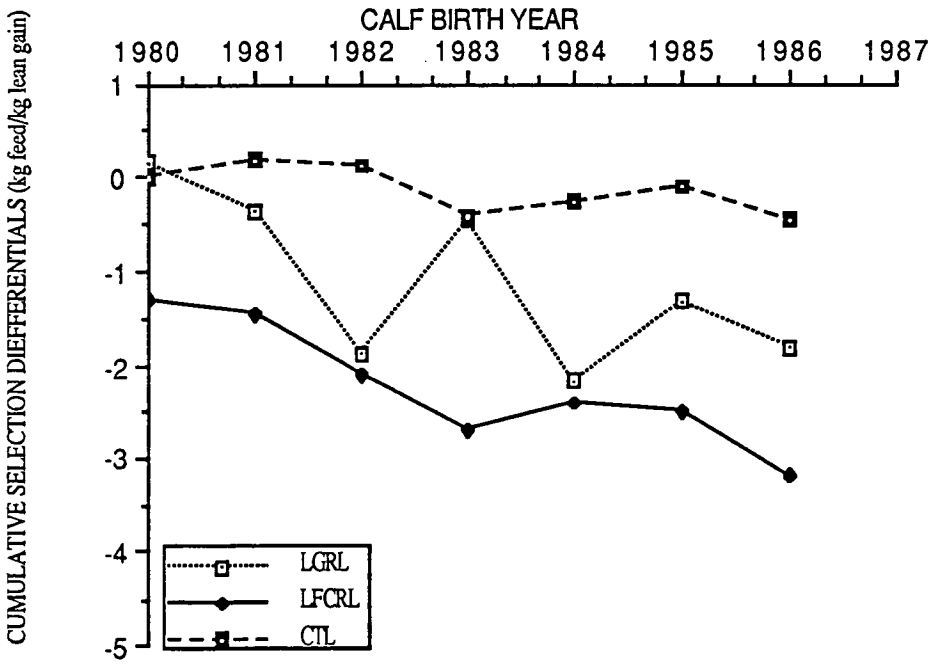

Fig. 4.2 Cumulative selection differentials for LFCR (CM) by line and year.

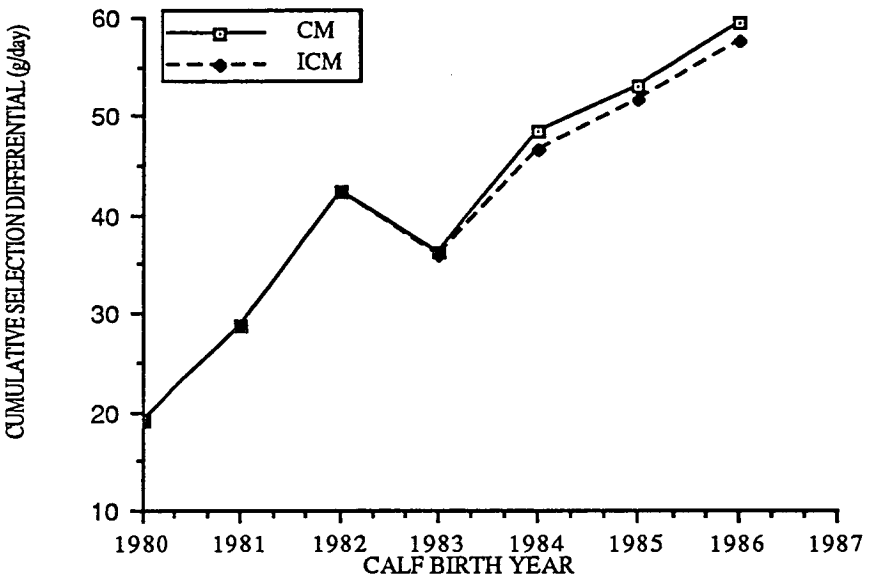

Fig. 4.3 Cumulative selection differentials for LGR by the correct (CM) and incorrect (ICM) methods.

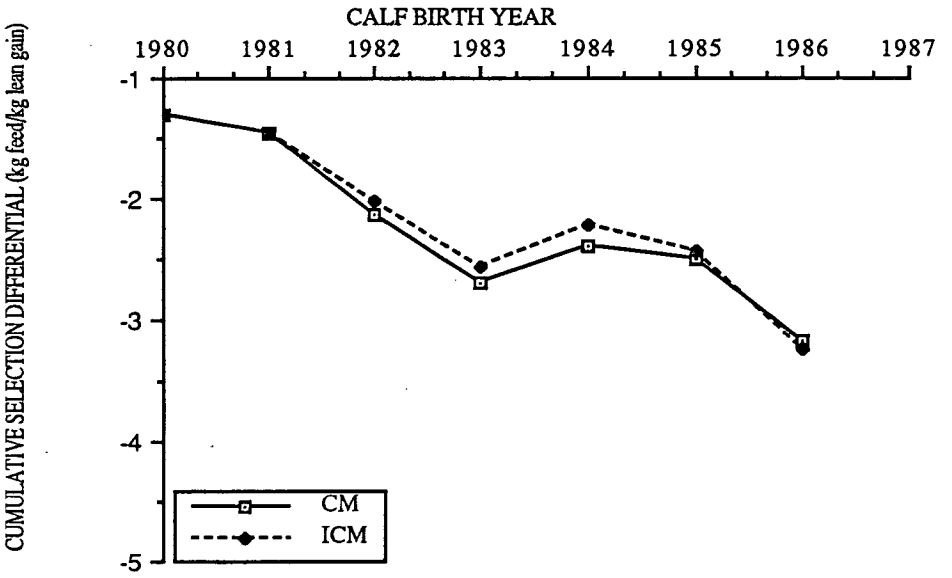

Fig. 4.4 Cumulative selection differentials for LFCR by the correct (CM) and incorrect (ICM) methods.

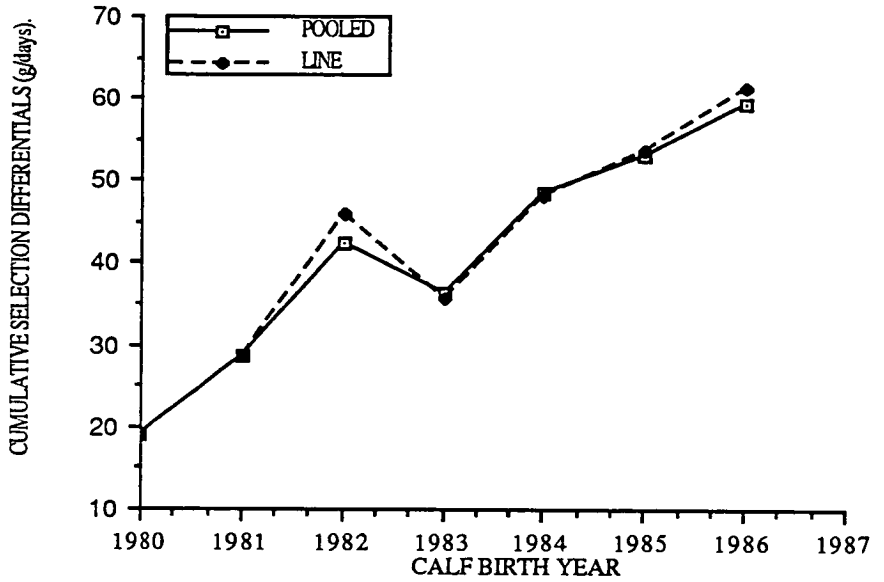

Fig. 4.5 Cumulative selection differentials for LGR, pooled and line estimates.

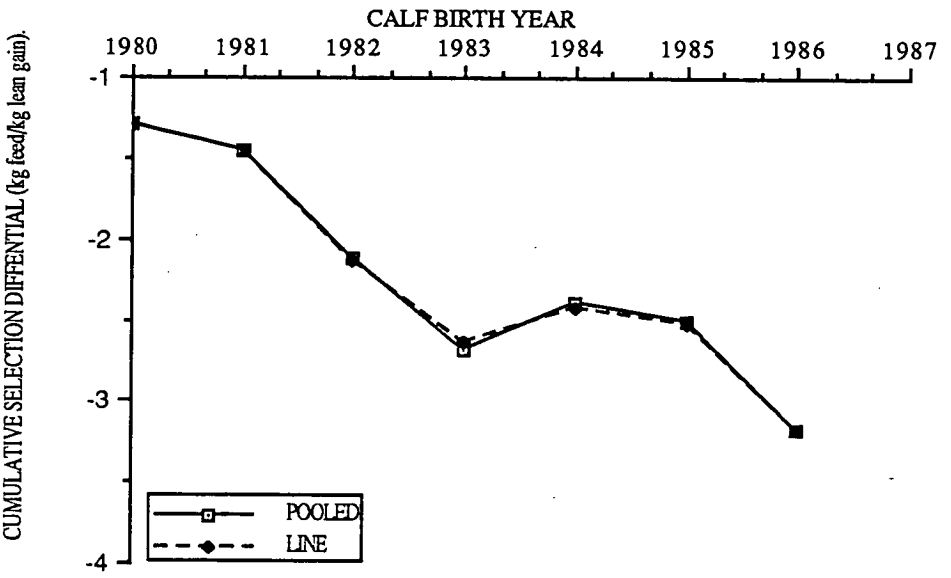

Fig. 4.6 Cumulative selection differentials for LFCR, pooled and line estimates.

Therefore all subsequent discussions on CSD are restricted to the pooled estimates calculated by the correct method. Direct sire selection accounted for 67% of the CSD for LGR and 65% for LFCR in their respective lines, and the use of heifers which were progeny of previously selected bulls accounted for the rest.

Regression coefficients of cumulative selection differentials on years in standard deviation unit indicating the rate of accumulation of selection pressures applied over the years are presented in Table 4.7. Cumulative selection differential increased at the rate of 0.21 SDU per year for LGR and -0.16 for LFCR in their respective line, indicating that the selection differential accumulated at a slightly faster rate for LGR.

Secondary CSD for LGR in the LFCR line and LFCR in LGR line were 47% and 57% respectively of the primary CSD from direct selection for these traits in their respective lines. However the rate of increase of secondary CSD for LFCR in LGR line was of the same magnitude as the primary CSD for LFCR, but the pattern of accumulation was rather erratic (Table 4.7 and Fig. 4.2).

Plots of mean CSD in standard deviation units for LGR and its component traits, growth rate and LEAN in the LGR line by calf birth year (Fig. 4.7) indicated that the pattern of accumulation of selection differential for LGR was much more similar to that of growth rate than to LEAN. In terms of SDU, the secondary CSD for growth rate was 89% of the primary CSD for LGR, while that of lean was only 42%. This indicates that much of the selection pressure on LGR was on growth rate rather than on LEAN. Similar plots of mean standardised CSD for LFCR, FCR and LEAN (Fig. 4.8) showed a somewhat similar pattern of accumulation for LFCR and its component

TABLE 4.7

Regression coefficients of primary cumulative selection differentials on calf birth year in standard deviation units

	Traits						
Line	BW	LEAN	FEED	GRT	LGR	FCR	LFCR
LGRL	-0.009	0.130	0.11	0.169	0.209	-0.112	-0.171
LFCRL	-0.014	0.138	-0.055	0.064	0.120	-0.118	-0.164
CTL	0.020	0.043	-0.046	-0.037	0.05	-3.078	-0.063

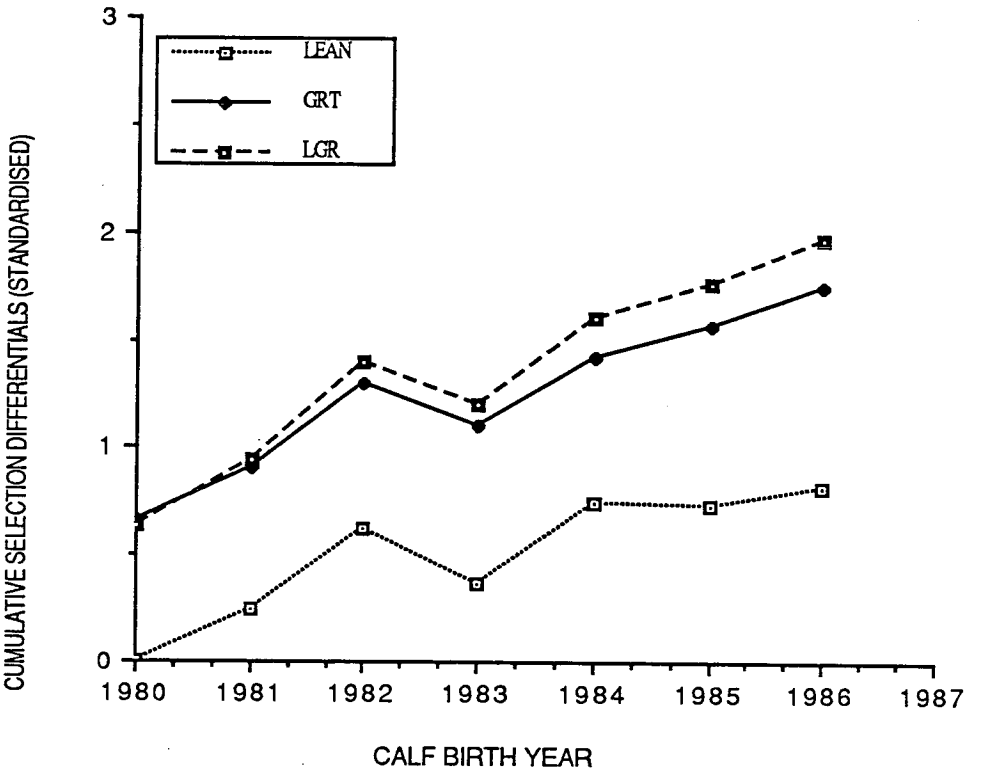

Fig. 4.7 Cumulative selection differentials for LGR, GRT and LEAN in the LGR line.

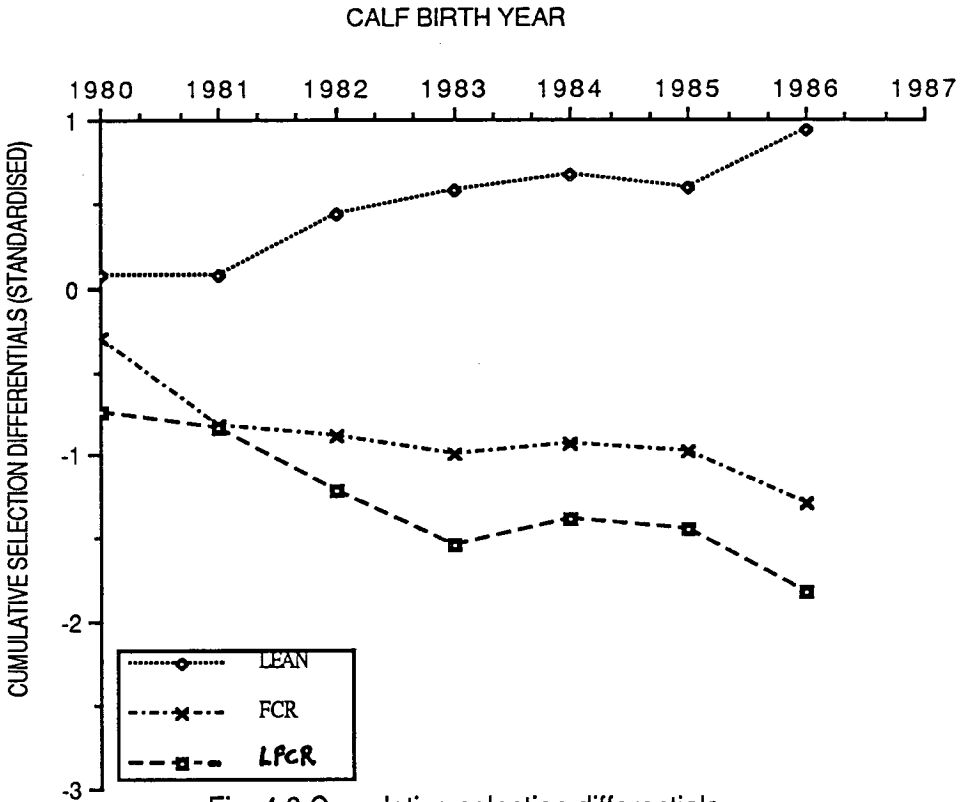

Fig. 4.8 Cumulative selection differentials for LFCR, FCR and LEAN in the LFCR line.

traits: LEAN (although in the opposite direction) and FCR. However, the secondary CSD for FCR and LEAN in the LFCR line were 70% and 51% of the primary CSD for LFCR.

The secondary CSD for growth rate in the LFCR line was only 41% of that realised in the LGR line (0.73 versus. 1.76 SDU) and the reverse was true for FCR in both lines. There was a difference of 37% between the secondary CSD for FCR realised in the LGR line and LFCR line, in favour of the latter. However secondary CSD for FEED and LEAN were about the same in both lines but were in opposite directions for FEED.

In the control line, there was a slight amount of selection for LGR and LFCR. This was due primarily to the use of heifers which were progeny of bulls in the foundation herd as dams in the control line.

(ii) Actual and maximum potential selection differentials

The annual selection differentials for selected sires in actual and standard units are given in Table 4.8. About 0.648 and -0.680 standard deviation of selection have been applied on LGR and LFCR each year in their respective lines. Selection differentials on a generation basis (that is, EFSD) were about twice the annual selection differentials because sires had their progeny at about two years of age and were used once in most cases (Table 4.9).

Comparison of the actual (effective) selection and expected selection differential (Table 4.10) indicates that actual selection differentials for LGR and LFCR were 100% and 83% respectively of their expected values in their respective lines. This seems to show that little natural selection was operating

TABLE 4.8

Annual selection differentials for selected sires in actual units and standard measure

Trait	In actual measure		In standard measure	
	LGRL	LFCRL	LGRL	LFCRL
BW (kg)	0.214	0.669	0.067	0.210
LEAN (%)	0.473	0.651	0.206	0.283
FEED (kg)	22.871	-25.16	0.187	-0.206
GRT (g/day)	46.16	22.917	0.588	0.292
+LGR (g/day)	19.59	12.268	0.648	0.406
FCR (kg feed/kg gain)	-0.001	-0.280	-0.002	-0.465
+LFCR (kg feed/ kg lean gain	-0.442	-1.180	-0.254	-0.680

+ Primary selection differentials
All other estimates are secondary selection differentials

TABLE 4.9

Mean selection differentials per generation for selected sires in actual units and standard measure

Trait	In actual measure		In standard measure	
	LGRL	LFCRL	LGRL	LFCRL
BW	0.415	1.460	0.130	0.457
LEAN (%)	0.970	1.311	0.422	0.570
FEED (kg)	46.49	-53.05	0.381	-0.434
GRT (g/day)	92.71	44.45	1.182	0.567
+LGR (g/day)	39.33	24.23	1.300	0.801
FCR (kg feed/kg gain)	-0.002	-0.597	-0.003	-0.993
+LFCR (kg feed/ kg lean gain)	-0.880	-2.478	-0.507	-1.428

+See Table 4.8 for explanation of symbol

against LFCR.

Similarly, comparison of the selection differential achieved and the maximum potential selection differential (MPSD) for each primary trait provides an evaluation of how effective actual selection was relative to the intended selection. The MPSD are presented in Table 4.10. Usually, most comparisons of the selection differentials realised and the maximum potential have been between the effective (weighted) selection differential (EFSD) and maximum potential calculated as the highest mean ISD possible (Frahm et al., 1985a; Aaron et al., 1986a). Since the weighting of the selection differential partly accounts for the effects of natural selection (Falconer, 1981), a comparison of the EFSD to the MPSD does not seem appropriate especially if natural selection is of importance. For instance, if natural selection is operating in favour of a trait through differences in fertility, the EFSD might be higher than the MPSD as high ranking individuals might tend to have more progeny. It seems therefore that a comparison of unweighted selection differential (EXSD) and MPSD might be more appropriate for evaluating the effectiveness of the selection achieved relative to the maximum possible. In the LGR line, the selection differential achieved for LGR was 97% of the maximum potential for sires on the basis of selection within replicates; while the corresponding estimate of LFCR was 89% in the LFCR line. A similar estimate was obtained for LFCR when the achieved selection differential was compared with MPSD calculated on the basis of selection within lines; however that of LGR dropped to 90%. This further confirms that selection within replicates rather than within lines did not drastically affect selection differentials achieved in

TABLE 4.10

Unweighted actual and maximum selection differential for selected sires in both lines

Line	Trait	Actual[1]	Maximum[2]	
			Pooled	Line
LGRL	LGR g/day	39.40	40.69	43.62
LFCRL	LFCR kg feed/ kg lean gain	-2.054	-2.312	-2.346

[1]Not weighted by the number of progeny contributed to the next generation

[2]Maximum selection differential was calculated on two basis within replicates and pooled, and in overall line.

this experiment.

4.4 Discussion

Although selection was applied only on males, the 1.5 generations of selection observed in both selected lines, corresponding 4.67 years per generation, is similar to the results from other selection experiments in beef cattle with both bulls and heifers selected. After 15 years of selection, Frahm et al. (1985a) reported 3.22 and 3.21 generations of selection respectively for their weaning (WW) and yearling (YW) lines corresponding to 4.66 and 4.67 years per generation respectively. Aaron et al. (1986a) reported slightly higher number of generations of selection 3.87 and 3.72, for two lines of Angus selected for WW and YW respectively after 16 years of selection. Compared with the selected lines of Irgang et al. (1985a) in which selection was similarly applied only on males, the generation turnover observed in this study is much higher. They reported about 2.0 generations of selection in each of the two lines selected for weaning weight and post weaning gain after 12 years of selection, corresponding to about 6 years per generation. The rapid rate of generation turnover is due to the design of the experiment; selected bulls were used for breeding at an early age (about 1 year of age) and were used only once. In addition, heifers which were daughters of previously selected bulls were used early as replacement for foundation cows.

The inbreeding coefficients for calves observed are higher than those reported by Buchanan et al. (1982a) and Irgang et al. (1985a), accounting for differences in the number of years animals have been selected. Although selection was similarly only on males

and within sire family on the selected lines of Irgang et al. (1985a), selection was in addition within replicates in this study, with about 2 sires per replicate. This small number of sires per replicate may account for the slightly higher inbreeding coefficients of calves observed. However, inbreeding coefficients were much higher in the study of Nelms and Stratton (1967).

Most reported estimates of cumulative selection differential in the literature are averages of sires' and dams' CSD (midparent CSD) and are usually expressed in terms of rate of increase per year (by regression on years of selection). Chevraux and Bailey (1977) reported a rate of 0.22 SDU per year for midparent CSD in the line selected for postweaning gain ; Buchanan et al. (1982a) reported increases of 0.24 SDU per year for both WW and YW and Aaron et al. (1986a) observed rates of 0.27 and 0.25 SDU respectively in their WW and YW lines. The rates of 0.21 SDU and -0.16 SDU per year observed respectively in the LGR line and LFCR line for the increase of CSD through only sire selection are similar to the estimates from the reports mentioned above, since sire selection accounted for about 70 to 84% of the selection pressure applied in those studies.

Atkins (1985) and James (1986) have demonstrated that with overlapping generations, the Pattie (1965) (ICM) method for calculating CSD is biased upwards and tends to underestimate realised heritability, while the method of Newman et al. (1973) was correct. In this experiment, estimates of CSD by both methods were similar, although slightly lower for ICM. Frahm et al. (1985a) have reported that D.S. Buchanan (unpublished data) obtained very similar average CSD for any particular year by both methods in the

Nebraska study. The similarity between estimates of CSD by both methods in this study could be attributed to the following reasons:

1. As mentioned earlier, James (1986) showed that the total CSD estimated by the ICM in any year is equivalent to weighting the phenotypic deviations of all previous parents by their proportionate genetic contribution to individuals in that year. He therefore argued that the better parents in any generation will tend to have above average progeny, and so will have more progeny than average selected. Thus their genetic contribution to the grand-progeny generation will be greater than to the progeny generation. The consequence is that higher deviation will receive progressively more weight for some generation resulting in CSD being biased upwards. However, in this study selection was within replicates and sire families, and with only two bulls per replicate, the contribution of male progeny to the next generation was not always higher in some years for the superior of the two bulls. The consequence is that ICM tends to underestimate CSD compared to the CM, as it does not take account of the worth of contemporaries. Actually in one of the replicates (the second replicate) in the LGR line the estimate of CSD by the ICM were about 17% lower than by the correct method. The pooled estimate of CSD by the ICM for LGR in the LGR line was consistently about 2% lower than by the CM in the last 3 years.

2. Secondly, a few years after the selection commenced, dams consisted of foundation cows and heifers which were progeny of previously selected bulls. If the selected bulls in any such year were progeny of foundation cows, the ICM ignores the selection

differential accumulating through the heifers, which are progeny of previously selected bulls, in calculating the CSD for the next generation. The CM however incorporates such selection pressure in estimating CSD for the next generation, because it takes account of the genetic worth of all contemporaries of selected bulls.

The above therefore indicates that ICM, by ignoring the genetic worth of contemporaries in estimating CSD, could lead either to an upward or downward bias in CSD. The bias may not be apparent in this study because of the within sire family selection practised with only two sires per replicate, thereby limiting the range of selection.

In practice, since selected individuals in most selection experiments of beef cattle are usually deviated from their contemporary line-year-sex mean rather than from the average of progeny of the individual's parents, most recent workers (Buchanan et al., 1982a; Frahm et al., 1985a; Irgang et al., 1985a; Nicholl and Johnson, 1986) have shown preference for and/or used the correct method in calculating CSD.

In most beef selection experiments about 0.20 SDU of annual midparent selection differential has been reported on the basis of selection on individual performance. With sire selection accounting for about 70 to 80% of the selection applied, this is equivalent to approximately 0.30 SDU of annual selection differential applied through sires. Specifically, Koch et al. (1974a) reported an unweighted average annual selection differential of 0.31 for WW in the WW line and 0.38 for YW in the YW line through sire selection. Chevraux and Bailey (1977) reported 0.36 for postweaning gain. However, high values of 0.64 and 0.68 have been

observed for LGR and LFCR respectively in their individual lines. This may be attributed to the low average age of bulls in this study. The average age of sires was about 2.0 years compared to 4.06, 3.37 and 3.0 reported respectively by Koch et al. (1974a), Chevraux and Bailey (1977) and Irgang et al. (1985a). The above seems to be confirmed by the fact that on a generation basis, the selection differentials observed are consistent with the reports of other workers. For instance, Chevraux and Bailey (1977) and Buchanan et al. (1982a) reported an average selection differential of 1.55 SDU per generation from direct sire selection for postweaning gain and weaning weight respectively. Koch et al. (1974a) reported a similar estimate of 1.51 SDU for WW and 1.18 for YW and Aaron et al. (1986a) 1.30 and 1.52 SDU for WW and YW respectively in their individual lines. Thus the selection pressure in this study are as intense as in most beef selection experiment but are higher on an annual basis because of the rapid generation turnover. The theoretical selection differentials for the top 6 bulls in a normally distributed population with n=20 is about 1.11 standard deviations (Falconer, 1981) and this is close to the estimates observed.

One of the arguments against selection for growth rate in beef cattle is the problem of increased birth weight (BW) resulting in increased incidence of dystocia and calf mortality. It may be worthwhile to compare estimates of secondary selection differential for BW in this study to those obtained from direct selection for growth rate. The secondary selection differentials obtained per generation by Koch et al. (1974a), Buchanan et al. (1982a) and Frahm et al. (1986a) for BW from sire selection for WW were 0.58, 0.90 and

0.59 SDU respectively. Corresponding estimates from YW selection were 0.58, 0.77 and 0.75 SDU respectively. In the LGR line, the secondary selection differential for BW per generation was much lower than the reported estimates; but in the LFCR line, the estimate was only slightly lower. This implies that the selection pressure on BW in the LGR line and LFCR line was not as intense as with direct selection for growth rate.

As in most selection experiments on beef cattle, only a proportion of the maximum possible selection differential has been achieved in both selection lines. The proportions achieved are however similar to estimates by other workers (Irgang et al. 1985a; Nicholl and Johnson, 1986). Failure to realise the maximum possible selection differential was due to the within sire family selection practised.

CHAPTER 5

DIRECT AND CORRELATED RESPONSES FOR LGR AND LFCR IN SELECTED AND OPEN LINES

5.1 Introduction

Direct and correlated cumulative responses to selection for LGR and LFCR in selected and open lines are examined in this chapter. The annual rates of genetic change achieved and estimates of realised genetic parameters from various methods of analyses are reported.

5.2 Materials and methods

5.2.1 Description of lines

The structure of the two selected lines, the open and control lines, the management of animals and selection procedure have been described in Chapter three.

5.2.2 Statistical methods

Response to selection was evaluated using three methods:

a. deviation from a control population,

b. the recursive prediction of progeny breeding value and

c. the estimation of (co)variance components and prediction of genetic trend by Restricted Maximum Likelihood.

(a) Deviation from control population

(i) Estimation of cumulative response

Cumulative direct response to selection for LGR and LFCR each year in their respective lines were calculated as the deviation of the mean phenotypic performance of each selection line from the mean performance of the control line. To provide a measure of average response over time, yearly genetic responses were regressed on calf birth year as suggested by Falconer (1981). Usually in beef selection experiments these regressions are considered as the genetic

(time) trends with the variances equal to the estimated variances from the regressions fitted. This is based on the assumption that the variance of response is consistent over years and the responses are independent each year. This may be inappropriate, because Hill (1972b,c) has indicated that the variance of response increases each year due to drift and that responses in different years are correlated. Using a variance-covariance matrix developed for response (see equation (9)), the variance of annual genetic change was estimated as:

$$(X'X)^{-1}X'V \quad X(X'X)^{-1} \qquad (1)$$

where

X = vector of calf birth year

V = variance-covariance matrix of response

The same procedure was used to evaluate correlated responses.

Since the open line was not derived from the same base population as the control, genetic trends estimated as for the selected lines would not be appropriate. The bulls used in the open line were superior bulls from AI stations and would be expected to be of higher genetic merit than the control even in the first year they were used. Genetic trends in the open line were therefore estimated relative to the difference between the open and control lines in the first year; that is, the deviation of the open line from the control in the first year was used as the intercept through which the regression of the deviations of the open from the

control on years was forced. This was carried out by fitting the following model using the Genstat statistical package on a data set consisting of the control and open line.

$$Y_{ijk} = u + t_i + B.x_{ij} + D.z_{ik} + e_{ijk} \quad (2)$$

where

Y_{ijk} = observations for the open and control lines

u = overall mean

t_i = ith calf year effect

x_{ij} = a variate of ones representing the open line and zeros for the control lines

z_{ik} = a variate which was equal to one for the open line in the first year and increased linearly by one every subsequent year for the open line otherwise it was zero

B = regression coefficient of Y on x_{ij}, provides an estimate of the difference between open and control lines in the first year

D = regression coefficient of Y on z_{ij}, estimates linear changes in the open relative to the control across years

e_{ijk} = random error

The D in the above model represents an estimate of genetic trend in the open line relative to the initial difference between the open and control lines. The above method was checked by actually deviating the open line from the control every year and regressing the deviations on years. Similar estimates were

obtained as when the above model was fitted, but the use of the model was preferred as standard errors were estimated from the actual observations rather from the mean of observations with account not being taken of number of records used to estimate the means. Using the model above, genetic trends were estimated for LGR and LFCR in the open line.

(ii) Realised heritabilities

Realised heritabilities for LGR and LFCR were estimated as the linear regression of cumulative direct response in each respective line on deviations of mean cumulative selection differential in each line from CSD in the control line. Because control animals were selected at random the mean CSD in this line is expected to be zero.

Hill (1972c) showed that the variance of an unweighted regression of response on CSD is biased downwards since the individual year observations are assumed to have equal variance and to be uncorrelated, when in reality the variance of the population mean increases and are correlated due to genetic drift. In replicated selection experiments, an appropriate variance of response can be estimated directly from the variance among replicates (Hill, 1971). Such variance of response between replicates represents the sum of genetic drift and random error. However, with only three replicates per line, the variance that has to be estimated has only two degrees of freedom. Such an estimate of between line variance, although unbiased, is unreliable (Hill, 1980) hence an alternative method was used to estimate the variance of response.

In random mating populations, the process of genetic drift

is well understood. Gene frequency changes due to genetic drift in different generations are independent, but cumulative drift in a particular generation is the result of the sum of random deviations in all previous generations. Hence, the variance of the genetic mean increases each generation and means of different generations become correlated.

However in directionally selected lines, the variation between means is less well understood. Briefly, as stated by Sorensen and Kennedy (1983), selection leads to the following phenomena:

(i) Selected individuals tend to be genetically more alike due to increase in homozygosity than randomly chosen ones and this tends to reduce the variance of response.

(ii) The within-line genetic variance differs between lines due to finite population size (Avery and Hill, 1977) and results in real differences in response in different lines. This effect will tend to increase the variance between lines.

(iii) Selection causes negative covariances of gene frequencies in gametes, that is, negative linkage disequilibrium. This leads to a reduction in the additive genetic variance within lines (Bulmer, 1971) and this will decrease variance between lines.

(iv) Finally, directional selection causes changes in gene frequency, changes in gene frequency can have an effect on drift variance in either direction depending upon the initial distribution of gene effects and frequencies. All these phenomena have opposing effects on the variance of selection response and a simple operational compromise is to assume that they cancel each other out

approximately.

The effect of drift on the genetic mean cannot be predicted in any one replicate but the magnitude of variances between lines due to genetic drift can be quantified from the knowledge of the population structure before the experiment is carried out. Hill (1971, 1972b,c) using this a priori approach, developed formulae for the estimation of the variance of response.

However, Sorensen and Kennedy (1983) recently showed that the inclusion of the matrix of the additive genetic relationships among individuals (the relationship matrix) in the computation of sampling variance of estimates of genetic means accounts for variance due to drift (assuming an infinitesimal model and additive gene action). The relationship matrix (A) for a group of animals is defined as the matrix with the ijth off-diagonal element equal to the numerator of Wright's (1922) coefficient of relationship of the ith and jth animals and with the ith diagonal element equal to $1+F_i$, where F_i is the coefficient of inbreeding of the ith animal. They indicated that the variance of genetic mean in any particular generation that takes account of the correlated structure among observations can be estimated by the equation below:

$$V(b) = (X'X)^{-1}X'ZAZ'X(X'X)^{-1}\sigma_a^2 + (X'X)^{-1}\sigma_e^2 \qquad (3)$$

where

b = the vector of generation or year effects (means)

X = the incidence matrix of ones and zeros representing generations or years

Z = incidence matrix for number of records per individual; with one record per individual Z is equal to I

A = relationship matrix

σ_a^2 and σ_e^2 = are the additive genetic and residual variances respectively in the base population

The first term in expression (3) is due to drift and for a particular generation represents the average additive genetic variance and covariance between individuals in that generation. Sorensen and Kennedy (1983) stated that the use of the relationship matrix being essentially a retrospective approach accounts for reduction in effective population size due to selection (Robertson, 1961) with associated increase in drift variance.

Using the above approach, pedigrees consisting of each selected line and the control animals were set up and used to compute the relationship matrix. The variance and covariance matrix for the vector of phenotypic means of the ith and jth year-line combinations (i<j) was estimated using expression (3), which could also be written illustratively as

$$V(b) = \begin{bmatrix} a_{11} & a_{12} \cdots a_{it} \\ a_{21} & a_{22} \cdots a_{2t} \\ \cdot & \cdot \quad \cdot \\ \cdot & \cdot \quad \cdot \\ \cdot & \cdot \quad \cdot \\ a_{t1} & a_{t2} \cdots a_{tt} \end{bmatrix} h^2\sigma_p^2 + (X'X)^{-1}(1-h^2)\sigma_p^2 \qquad (4)$$

$$= \bar{A}h^2\sigma_p^2 + (X'X)^{-1}(1-h^2)\sigma_p^2 \qquad (5)$$

with

b = vector of phenotypic mean for the year-line combinations

X = incidence matrix for year-line combinations

h^2 = initial heritability from unweighted regression of response on CSD

σ_p^2 = phenotypic variance of trait estimated from within year analysis (Hill, 1972c)

$\bar{A}$ = a symmetric matrix of the average additive genetic relationship between individuals in the ith and jth year-line combinations ($i = 1, \ldots t$; $j = 1, \ldots .t$); t equals twice the number of years of selection (m).

Genetic response was however estimated as a deviation of the mean performance of the selected line from the control line. Therefore the variance of response, V(R), in the ith year was estimated as:

$$V(R_i) = (a_{isis} + a_{icic} - 2a_{isic})h^2\sigma_p^2 + (\frac{1}{n}_{isis} + \frac{1}{n}_{icic})\sigma_p^2(1-h^2) \quad (6)$$

and the covariance of response in the ith and jth year ($i<j$) as,

$$Cov(R_i,R_j) = (a_{isjs} - a_{isjc} - a_{icjs} + a_{icjc})h^2\sigma_p^2 \quad (7)$$

where s and c refer to the selected and control lines respectively and n is the number of animals in either of the lines.

Using matrices, the variance-covariance matrix of response was estimated as,

$$V(R) = (TPT')h^2\sigma_p^2 + [D_s^{-1} + D_c^{-1}]\sigma_p^2(1-h^2) \quad (8)$$

$$= Gh^2\sigma_p^2 + [D_s^{-1} + D_c^{-1}]\sigma_p^2(1-h^2) \quad (9)$$

where

$P = X'AX$

$T_{i+i-1,\ 2i} = \frac{1}{n_{is}},\ -\frac{1}{n_{ic}}$; i=1 to m (the number of years of selection)

T_{ij} = 0 otherwise

$D_{sii} = n_{is}$

D_{sij} = 0 otherwise

$D_{cij} = n_{ic}$

D_{cij} = 0 otherwise

Although expression (9) takes care of the genetic drift in estimating the variance of response, it has not however accounted for the regression fitted. The regression of cumulative response on cumulative selection differential is equivalent to the regression of the breeding value of offspring on that of either parents or on mid-parental mean, depending on the type of selection practised (Falconer, 1981). With only sires selected in this experiment, it is equivalent to regression of the breeding value of an offspring (a_o) on that of its sire (a_s), which can be expressed as

$$a_o = (1/2)a_s + e \quad (10)$$

where e has variance σ_w^2 which is the residual variance of an offspring given one parent. The residual variance σ_w^2 is equal to

(Thompson, personal communication):

$$V_p - V((1/2)a_s); \text{ with } V_p = \text{phenotypic variance of offspring} \qquad (11)$$

$$= \sigma_e^2 + \sigma_a^2 - (1/4)h^4(\sigma_e^2 + \sigma_a^2) \qquad (12)$$

$$= o_e^2 + o_a^2 - (1/4)\sigma_a^4/(\sigma_e^2 + \sigma_a^2)$$

$$= \sigma_e^2 + (3/4)\ \sigma_a^2 + (1/4)\ \sigma_a^2\ (1-h^2) \qquad (13)$$

where $(3/4)\sigma_a^2$ is the contribution to the variance from dam and mendelian sampling and the contribution from the sire is reduced in proportion $(1-h^2)$.

Incorporating the matrix G in expression (9), which represents the additive genetic relationship between response in different years, expression (13) can be written as,

$$(G - 3/4I)\sigma_a^2(1-h^2) + (3/4)I\sigma_a^2 + I\sigma_e^2 \qquad (14)$$

approximately arguing that the covariance between relatives should be reduced by the same order as the reduction of the sire variance contribution to (13); this is an approximate argument for half sibs and for other relatives.

Re-arranging expression (14) gives,

$$G\sigma_a^2(1-h^2) + (3/4)h^2\sigma_a^2I + I\sigma_e^2 \qquad (15)$$

The variance and covariance of response (expression 9) can now be

written as

$$V(R) = G\sigma_a^2(1-h^2) + [D_s^{-1} + D_c^{-1}][(3/4)h^2\sigma_a^2 I + I\sigma_e^2] \quad (16)$$

approximately with σ_e^2 and σ_a^2 being equivalent to $\sigma_p^2(1-h^2)$ and $h^2\sigma_p^2$ respectively in expression (9).

Compared to equation (9), the first term in equation (16) represents a decrease in the additive genetic variance and covariance (drift variance) between response in different years due to fitting the regression and the term $(3/4)h^2\sigma_a^2 I$ in the second part of the expression represents the contribution to the error variance from the fitted regression. Using the variance-covariance matrix developed in (16), an estimate of realised heritability (h_R^2) was obtained from a generalised least-squares solution of the regression of response on selection differential as,

$$h_R^2 = (X'V^{-1}X)^{-1}X'V^{-1}Y \quad (17)$$

and the variance of h_R^2 was estimated as,

$$V(h_R^2) = (X'V^{-1}X)^{-1} \quad (18)$$

where

X = vector of cumulative selection differentials

Y = vector of cumulative responses

V = variance-covariance matrix of cumulative response from (16).

(iii) Realised genetic correlation

A joint estimate of the genetic correlation (r_g) between LGR and LFCR was obtained (Falconer, 1981) as:

$$r_g = \left[\frac{CRS_{LGR} * CRS_{LFCR}}{DRS_{LGR} * DRS_{LFCR}} \right]^{1/2} \qquad (19)$$

where CRS and DRS represent estimated correlated and direct responses per year respectively. An approximate standard error for r_g was calculated as suggested by Hill (1971), using the variances of heritabilities estimated from equation (18).

(b) Prediction of progeny breeding values

This method is essentially concerned with prediction of breeding values of progeny from their own performance and their parents with account being taken of the changes in the regression coefficient in each generation of selection. The heritability that minimises the sums of squares of deviations between predicted and observed progeny value is an estimate of realised heritability. As mentioned in chapter four, this method is a combination of the correct and incorrect methods for estimating cumulative selection differential. Both the correct and incorrect methods ignores the reduction in genetic variation due to selection and yield downward biased realized heritability estimates. This method accounts for the reduction in genetic variation and utilises both ancestral and contemporary information with the relative weight depending on the value of the heritability (Juga and Thompson, 1988).

We will briefly illustrate how the breeding value of progeny might be predicted from parental values and their values in a single generation and later on describe how this could be done recursively across several generations by means of BLUP. The details of the methodology are given by Juga and Thompson (1988). Suppose a sire is measured in year zero with a value of Y_F and an offspring with a value of Y_G is measured in year one. The mean of unselected animals in year i is assumed to be u_i. Suppose the trait has variance 1, genetic variance and heritability h^2; the predictor of the breeding value of the sire is then

$$A_F = h^2(Y_F - u_o)$$

and the predictor of the offspring from the sire is

$$A_{GP} = (A_F)/2,$$

and using the offspring's own information

$$A_G = A_{GP} + h_1^2(Y_G - u_1 - A_{GP}) \qquad (20)$$

with $h_1^2 = [(h^2 - 0.25h^4)/(1-0.25h^4)]$

Expression (20) can be derived with a selection index or by noting that the genetic regression of Y_G on Y_F and $Y_G - A_{GP}$ are $h^2/2$ and h_1^2 and that Y_F and $Y_G - A_{GP}$ are uncorrelated.

The argument can be extended to predict the breeding values of animals successively for each generation using individual

information and predictions from parents (based on their own and parental predictions). Using Best Linear Unbiased Prediction (BLUP) and mixed model arguments (Henderson, 1973) it is shown in the appendix that a predictor of an offspring with measurement Y_G in year i from sires only is:

$$A_G = A_{F/2} + h_G^2(Y_G - u_i - A_{F/2}) \text{ with} \qquad (21)$$

$$h_G^2 = \frac{3h^2/4 + (1-h^2)\, h_F^2/4}{1-h^2/4 + (1-h^2)\, h_F^2/4}$$

where A_F is the predictor of the sire value and h_F^2 is the regression coefficient involved in deriving A_F. In year zero, when $h_F^2 = h^2$, $h_G^2 = h_1^2$. The coefficients h_G^2 estimated every generation can be interpreted as genetic regression coefficient given ancestral information. In the early years of the experiment, when records were available only on progeny and sires, equation (21) was used for the prediction of progeny breeding value. However in later years when female progeny of selected bulls were used as dams, prediction of progeny breeding value also included information from grand maternal sires. Using similar arguments to the derivation of expression (21) it is shown in the appendix that the predictor of progeny breeding value from its own value, sire and grandmaternal values is:

$$A_G = (A_{M/4} + A_{F/2}) + h_G^2\,(Y_G - u_i - (A_{M/4} + A_{F/2})) \qquad (22)$$

$$\text{with } h_G^2 = \frac{11h^2 + (1-h^2)\,(4h_F^2 + h_M^2)}{16-5h^2 + (1-h^2)\,(4h_F^2 + h_M^2)}$$

where A_M and A_F are predictors of grandmaternal sire and sire breeding values respectively and h_M^2 and h_F^2 are the regression coefficients in deriving A_M and A_F.

Using each selected line and the control line with an initial heritability input, equations (21) and (22) were used to predict progeny breeding value in each generation of selection and the heritability estimate (an estimate of realised heritability) which minimised the sums of squared residuals, that is, difference between predictions and observed values was found by iteration.

A 97.5% confidence interval for the realised heritability estimate was constructed (Thompson, personal communication) as

$$CI = F_{0.975} \times MSS(h^2) + RSS(h^2) \qquad (23)$$

where RSS = residual sums of squares, that is, the difference between progeny predicted and observed values

MSS = residual mean squares, that is, RSS divided by degrees of freedom

$F_{0.975}$ = 2.5% F value from tabulated values of F distribution

CI = lower and upper limits of confidence interval which are equal to the lower and higher h^2 respectively with RSS equal to the right hand side of (23).

(c) REML to estimate (co)variance components and predict genetic trend

A full description of the principles and procedures of REML for the estimation of variance components has been given by Patterson and Thompson (1971) and only a few salient points as far a it relates to the model fitted are stated.

The model

$$y = Xb + Z_1u + e \qquad (24)$$

where

y = nx1 vector of observations

b = tx1 vector of fixed effects (calf birth year, age of dam, rearing type, day of birth and initial weight on test (for LFCR only)

u = qx1 vector of random effects

e = vector of random error effects

X = the incidence matrix pertaining to b

Z_1 = the incidence matrix pertaining to u; Z_1=1 since each animal had one record

Let

$$E \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} Xb \\ o \\ o \end{bmatrix}$$

$$\text{Var}\begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & o \\ o & I\sigma_e^2 \end{bmatrix}$$

$$V(y) = Z_1 G Z_1' + I\sigma_e^2$$

with $G = A\sigma_a^2$

It was thought that the use of dams for several years might induce maternal environmental covariances between performance of calves of the same dam across years. The data were initially analysed using the above model (equation 24) and the maximum likelihood was calculated for each trait in a univariate analysis. Dams were then included in the model as a random effect which was absorbed with an initial input of α , the ratio of the error variance (σ_e^2) to the dam variance component (σ_D^2).

An estimate of the dam variance component therefore equals

$$\sigma_D^2 = \frac{\sigma^2_e}{\alpha}$$

If there is a high maternal environmental covariance between progeny of the same dam, then σ_D^2 which is estimate of the variance between families, would be large. Consequently, the maximum likelihood calculated should increase with decreasing values of α for such a trait. One other other hand, when maternal environmental covariance is minimal, σ_D^2 will similarly be very low or negligible, therefore

the maximum likelihood should increase with increasing values of α. The likelihood was calculated with various values of α. It was discovered that the likelihood increased for both selected traits as the value of α increased and an α value of 10,000 gave the maximum likelihood which was essentially the same likelihood obtained when no dams were fitted in the model. This implies that maternal environmental effects were not of significant importance in these traits and were dropped from the model.

The mixed model equations (MME) pertaining to expression (24) are:

$$\begin{bmatrix} X'X & X'Z_1 \\ Z_1'X & Z_1'Z_1 + A^{-1}\gamma^{-1} \end{bmatrix} \begin{bmatrix} b \\ u \end{bmatrix} = \begin{bmatrix} X'y \\ Z_1'y \end{bmatrix} \qquad (25)$$

with $\gamma = \sigma_a^2/\sigma_e^2$.

The objective is to estimate the variance between (σ_a^2) and within (σ_e^2) levels of the random effect. For an iterative estimation procedure, the numerator relationship matrix which describes the covariance structure between levels of the random effects can be incorporated into the design matrix so that the random effects are independently distributed, yielding an equivalent model to (24) (Quass, 1984). Under the equivalent model, variance components can be estimated as if animals were unrelated, reducing computational effort. The relationship matrix, being a covariance matrix, is (semi) positive definite, hence a lower triangular matrix L always exists such that A=LL'. The variance of Y can be expressed as,

$$V(y) = Z_1'LL'Z_1'\sigma_a^2 + I\sigma_e^2$$

Defining $Z = Z_1L$ then yields an equivalent model to (24):

$$y = Xb + Zu^* + e \qquad (26)$$

with $V(u^*) = I\sigma_a^2$ and

$$u^* = L^{-1}u$$

The computational procedures involved in incorporating A as LL' to yield the equivalent model are fully described by Meyer (1987). A faster algorithm developed in the course of this work is presented in chapter nine. The MME pertaining to (25) for random effects absorbing fixed effects are:

$$[Z'SZ + \gamma^{-1}I] \quad u^* = Z'Sy$$

This gives solutions:

$$u^* = (Z'SZ + \gamma^{-1}I)^{-1} Z'Sy = C\,Z'Sy \qquad (27)$$

$$u = Zu^*$$

REML equations to estimate σ_a^2 and σ_e^2 using an EM-algorithm are (Meyer, 1987).

$$\sigma_a^2 = u^{*\ell}u^*/[ns - \gamma^{-1}tr(C)] \qquad (28)$$

$$\sigma_e^2 = [y'Sy - y'SZU^* - \gamma^{-1}u^*u^*]/[n-r(X) - ns + \gamma^{-1}tr(C)] \qquad (29)$$

where ns denote the number of levels of the random effect, n the number of observations and r(X) the rank of X.

The analysis of data was carried out using univariate and multivariate programs written by Karin Meyer (see Meyer, 1983; 1985). A univariate analysis was carried out for LGR and LFCR in their respective lines (LGRL or LFCRL) or in their respective lines plus the control (POP1 or POP2). For the estimation of variance and covariance components of LGR and LFCR a multivariate analysis was done firstly in each of the selected lines only, secondly in either of the selected line plus the control and thirdly in all three lines (POP3). From (24) it can be seen that the design matrices for LGR and LFCR are different, but Meyer's programs were for traits with equal design matrices. The weight at beginning of test (IWT) fitted as a covariate is only relevant to LFCR. To overcome this problem, an initial multivariate analysis was carried out for LGR, LFCR and IWT in POP3 with all other fixed effects fitted. This yielded estimates of genetic and phenotypic correlations between the three traits. The regression coefficient for the regression of LFCR on IWT was estimated from the phenotypic correlation between the two traits and their phenotypic standard deviations. The estimated regression coefficient was comparable to a pooled estimate from yearly estimates which were used for adjustment during the actual selection of animals. Using the regression coefficient estimated, LFCR was adjusted for the effects of IWT. This was followed by another multivariate analysis on LGR, adjusted LFCR and IWT to check if the adjustment was effective. The phenotypic correlation between the adjusted LFCR and IWT was essentially zero, indicating that the adjustment was effective.

The results reported were based then on the multivariate analysis of LGR and the adjusted LFCR.

5.3 Results

5.3.1 Genetic change or response

Direct and correlated cumulative responses for LGR and LFCR per year from deviation of selected lines from control method (1) are shown in Figures 5.1 and 5.3. Estimated linear genetic time trends are presented in Table 5.1. Direct genetic changes were 5.0±1.6 g/day for LGR and -0.13±0.08 kg feed/kg lean gain for LFCR in their respective lines from method (1); only the former estimate was significant. Corresponding estimates from REML (method 3) represent means of predicted breeding values of animals in each year (Figs. 5.2 and 5.4) regressed on calf birth year (Table 5.1). Estimates of genetic trends from REML were similar to those from method (1) but were more precise and were over a 7-year period. The measurement of animals in the control line commenced in 1981, therefore estimated genetic trends from method (1) are over a 6-year period. Genetic trends from REML over the same time period as method (1) tended to be slightly higher. The variance of the annual genetic change from REML was estimated using a variance-covariance matrix developed from the average additive genetic (co)variance between animals (see equation 3) using expression (1). REML estimates of direct genetic change from the various populations from the univariate and multivariate analyses were similar, therefore the estimates presented were from a multivariate analysis, as they simultaneously estimate direct and correlated genetic changes.

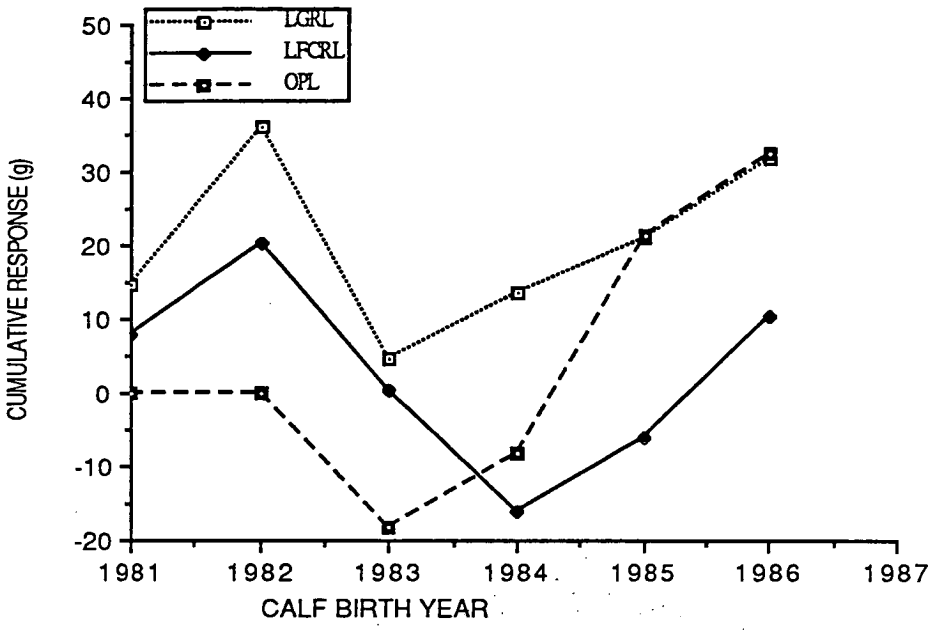

Fig. 5.1 Direct and correlated responses for LGR by year and line (deviation from control line).

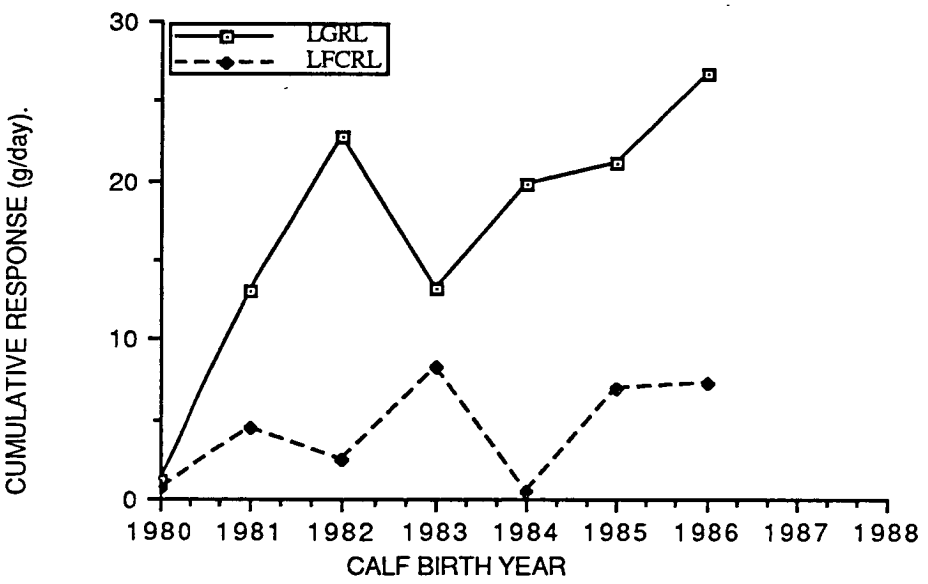

Fig. 5.2 Direct and correlated responses for LGR from REML analysis.

TABLE 5.1

Direct and correlated responses (per year) for LGR and LFCR

Trait	Line	Method 1	Method 3			
			Line only	POP1	POP2	POP3
LGR g/day	LGRL	4.96*	4.26**	4.00**		4.24**
		[a](1.4)	(0.45)	(0.45)		(0.40)
		[b](1.6)	(0.84)	(0.81)		(0.81)
	LFCRL	0.202	0.130		1.04	1.10
		(1.38)	(0.47)		(0.23)	(0.40)
		(1.54)	(0.80)		(0.77)	(0.87)
LFCR kg/feed/ kg lean gain	LGRL	-0.173*	-0.086	-0.150*		-0.143*
		(0.06)	(0.02)	(0.02)		(0.02)
		(0.08)	(0.05)	(0.05)		(0.05)
	LFCRL	-0.127	-		-0.121	-0.111
		(0.13)			(0.02)	(0.02)
		(0.08)			(0.05)	(0.05)

[a] Standard error of regression coefficient

[b] Standard error estimate using the variance-covariance matrix of response from equation 16

Method 1 = Deviation of selected lines from control line
Method 3 = REML

* $P<0.05$
** $P<0.01$, the test of significance based on standard error estimates from variance-covariance of response

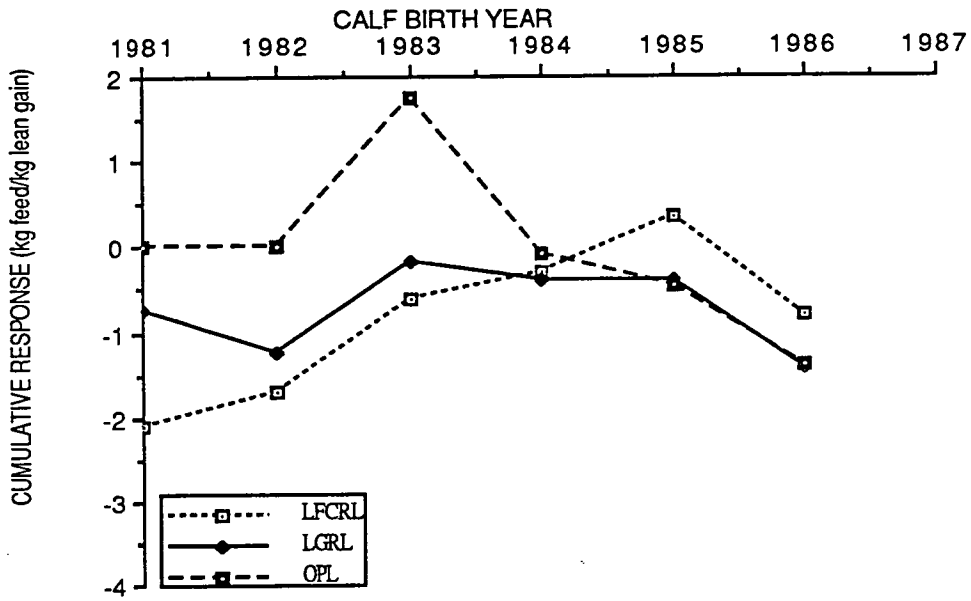

Fig. 5.3 Direct and correlated responses for LFCR by year and line (deviation from control line).

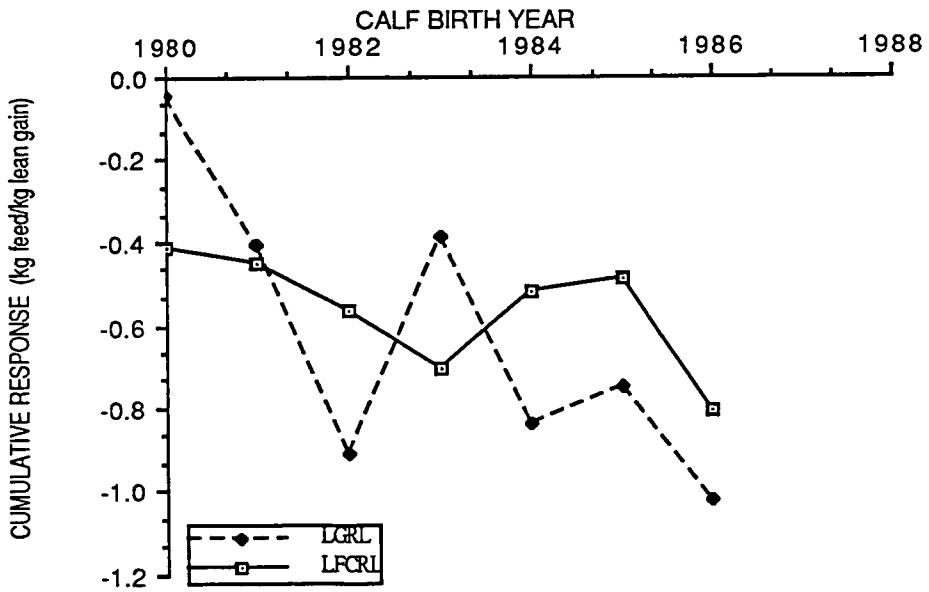

Fig. 5.4 Direct and correlated responses for LFCR by year and line from REML analysis.

Data were only available for the open line in the last four years and from Figs. 5.1 and 5.3, it can seen that genetic change for LGR was negative in the first two years and it was almost the same for LFCR. Although genetic changes were negative and significant in the first year for LGR and LFCR, the genetic trends estimated in the open line relative to genetic changes in the first year were positive (Table 5.2). This indicates there was a slight improvement in LGR and LFCR in the open line over the years.

Comparing the standard errors for genetic trends in the selected lines obtained from the variance of the regression and those from the variance-covariance of response indicates that the former are biased downwards.

Correlated responses for LGR and LFCR were 0.202+1.54g/day and -0.173+0.08 kg feed/kg lean gain respectively in the LFCR and LGR lines from method (1); only the later estimate was significant. Corresponding estimates from REML were similar. Thus the correlated response in LFCR from selection for LGR was greater than the response obtained by selecting directly for LFCR. Expressed as a percentage of the mean (Smith, 1984), the direct rate of genetic change for LGR and LFCR in their respective lines were 1.51 and 0.75% per year.

5.3.2 Realised heritabilities

The unweighted regression of cumulative response on cumulative selection differential gave realised heritability estimates of 0.533±0.110 and 0.349±0.178 for LGR and LFCR respectively (Table 5.3). Using the variance-covariance matrix of response generated from the relationship matrix (equation 9) and the

TABLE 5.2

Estimates of genetic change per year (and standard errors) for LGR and LFCR in the open line

Trait	[a]Intercept	[b]Genetic change
LGR g/day	-38.72* (18.75)	18.12** (6.06)
LFCR kg feed/ kg lean gain	2.258* (1.06)	-0.929** (0.34)

[a] Estimated difference between the open line and the control in the first year

[b] Genetic change per year relative to the intercept

* P<0.05
** P<0.01

TABLE 5.3

Realised heritability estimates (and standard errors) from the various regression methods

Regression method	Trait	
	LGR	LFCR
1	0.533 (0.11)	0.349 (0.18)
2	0.533 (0.17)	0.380 (0.14)
3	0.533 (0.14)	0.379 (0.13)

[1] Unweighted regression of response on cumulative selection differential (CSD)

[2] Generalised least square solution for the regression of response on CSD using the variance-covariance matrix from equation (9).

[3] Generalised least square solution for the regression of response on CSD using the variance-covariance matrix from equation (16).

initial heritability estimate to account for drift variance, generalised least-squares estimates of 0.533±0.165 and 0.380±0.142 were obtained for realised heritability respectively for LGR and LFCR. Accounting for the reduction in the sum of squares due to the regression fitted (equation 16) resulted in generalised least-squares estimates of 0.533±0.137 for LGR and 0.379±0.132. The above heritability estimates were from CSD estimated by the correct method. Using CSD estimated by the incorrect method resulted in slightly higher heritability estimate (Table 5.4). The very large standard error of the unweighted regression of cumulative response on CSD for LFCR seems difficult to explain. The same phenomenon was observed in estimating the variance of genetic trend (Table 5.1). It may be due to the small degrees of freedom used in estimating the variance. Generally yearly cumulative response in this line were subject to large fluctuations and declined gradually with selection (see Fig. 5.3). From Hill (1972a) the only factor contributing to the variance of response associated with the type of design in this experiment not yet considered is genotype-environmental interaction. With the selected line and control derived from the same base population the magnitude of the variance from genotype-environmental interaction is likely to be small. However, it may be possible that the significantly high ($p<0.01$) response observed at the initial stages of selection in this line (which is indicative of genetic difference between individuals in the selected and control lines) accompanied by a gradual decline in response resulting in reversal of rank between the LFCR and control lines in 1985, could result in some genotype-environment interaction (see Fig. 5.3).

TABLE 5.4

Realised heritabilities and standard errors from methods (1) and (2)

Method	Trait	
	LGR	LFCR
1a	0.533 (0.14)	0.379 (0.13)
1b	0.542 (0.14)	0.394 (0.14)
II	[c]0.443	[d]0.219

1a cumulative selection differential used to estimate realised heritability calculated by the correct method.

1b cumulative selection differential used to estimate realised heritability calculated by the incorrect method

II generalised method; fixed effects corrected by estimates from REML

[c] lower and upper limits of 0.975% confidence interval for estimate = $\pm$ 0.220

[d] lower and upper limits of 0.975% confidence interval for estimate = $\pm$ 0.260

Realised heritability estimates from method (2) were 0.443 for LGR and 0.219 for LFCR (Table 5.4). Estimates of heritability by this method were more related to those from REML as expected, due to the similarity in adjustment factors for fixed effects, and both also account for reduction in genetic variance (assuming an infinitesimal model and additive gene action). However, estimates from REML should be more efficient as method (2) uses information only from offspring-parent relationships while REML uses all available relationships. Variance components and heritability estimates from REML using the various populations are shown in Table 5.5. The estimates of heritabilities and variance components from POP3 were from a multivariate REML analysis. The results presented for each of the selected lines only or POP1 or POP2 are from univariate REML analysis. The univariate analysis for LFCR in LFCR line only yielded a zero estimate for the additive genetic variance component during the process of iteration and it was not possible therefore to achieve convergence. However a multivariate analysis for LGR and LFCR using only the LFCR line converged but yielded essentially a heritability estimate of zero for LFCR which seems to confirm the univariate analysis. The heritability estimates for LGR from the different populations were quite consistent. This is also true for LFCR except for the zero estimate from LFCR line only. Generally the precision of the heritability estimates from REML increased with population size. An approximate estimate of the gain in information associated with increase in population size can be calculated from the variances of the heritability estimates. In data with a simple structure such as offspring sire regression, the variance of heritability, $V(h^2)$, is proportional to the inverse of

TABLE 5.5

Variance components, heritability estimates and standard errors for LGR and LFCR from REML analysis

Trait	Population	Variance components		
		Additive genetic	Residual	Heritability
LGR (g/day)	LGRL	538.5 (191)	498.9 (150)	0.522 (0.16)
	POP1	460.8 (122)	518.8 (99.7)	0.470 (0.11)
	POP3	461.1 (118)	537.1 (93)	0.462 (0.09)
LFCR[1] kg/feed kg lean gain	POP2	1.027 (0.61)	2.613 (0.55)	0.288 (0.16)
	POP3	1.264 (0.43)	2.727 (0.27)	0.317 (0.10)

Standard errors in brackets

[1] Analysis on LFCR line only could not converge as additive genetic variance became zero during iteration.

the number of records used in estimating the heritability:

$V(h^2) \propto 1/n$

and an estimate of the amount of information ($1/V(h^2)$) used is proportional to the number of records. Using the same approach, approximate estimates of the amount of information used in estimating heritability in the various populations in the analyses of LGR are indicated in Table 5.6. Including the control line in the analysis resulted in a gain of about 118% in information used in estimating heritability and its variance. Using POP3 in the multivariate analysis represent a gain of about 51% in information compared with using POP1. Partitioning the gain in information due to including only the control to the LGR line (using the numbers of animals in the different lines) indicated that about 26% of the gain in information is from the control line while 74% is from the contrast between the selected line and control. The 51% gain in information from using POP3 comes from the LFCR line, the contrast between LFCR and LGR lines, and the control line.

5.3.3 Genetic correlations

The joint estimate of realised genetic correlation from method (1) between LGR and LFCR was -0.235 ± 0.21. Although this is consistent with little or no correlated response for LGR in the LFCR line (Table 5.1), it is inconsistent with the observed correlated response for LFCR in LGR line. Attempts were therefore made to estimate the genetic correlation within each of the lines. The regression of correlated response on CSD has the following

TABLE 5.6

Estimates of information utilised from the variances of heritabilities for LGR

Population	n[3]	se	Variance	Information
LGRL[1]	275	0.158	0.0250	40
POP1[1]	351	0.107	0.0114	87
POP3[2]	500	0.087	0.0076	132

se = standard errors (developed with the help of Robin Thompson)

1 Standard errors are from second partial differentials of log likelihood utilising actual observations including residual sums of squares

2 Standard errors are from quadratic approximation of log-likelihood

3 Number of records, includes base population animals

expectations:

$$b = r_G h_1 h_2 o_2 / o_1$$

where

r_G = genetic correlation
h_1^2 = heritability of selected trait
h_2^2 = heritability of correlated trait
o_1 = phenotypic standard deviation of selected trait
o_2 = phenotypic standard deviation of selected trait

Estimates of genetic correlation between LGR and LFCR using the above equation were -0.176 ± 0.211 in the LFCR line and -0.755 ± 0.134 in the LGR line. Falconer (1981) has commented on the problem of variation in estimates of genetic correlations. He mentioned that double selection experiments are often inconsistent in the estimates of the genetic correlation that they give which may be attributed to the fact that genetic correlations are strongly influenced by gene frequency changes and so may differ markedly in different populations. Secondly, genetic correlation estimates are often low in precision because they are subject to rather large sampling errors. The latter reason seems more likely in this situation due to the short duration of the experiment.

The line differences in estimates of genetic correlation are consistent with the observed correlated responses. Moreover the estimate of genetic correlation from LGR line is consistent with estimates from POP2 and POP3 using REML. The covariance and

TABLE 5.7

Covariance components, genetic and phenotypic correlations between LGR and LFCR from REML

Population	Covariance components		Correlations	
	Additive genetic	Residual	r_G^1	r_P^2
LGR2	-12.90 (9.28)	-26.697 (8.04)	-0.531 (0.24)	-0.567 (0.05)
POP1	-18.03 (7.31)	-18.02 (6.19)	-0.807 (0.15)	-0.565 (0.04)
POP2	-9.89 (6.38)	-19.25 (5.81)	-0.579 (0.23)	-0.519 (0.04)
POP3	-16.94 (5.84)	-18.92 (4.81)	-0.702 (0.12)	-0.568 (0.03)

[1] r_G = genetic correlations

[2] r_P = phenotypic correlations

Standard errors are in brackets

genetic correlations estimates from REML are shown in Table 5.7. The estimates of genetic correlations from POP1 and POP3 were similar, -0.807±0.151, -0.702±0.122 but slightly higher than estimates from the LGR line alone (-0.521±0.236) and POP2 (-0.579±0.229). Again, the precision of genetic correlation estimates from REML increased with population size.

5.4 Discussion

The rates of genetic change observed indicate that selection for LGR and LFCR has been effective. The annual rate of change of 1.5% for LGR is consistent with the possible rate of 1.4% for growth rate in beef cattle reported by Smith (1984). This high rate of change may be due to the effective selection practised (97% of the maximum possible selection differential was achieved) and the high heritability. The average percentage rate of change from a summary of selection experiments in beef cattle reported in the literature was about 0.63, 0.80 and 2.03 respectively for weaning weight, yearling weight and postweaning gain. Selection was however applied to both sires and dams in most of the experiments and in some cases, was on the basis of an index.

Compared to LGR, response in LFCR was much lower. Most of the response in LFCR estimated from method (1) occurred in the first two years of selection (which were significant at 1% level of probability) and declined gradually in subsequent years, although the mean predicted breeding value per year from REML were more or less constant over the years of selection. The observed response in LFCR was only 66% of the predicted response using the genetic parameters from REML analysis, but the observed response in LGR was

consistent with predicted response (about 103%).

Heritability estimates based on cumulative selection differentials estimated by the incorrect method were generally slightly higher than estimates obtained and calculated by the correct method. This is contrary to the indications of James (1986) and the simulation results of Juga and Thompson (1988) in which heritability estimates based on CSD calculated by the incorrect method were biased downwards. The contrary results obtained are due to the fact that the incorrect method underestimated CSD compared with the correct method and hence the upward bias in heritability estimates. The conditions under which the incorrect method can result in lower CSD estimates compared with the correct have been discussed in chapter four.

Method (2) and REML account for changes in additive genetic variances due to selection assuming an additive genetic model with infinite number of loci and therefore give unbiased estimates of base population genetic parameters (Rothschild, Henderson and Quass 1979; Thompson and Meyer, 1986; Juga and Thompson, 1988). Method (1) consistently gave higher heritability estimates compared with REML (although differences were not significant) and method (2). Although Hill (1972c) showed that linear estimators of realised heritability such as regression of cumulative response on cumulative selection differential are efficient and unbiased over most relevant range of parameters, Falconer (1981) and Sorensen and Kennedy (1984) have indicated that they may not necessarily give unbiased estimates of base population heritability. In method (1), the estimator assumes that the response per unit selection differential applied is linear. This may not be applicable if variances change as a result

of selection, random drift and (or) gametic disequilibrium generated by selection. Due to the short duration of this experiment, the non-significant higher estimates of heritabilities from method (1) compared with those from REML and method (2) may result mainly from sampling error.

Generally, the precision of genetic parameters from REML analyses increased with increases in population size, accompanied by substantial gains in information with which these parameters were estimated. If we assume that the total number of animals used in the LGR and control lines were used only in the LGR line, the gain in information would only be about 28% compared with 123% from POP1. The former was estimated by scaling the variance of heritability from only LGR line by the number of records in POP1. The above does indicate much of the gain in information is from the contrast between the selected and control lines. This is consistent with the observation of Thompson (1986). Thus the intended use of REML or BLUP to evaluate genetic change should not exclude the establishment of control line from the design if facilities are available.

Correlated response for LFCR in the LGR line was higher than the response from direct selection for LFCR. In view of the high cost involved in recording individual feed intake of animals, it might be argued that selection for LGR alone is adequate in increasing the rate and efficiency of lean gain, and selection for LFCR should be ignored. However, it is worthwhile to examine correlated responses to selection for LGR and LFCR before ascertaining whether selection for LFCR is necessary or not. In the next chapter, correlated responses in recorded secondary traits

in both selection lines are examined.

5.5. Appendix

1. Prediction from progeny and sire values

Suppose sires in generation zero have prediction A_F and let $d_F = 1/h^2$. Then $d_F A_M = Y_F - U_o$ and BLUP equations for the sire and its offspring can be written in the form

$$\begin{bmatrix} d_F+g/3 & -2g/3 \\ -2g/3 & 1+4g/3 \end{bmatrix} \begin{bmatrix} A_{FG} \\ A_G \end{bmatrix} = \begin{bmatrix} d_F A_M \\ Y_G - U_1 \end{bmatrix} \qquad A1$$

with $g = (1-h^2)/h^2$, and A_{FG} is a predictor for the sire incorporating the offspring value Y_G. The g terms come from linking offspring to the sire when the inverse of the relationship matrix A is found.

Re-arranging A1, we get

$$\begin{bmatrix} \hat{A}_{FG} \\ \hat{A}_G \end{bmatrix} = 1/D \begin{bmatrix} 1+4g/3 & +2g/3 \\ +2g/3 & d_F+g/3 \end{bmatrix} \begin{bmatrix} d_F A_M \\ Y_G - U_1 \end{bmatrix} \qquad A2$$

with $D = d_F + g/3 + (4g/3)\, d_F = g/3 + d_F\,(1+4g/3)$

$$A_G = \frac{2g/3\; d_F A_M + [d_F + g/3]\; Y_G - U_1}{d_F + g/3 + (4g/3)\, d_F}$$

$$= A_M/2 + \frac{d_F + g/3}{d_F + g/3 + (4g/3)\, d_F} (Y_G - U_1 - A_M/2)$$

$$= A_M/2 + h_G^2 (Y_G - U_1 - A_M/2) \text{ with}$$

$$h_G^2 = \frac{3h^2/4 + (1-h^2)\, h_F^2/4}{1-h^2/4 + (1-h^2)\, h_F^2/4}$$

which is equation (20).

2. Prediction from grandmaternal sires, sires and progeny values. Using the same argument outlined for prediction from sire and progeny values, equations for grandmaternal sire, sire and their progeny are:

$$\begin{bmatrix} d_M + g/11 & 2g/11 & -4g/11 \\ 2g/11 & d_F + 4g/11 & -8g/11 \\ -4g/11 & -8g/11 & 1+16g/11 \end{bmatrix} \begin{bmatrix} A_{MG} \\ A_{FG} \\ A_G \end{bmatrix} = \begin{bmatrix} d_M A_M \\ d_F A_F \\ Y_G - U_1 \end{bmatrix} \qquad \text{A3}$$

where A_{MG} and A_{FG} are predictors for grandmaternal sires and sires incorporating the offspring value Y_G. The g terms again arise from inverting the relationship matrix between grandmaternal sires, sires and progeny.

Re-arranging A3, predictors for the parents are

$$\begin{bmatrix} \hat{A}_{MG} \\ \\ \hat{A}_{FG} \end{bmatrix} = 1/D \begin{bmatrix} d_F + 4g/11 & -2g/11 \\ \\ -2g/11 & d_M+g/11 \end{bmatrix} \begin{bmatrix} d_M A_M + 4g/11\ A_G \\ \\ d_F A_F + 8g/11\ A_G \end{bmatrix} \qquad A4$$

with $D = d_M d_F + (g/11)\ [4\ d_M + d_F]$

Absorbing the parents equations into offspring equation, we get

$$[1+16g/11-(16g^2/11^2 D)(d_F+4d_M)]A_G=(Y_G-U_1)+((d_F + d_M)/D)\ 4g/11(A_M+2A_F)$$

$$= \left\{ \frac{1+(16g/11)d_M d_F+g/11(4d_M+d_F)}{D} \right\} A_G = \frac{(Y_G-U_1)D+d_M d_F(4g/11)(A_M+2A_F)}{D}$$

Substituting D and rearranging.

$$A_G = \frac{[1+g/11(4/d_M + 1/d_F)Y_G - U_1}{1+16g/11+g/11\ (1/d_M+4/d_F)} \qquad \frac{4g/11(A_M + 2A_F)}{1+16g/11+(g/11)(1/d_M+4/d_F)}$$

$$= \frac{(A_M/4 + A_F/2) + 1+g/11(4/d_F+1/d_M) \qquad (Y_G-U_1(A_M/4+A_F/2))}{1+16g/11+g/11(4/d_F+1/d_M)}$$

$$= (A_M/4 + A_F/2) + h^2_G\ (Y_G - U_1 - (A_M/4 + A_F/2))$$

with $$h^2_G = \frac{11h^2 + (1-h^2)(4h^2_F + h^2_M)}{16-5h^2 + (1-h^2)\ (4h^2_F + h^2_M)}$$

which is equation (21).

CHAPTER 6

CORRELATED RESPONSES FOR SECONDARY TRAITS MEASURED ONLY IN RECORDED BULLS

6.1 Introduction

In this chapter, realised correlated responses to selection in the LGR and LFCR lines for birth weight, lean percent, growth rate, feed intake and food conversion ratio in recorded bulls are considered. Using the estimated selection differentials and genetic parameters from REML (which represent base population parameters) correlated responses in the above traits were predicted and compared with realised correlated responses.

6.2 Material and methods

6.2.1 Management

The management of animals, recording of traits and selection procedure have been described in chapter three.

6.2.2 Statistical methods

Correlated responses in the two selection lines were evaluated by two methods:

1) Deviation of selected lines from control and

2) Multivariate REML analysis to estimate (co)variance components and predict rate of genetic change.

The details of the two methods were as described in chapter five. The only exception was that the variances of annual correlated genetic changes from method (1) were estimated using variance components estimated by REML from POP3 in equation (9) (see chapter five).

In method (2), FEED and FCR were adjusted for the effects of

initial weight as was described for LFCR. To account for selection bias, the multivariate analyses involved each of the secondary traits and the selected trait in POP1 and POP2, while in POP3, it was based on two of the selected traits and each of the secondary traits. However a multivariate analysis was also carried out on all selected and secondary traits in POP3, to estimate the genetic correlations between all traits.

Correlated responses in each selection line were predicted using the formula (Falconer, 1981)

$$CR_Y = i_x h_x h_y r_A \sigma_{py}$$

where

CR_Y = correlated response in the secondary trait y

h_y = square root of the heritability of trait y

h_x = square root of the heritability of selected trait x

i_x = selection intensity of selected trait x

r_A = genetic correlation between x and y

σ_{py} = phenotypic standard deviation of y

Predicted correlated responses were expressed on an annual basis by dividing by the number of years per generation.

Genetic change in the open line for the secondary traits considered were estimated by fitting a similar model as described for LGR and LFCR (see equation 2, chapter five).

6.3 Results

The cumulative correlated responses per year are shown in Figures 6.1 to 6.10 and the estimated correlated genetic trends are presented in Table 6.1. The heritability and genetic correlation estimates from REML used in the prediction of correlated response are shown in Tables 6.3 and 6.4 respectively. Correlated responses in both lines for BW were generally not significant. Estimates for lean percent were 0.103±0.12 and 0.267±0.12 for the LGR and LFCR lines respectively from method (1); only the latter was significant. Corresponding estimates from REML were 0.107±0.05 and 0.124±0.07 respectively. The observed correlated responses for BW and lean were consistent with predicted values (Tables 6.1 and 6.2).

The largest difference between both selected lines in terms of observed correlated response was in growth rate. A significant positive genetic trend of 12.23+4.34 g/day (method (1)) was observed in the LGR line while a negative but non-significant trend of -2.75±4.4 g/day was estimated in LFCR line. Estimates from REML were similar for the LGR line although more precise. The high correlated response for GRT in the LGR line could be attributed to the high genetic correlation between LGR and GRT, about 0.958±0.033 in POP1, LGR being a product trait of GRT and LEAN. There was a high similarity in the rate of accumulation of direct response for LGR and correlated response in GRT in the LGR line (Fig. 6.11) compared with that of lean percent, which further confirms that much of the selection pressure in LGR has been through GRT as mentioned earlier in chapter four. The estimated genetic correlation between LFCR and GRT was -0.580±0.240 in POP2. The observed correlated response in GRT was therefore inconsistent with the estimated genetic

TABLE 6.1

Correlated responses for secondary traits per year in both selected lines

	LGRL				LFCRL			
		Method 3				Method 3		
Trait	Method 1	LGRL	POP1	POP3	Method 1	LFCR	POP2	POP3
BW(kg)	0.106	0.093	0.074	0.028	0.100	0.168	0.048	-0.004
	[a](0.11)	(0.01)	(0.01)	(0.01)	(0.05)	(0.02)	(0.01)	(0.01)
	[b](0.14)	(0.08)	(0.07)	(0.07)	(0.15)	(0.09)	(0.09)	(0.09)
LEAN %	0.103	0.106*	0.107*	0.106	0.267*	0.016	0.124	0.172*
	(0.05)	(0.05)	(0.05)	(0.06)	(0.06)	(0.01)	(0.02)	(0.02)
	(0.12)	(0.05)	(0.05)	(0.06)	(0.12)	(0.05)	(0.07)	(0.07)
GRT	12.23**	13.43**	11.01**	11.91**	-2.748	0.499	2.641	2.00
(g/day)	(2.83)	(1.48)	(1.33)	1.20	(3.51)	(0.94)	(0.88)	(1.12)
	(4.34)	(2.42)	(2.26)	(2.24)	(4.39)	(2.33)	(2.27)	(2.41)
FEED	5.973	5.03	0.175	2.108	-3.841	-7.066	-2.043	-1.826
(kg)	(3.36)	(0.87)	(0.02)	(0.39)	(2.61)	(0.11)	(0.03)	(0.07)
	(5.31)	(3.11)	(2.70)	(2.68)	(5.91)	(3.75)	(3.32)	(3.41)
FCR	-0.201	-0.165	-0.339*	-0.295*	-0.354	-0.023	-0.277	-0.238
(kg feed/	(0.27)	(0.04)	(0.06)	(0.04)	(0.51)	(0.01)	(0.07)	(0.06)
	(0.27)	(0.14)	(0.15)	(0.14)	(0.28)	(0.15)	(0.16)	(0.16)

[a] Standard error of regression coefficient

[b] Standard error estimated using the variance-covariance matrix of correlated responses

**P<0.01; *P<0.05, test of significance based on the second standard error (b)

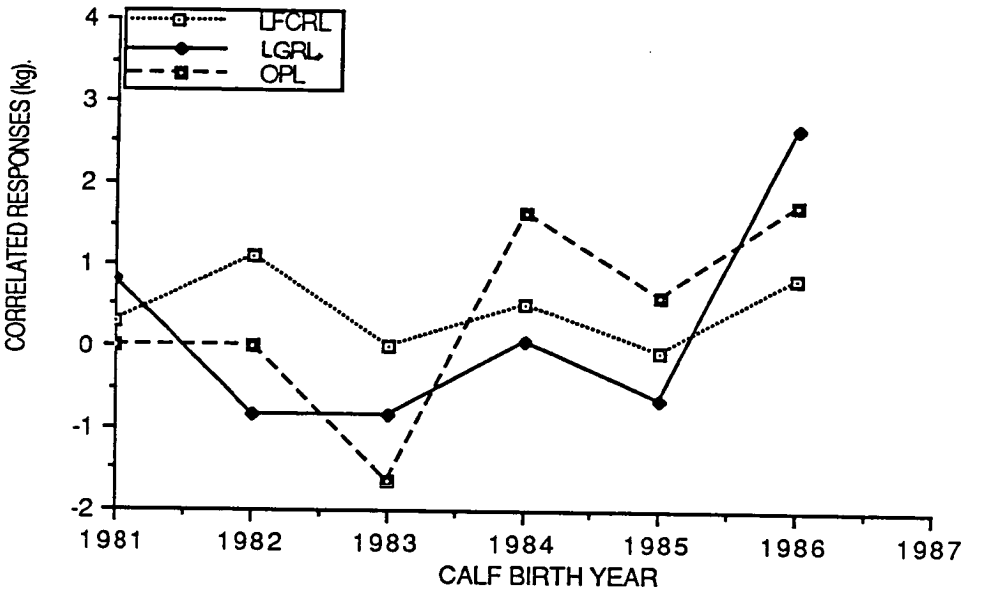

Fig. 6.1 Correlated responses for birth weight by year and line (method 1).

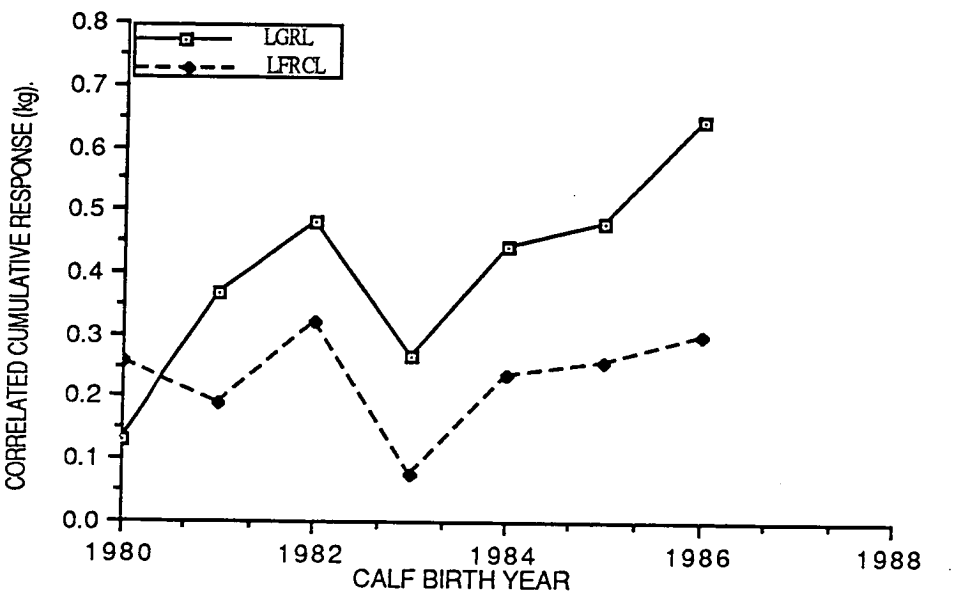

Fig. 6.2 Correlated responses for birth weight by year and line from REML analysis.

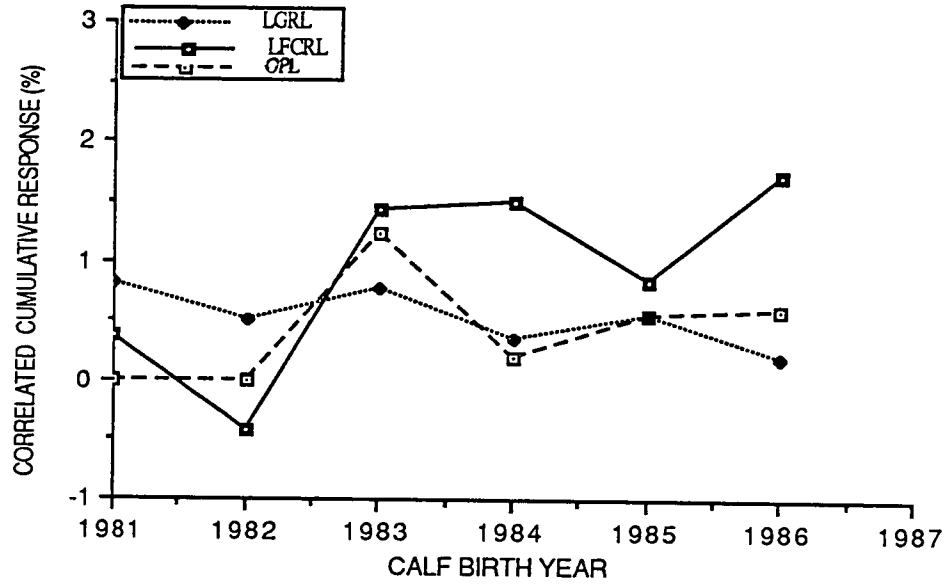

Fig. 6.3 Correlated responses for lean percent by year and line (method 1).

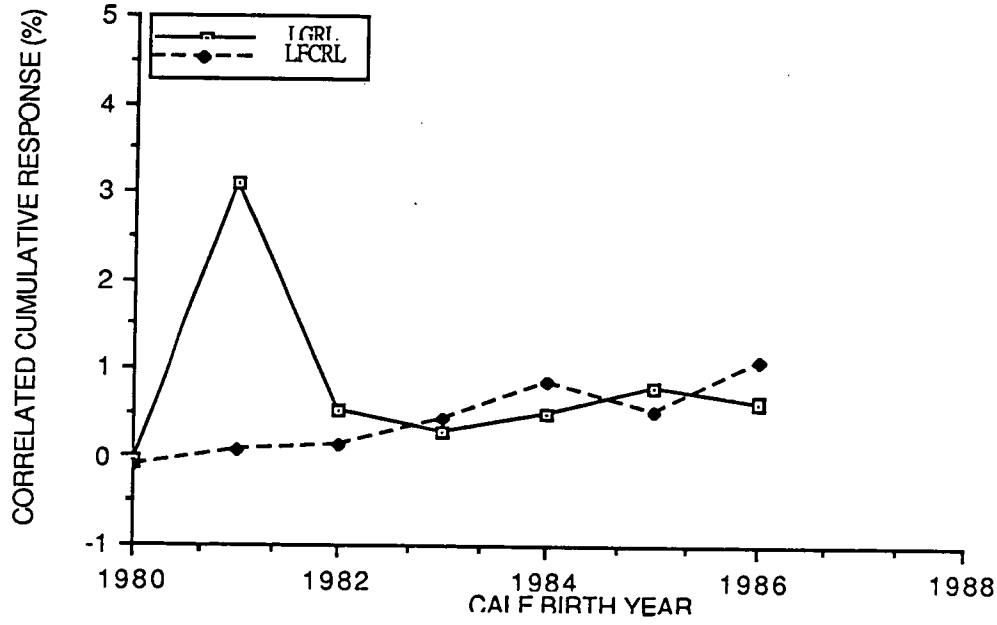

Fig. 6.4 Correlated responses for lean percent by year and line from REML analysis.

TABLE 6.2

Predicted annual correlated responses for secondary traits in selection lines

Traits	Predicted correlated response	
	LGRL	LFCRL
BW (kg)	0.093	0.032
LEAN	0.109	0.103
GRT (g/day)	13.07	5.612
FEED (kg)	0.311	-3.532
FCR (kg feed/ kg gain)	-5.648	-5.432

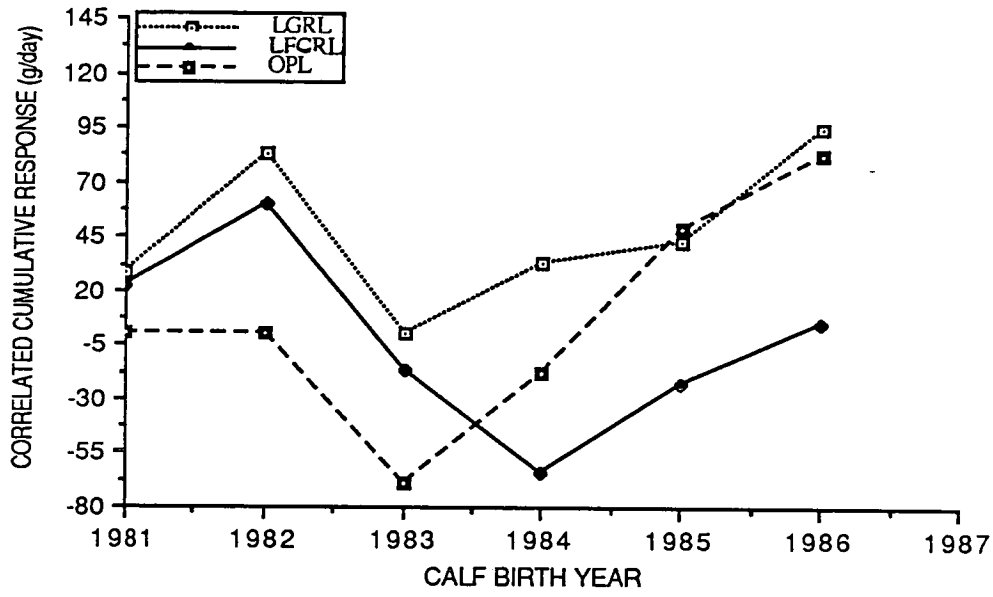

Fig. 6.5 Correlated responses for growth rate by year and line (method 1).

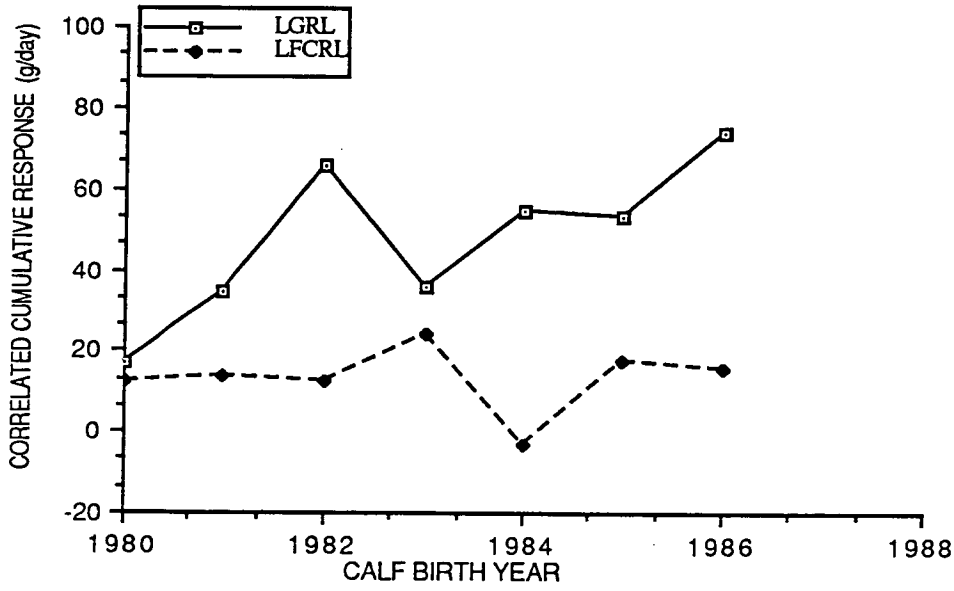

Fig. 6.6 Correlated responses for growth rate by year and line from REML analysis.

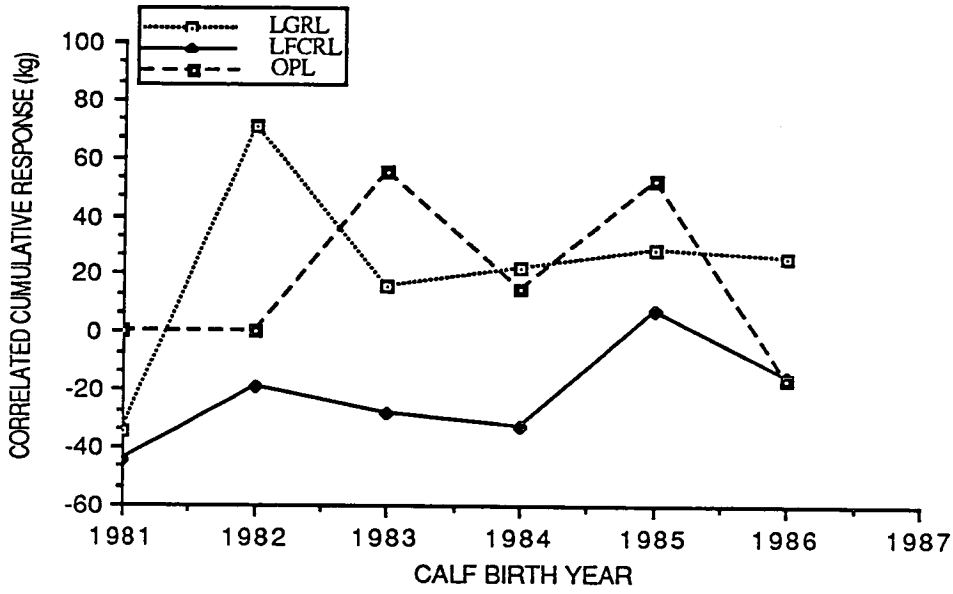

Fig. 6.7 Correlated responses for feed intake by year and line (method 1).

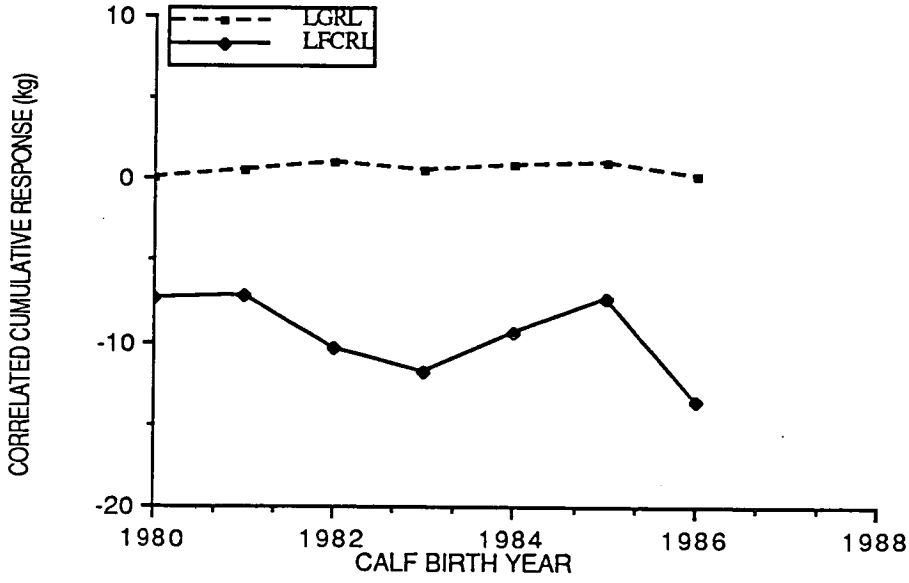

Fig. 6.8 Correlated responses for feed intake by year and line from REML analysis.

TABLE 6.3
Estimates of variance components (and standard errors) for secondary traits from REML analyses

Trait	Population	Variance components		
		Additive genetic	Residual	Heritability
BW (kg)	POP1	0.932 (1.33)	11.86 (1.54)	0.073 (0.10)
	POP2	1.228 (1.54)	12.19 (1.72)	0.092 (0.11)
	POP3	1.161 (1.04)	11.70 (1.21)	0.090 (0.08)
LEAN %	POP1	18.22 (7.48)	35.80 (6.62)	0.337 (0.13)
	POP2	27.69 (8.49)	26.84 (6.73)	0.508 (0.13)
	POP3	28.43 (6.72)	27.58 (5.11)	0.508 (0.10)
FEED (kg)	POP1	1.143 (34.52)	22445 (1732)	0.0001 (0.002)
	POP2	623.8 (907)	19406 (1909)	0.0311 (0.04)
	POP3	725.3 (988)	19845 (1451)	0.0365 (0.04)
GRT	POP1	3648 (11.36)	40.47 (910)	0.474 (0.13)
	POP2	2480 (1066)	4928 (955)	0.335 (0.13)
	POP3	3554 (906)	4171 (715)	0.460 (0.10)
FCR (kg feed/ kg gain)	POP1	11.82 (5.18)	27.26 (4.73)	0.303 (0.12)
	POP2	10.52 (5.17)	26.51 (4.82)	0.284 (0.13)
	POP3	9.97 (3.85)	28.13 (3.62)	0.262 (0.10)

TABLE 6.4

Covariance components, genetic and phenotypic correlations between secondary and selected traits from REML analysis

			Each selected line plus control				Both selected lines plus control (POP3)			
			Covariance components		Correlations		Covariance components		Correlations	
Trait	Selected trait	lines	Additive genetic	Residual	r_G	r_P	Additive genetic	Residual	r_G	r_P
BW (kg)	LGR	POP1	8.864 (10.18)	7.917 (9.54)	0.406 (0.49)	0.150 (0.05)	1.739 (8.01)	13.97 (7.53)	0.075 (0.34)	0.139 (0.04)
	LFCR	POP2	-0.177 (0.63)	-0.612 (0.64)	-0.152 (0.54)	0.112 (0.06)	0.269 (0.48)	-1.205 (0.48)	0.211 (0.40)	-0.130 (0.05)
LEAN (%)	LGR	POP1	10.41 (7.84)	16.44 (6.61)	0.359 (0.22)	0.369 (0.05)	14.92 (6.70)	11.51 (5.14)	0.411 (0.15)	0.353 (0.04)
	LFCR	POP2	-0.556 (0.50)	-1.149 (0.43)	-0.323 (0.24)	-0.381 (0.05)	-1.081 (0.42)	-1.06 (0.34)	-0.551 (0.15)	-0.452 (0.04)
GRT (g/day)	LGR	POP1	1252 (385)	1155 (304)	0.958 (0.03)	0.876 (0.01)	1217 (311)	12.53 (242)	0.951 (0.03)	0.898 (0.01)
	LFCR	POP2	-31.44 (18.2)	-29.70 (16.06)	-0.580 (0.24)	-0.370 (0.05)	-40.54 (15.3)	-31.46 (12.5)	-0.603 (0.15)	-0.410 (0.040)
FEED (Kg)	LGR	POP1	20.99 (373)	1564 (362)	0.919 (2.50)	0.339 (0.05)	172.8 (300)	1303 (298)	0.293 (0.47)	0.326 (0.04)
	LFCR	POP2	18.57 (22.6)	63.40 (24.02)	0.728 (a)	0.303 (0.05)	11.86 (18.4)	67.90 (19.5)	0.382 (0.46)	0.278 (0.04)
FCR kg feed/ kg gain	LGR	POP1	-5.462 (2.22)	-4.184 (1.84)	-0.727 (0.16)	-0.492 (0.04)	-3.387 (1.71)	-5.269 (1.44)	-0.645 (0.15)	-0.500 (0.04)
	LFCR	POP2	0.294 (0.16)	0.783 (0.15)	0.873 (0.07)	0.924 (0.01)	0.329 (0.12)	0.821 (0.11)	0.908 (0.04)	0.931 (0.01)

Standard errors in brackets

(a) standard error could not be estimated due to low additive genetic variance of feed intake (Table 6.3)

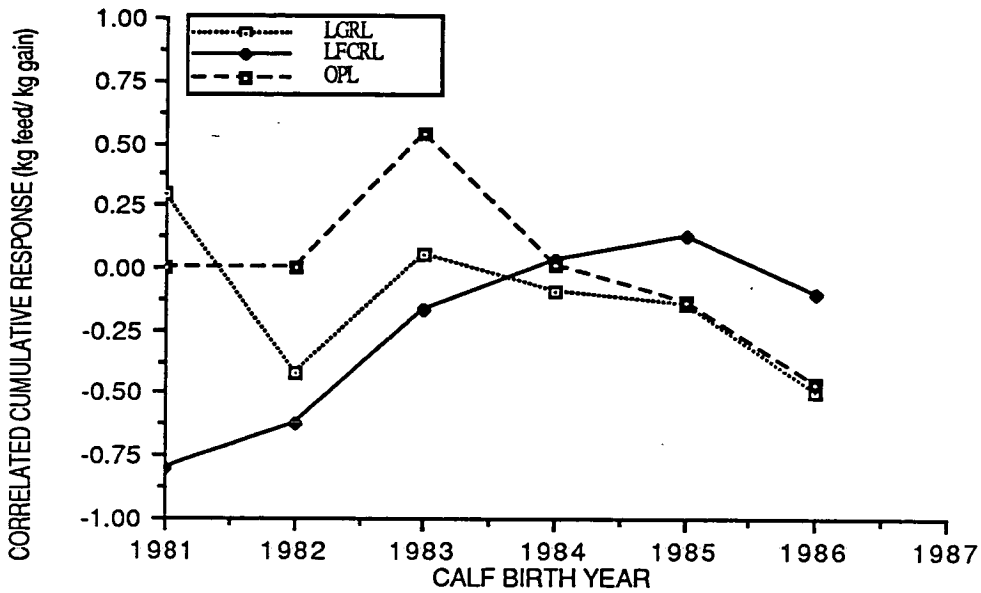

Fig. 6.9 Correlated responses for food conversion ratio by year and line (method 1).

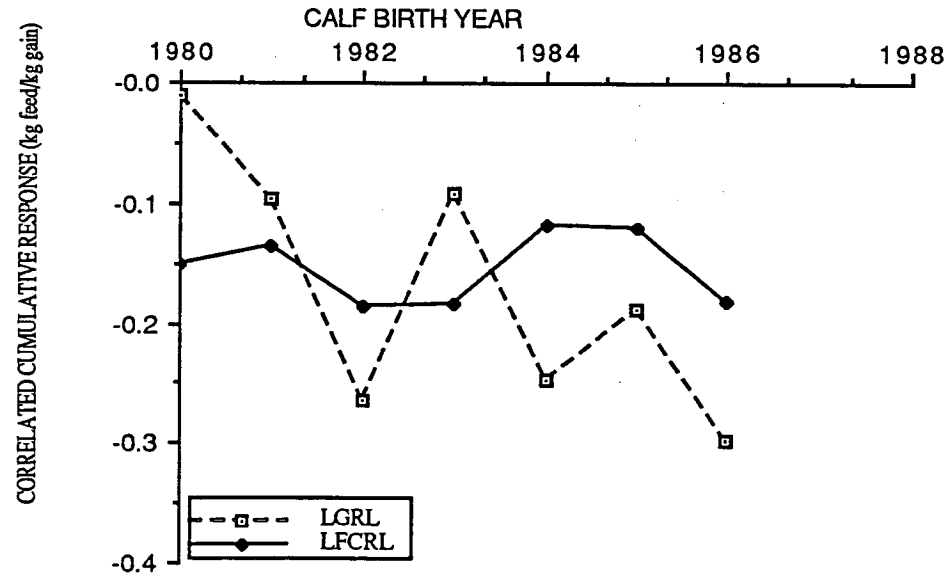

Fig. 6.10 Correlated responses in food conversion ratio by year and line from REML analysis.

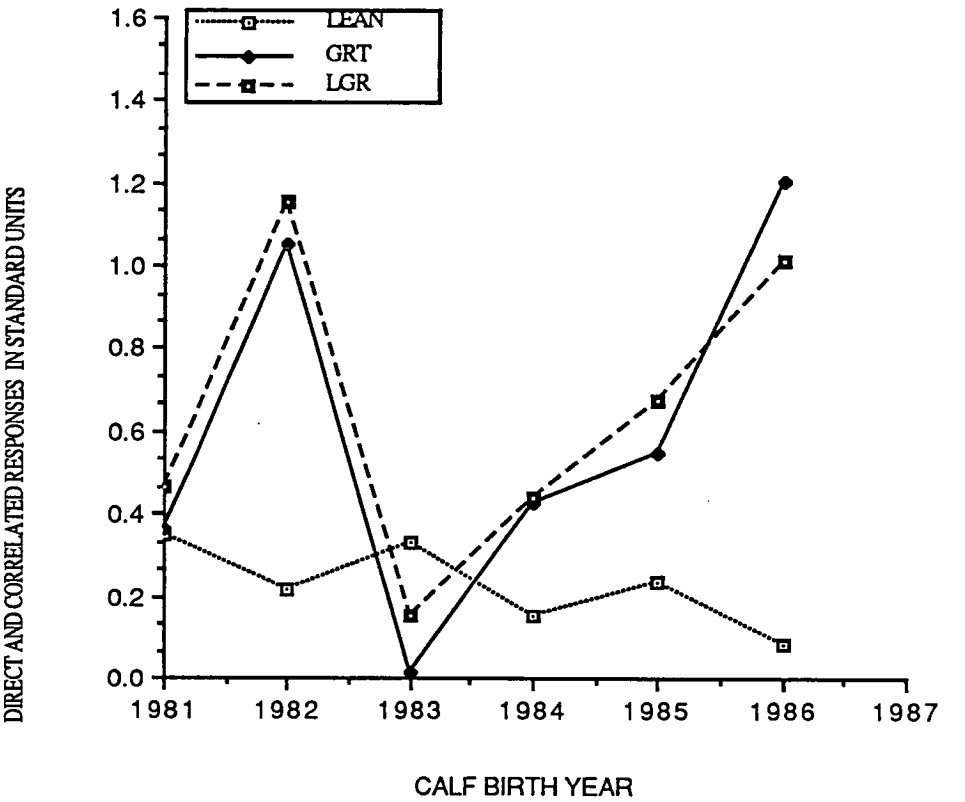

Fig. 6.11 Direct response for LGR and correlated responses for GRT and LEAN in the LGR line (method 1)

correlation probably due to the reduced feed intake which placed a limitation on rate of growth attained. Predicted genetic trends for GRT were 13.07 and 5.62 g/day in the LGR and LFCR lines respectively (Table 6.2). Correlated responses for FCR were about the same in both lines but were only significant in the LGR line from REML analyses on POP1 and POP3. Although genetic trends for FEED were in opposite directions in LGR and LFCR lines, the estimates had large standard errors due probably to: (1) the large variation in estimates of correlated responses from method (1) (Fig. 6.7), and (2) the large residual variance associated with FEED; this point is further examined in the discussion (section 6.4). The difference between the two lines in terms of estimated genetic trend for FEED is much more apparent from REML analyses of the individual selected lines only. The estimated trends were 5.03±3.11 and -7.07±3.75kg/day respectively in the LGR and LFCR lines although none was significant due to the large standard errors. In terms of cumulative correlated response in FEED in the last year, the LGR line was 2% higher and LFCR line -1% lower than the mean of the control line.

A summary of the heritability estimates and the genetic and phenotypic correlations between the selected traits and all secondary traits from a multivariate REML analyses on POP3 are presented in Table 6.5. These estimates might be useful in designing future improvement schemes for this herd and Hereford cattle in general.

The heritability estimates obtained for GRT, LEAN and FCR were consistent with values reported by Simm (1983) in an extensive survey of literature. He reported average values of 0.41, 0.39 and 0.42 for GRT, LEAN and FCR respectively from a total of 354, 14 and 45 estimates from paternal half sib analyses or offspring parent

TABLE 6.5

Estimates of heritabilities, genetic and phenotypic correlations and standard error for all traits

		1	2	3	4	5	6	7
LGR	1	0.47 (0.09)	0.15 (0.04)	0.35 (0.04)	0.89 (0.01)	-0.57 (0.03)	0.32 (0.04)	-0.50 (0.04)
BWT	2	0.55 (0.46)	0.03 (0.03)	0.06 (0.05)	0.17 (0.04)	-0.14 (0.04)	0.06 (0.05)	-0.14 (0.04)
LEAN	3	0.44 (0.15)	-0.50 (0.48)	0.45 (0.10)	-0.04 (0.05)	- 0.45 (0.04)	-0.16 (0.05)	-0.11 (0.05)
GRT	4	0.95 (0.02)	0.78 (0.34)	0.14 (0.18)	0.43 (0.10)	-0.41 (0.04)	0.38 (0.04)	-0.48 (0.04)
LFCR	5	-0.71 (0.11)	-0.12 (0.57)	-0.54 (0.14)	-0.60 (0.14)	0.39 (0.09)	0.29 (0.04)	0.93 (0.01)
FEED	6	0.09 (0.23)	0.59 (0.51)	-0.47 (0.21)	0.25 (0.22)	0.62 (0.16)	0.15 (0.06)	0.26 (0.04)
FCR	7	-0.64 (0.13)	-0.34 (0.59)	-0.22 (0.19)	-0.64 (0.14)	0.94 (0.30)	0.53 (0.20)	0.32 (0.09)

Lower traingle : Genetic correlations
Diagonal : Heritabilities
Upper triangle : Phenotypic correlations

regressions. However, the heritability estimate obtained for BW was very low compared with the average value of 0.46 he reported from 149 estimates.

In general LGR was positively genetically correlated with BW, GRT and LEAN but was negatively correlated with LFCR and FCR. LGR was not genetically correlated with FEED but the phenotypic correlation between both traits was 0.32±0.04. The situation was reversed for LFCR; it was negatively genetically correlated with BW, GRT and LEAN, but was positively correlated with FEED and FCR.

In the open line, significant annual genetic changes were observed only for GRT and FCR (Table 6.6). A significant genetic trend of 50.9±16.4g/day was observed for GRT in the open line with respect to an initial significant difference of -116.0±51.0 (g/day) between the open and control lines. This is consistent with Fig. 6.5 where deviations of the open line from the control line are plotted against calf birth year, correlated responses for GRT were negative in the first two years followed by a tremendous increase in later years. This is very similar to the pattern observed for LGR. FCR followed the same pattern, genetic change in the initial years were negative followed by a positive genetic in the later years (Table 6.6 and Fig. 6.9). Since neither the initial difference between the open and the control lines for FEED was significant nor the genetic trend in the open line, the above implies that the genetic improvement in food conversion ratio was essentially through rapid growth rate, as animals could be assumed to be eating more or less the same amount of food over the years.

TABLE 6.6

Annual genetic change in secondary traits in the open line

Trait	[1]Intercept	[2]Genetic trend
BW (kg)	-1.320 (2.11)	0.786 (0.68)
LEAN	8.50 (15.4)	-0.9.00 (4.96)
GRT (g/day)	-116.0** (51.0)	50.90** (16.4)
FEED (kg)	76.30 (78.8)	-20.3 (25.4)
FCR (kg feed/kg gain)	13.03** (6.09)	-5.36** (1.96)

1,2 see table 5.1 for explanation of terms

** P< 0.01

6.4 Discussion

In an extensive discussion on selection for growth rate and size in ruminants, Barlow (1984) concluded that selection for growth rate and leanness will continue to have a role in terminal sire breeds with the major reservation that strategies must be derived to minimise calving difficulties, which arises mainly from increased birth weight. Therefore the absence of correlated response in BW observed in both selected lines becomes very important in the light of his conclusions. This is more so in the LGR line where a significant correlated response in GRT was recorded. The correlated response in GRT observed in LGR line is similar to the estimate for the rate gain from birth to one year of age from direct selection on yearling weight reported by Aaron (1986b), lower than the estimate of Koch et al. (1974b) and higher than that of Frahm et al. (1986b) but higher correlated responses were however reported by these workers for BW (see Table 2.2). It does seem therefore that the inclusion of LEAN as a component trait in LGR acted as a check to increased correlated response in BW. The estimated genetic correlation between LEAN and BW in this study was -0.50±0.48 from multivariate REML analyses on POP3. Although the standard error is very large, it does however indicate a negative genetic relationship between BW and LEAN, which could act as a check on BW. The lower genetic correlation estimate of 0.55±0.46 between LGR and BW compared with 0.78±0.34 between GRT and BW in POP3 seems to confirm the above observation. However as pointed out in chapter two, not all selection experiments on growth rate have been accompanied by increased BW (see Frisch, 1981 and Bailey and Lawson, 1986). The magnitude and direction of change in BW as a result of selection on

growth traits might be influenced by environmental conditions, management and breed type.

A high correlated response in FEED was expected in the LGR line in view of the high correlated response in GRT observed in this line and the reverse was expected for the LFCR line. However correlated responses were generally low for FEED in both lines. These low correlated responses might be due to the low proportion of additive genetic variance associated with FEED in this study as indicated by the very low heritability estimate, and genetic correlations between FEED and both selected traits. However phenotypic variance for FEED was quite high (standard deviation was 143kg) which shows that a large proportion of variation in FEED was environmental (residual standard deviation equals 141kg) and could be related to variation in feed quality from year to year. A between year analysis on FEED, FCR and weight gain on test in the control line which represents environmental effects, showed a very significant ($P<0.01$) decline in total feed consumed and FCR in the last three years (1984 to 1986) of the experiment coupled with a very significant ($P<0.01$) increase in weight gain in 1984 and 1985 (Fig. 6.12). This might indicate a significant increase in feed quality in 1984 and 1985 which resulted in low feed consumption but in high weight gain. The environmental trend for FEED, FCR and weight gain estimated by regressing yearly means in the control line on years were -37.40 ± 10.7 kg, -2.88 ± 0.96kg feed/kg gain and 4.90 ± 3.36kg, the standard errors being taken from the regression analysis. The high residual variation in feed may partly account for large standard errors associated with estimates of correlated annual genetic changes in both lines.

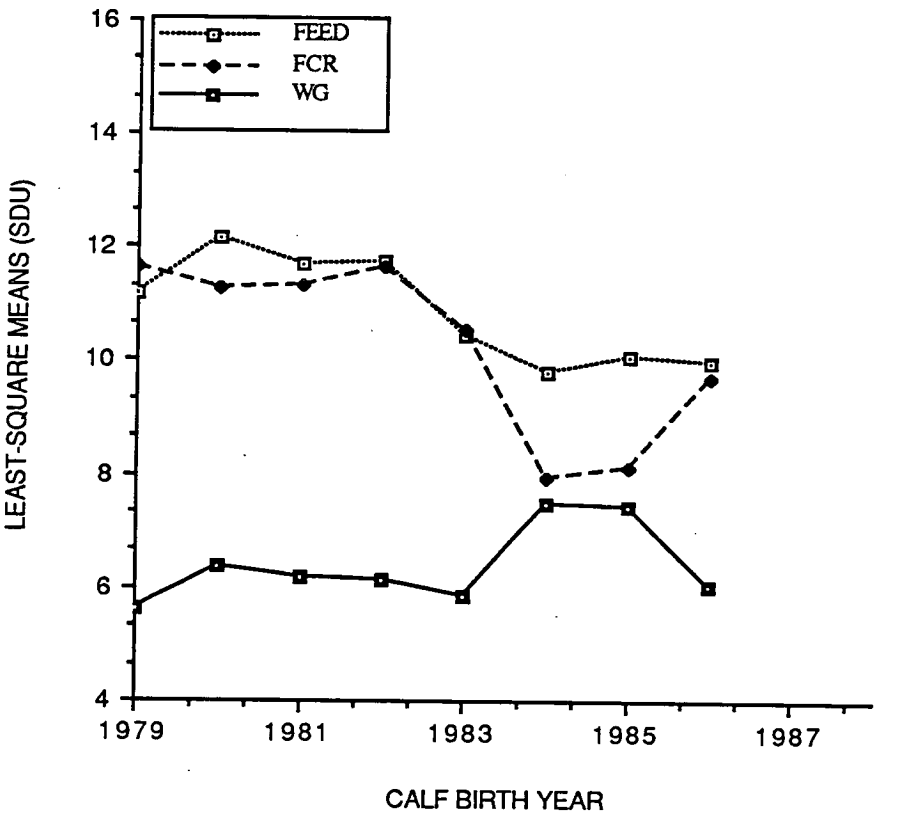

Fig. 6.12 Least-square means for FEED,FCR and weight gain (WG) in standard deviation units versus years.

In summary, selection for LGR has been accompanied by increases in growth rate, LEAN, and a decrease in FCR feed intake. In the LFCR line, there has been an increase in LEAN, a reduction in feed intake, FCR and little or no change in growth rate. Considering the direct and correlated responses, the answer to the issue raised on the last chapter as to whether selection for LFCR is necessary for improving rate and efficiency of lean gain, seems dependent on the conditions under which animals are commercially reared. In situations where feed availability is not a limiting factor, selection for LGR seems adequate to increase the rate and efficiency of lean gain. However where feed availability is a constraint, LFCR seems a better alternative selection in improving lean meat production.

CHAPTER 7

CORRELATED RESPONSES IN BODY WEIGHT AND MEASUREMENTS AT VARIOUS AGES AND REPRODUCTIVE TRAITS

7.1 Introduction

Correlated responses in body weight and body measurements at various ages in male and female calves, and reproductive traits in females are examined in this chapter. The literature indicates that there has been a lot of interest in environmental factors which are of importance in reproductive traits in beef cattle. The influence of various environmental factors on reproductive traits are therefore reported in addition to estimates of annual genetic change.

7.2 Materials and methods

The details of management for male and female calves have already been given in chapter three. The data analysed consisted of body weight measured approximately at one to two month intervals over an age period of 2 to 13 and 48 months respectively for male and female calves. Birth weight for female calves was also available. Data on body measurements: head length, first rib width, hook width, wither height, rump height and body length for females and scrotal circumference in addition for males, taken at about two to three months intervals over the same age period as body weight, were also analysed.

Reproductive traits studied included age at first calving, conception rate measured as the number of seasons mated divided by the number of successful pregnancies, calving date, calving difficulty score (score of 1 to 5; see Table 7.11 for definition of scores), calving and preweaning mortality rates and calving interval. Calving mortality rate was analysed as a binary trait with one assigned to dams whose calves died at birth or 24 hours after calving and zero to dams with calves surviving beyond 24 hours after calving.

Preweaning mortality rate was similarly analysed as a binary trait with one assigned to dams whose calves died at birth or before weaning; otherwise zero was assigned. All female records included female progeny born in the foundation years up to the 1985 calf crop, that is, over a six year period of selection.

7.2.1 Statistical analysis

(i) Body weight and measurements

Using a similar methodology as described in chapter five (equation 2), individual body weights and measurements at the various ages were adjusted for fixed effects and the deviations of the phenotypic means of the selected lines from the control each year regressed on calf birth year to obtain estimates of annual genetic change. The fixed effects fitted were calf birth year, weaning type, age of dam at the birth of their progeny, calving date and age at which body weights and measurements were taken. Weaning type and age of dam effects were classified as explained in section 4.2.2 (chapter four). The analysis was carried out separately for males and female calves. In estimating annual genetic changes (genetic trends) the regressions of yearly deviations of the mean performance of the selected lines from the control were forced through zero, since the selected and control lines were derived from same base population. Annual genetic changes in the open line were estimated relative to the initial difference between the open and control lines as explained in chapter five.

(ii) Reproductive traits

The same methodology employed for body weight was used to

estimate genetic trends for the various reproductive traits considered, with the relevant fixed effects fitted in the model. The fixed effects fitted in the model were, for

*age at first calving	year of birth, calving date, dam age, weaning type, birth weight and calving difficulty score.
*conception rate	year of birth
*calving date	year of birth, year of calving, dam age, sex of calf, dam age by sex of calf interaction and birth weight of calf
*calving difficulty	year of birth, year of calving, calving date, age of dam, sex of calf, dam age by sex interaction, and birth weight of calving
*calving and preweaning mortality rate	same as for calving difficulty
*Calving interval	year of birth, year of calving, calving date, sex of previous calf, dam age at calving, birth weight of previous calf and calving score of previous calf

Where appropriate, analyses of reproductive traits was carried initially utilising only first parity records and then over all available parities. For females born within the herd from the foundation year of 1978, records were available to a maximum of six parities. Analysis on only first parity performance involved about 653 reproductive records while about 1875 records were available over all parities.

The standard errors for the annual genetic changes for body weights and measurements, and reproductive traits were from the

regression analyses. They are therefore biased downwards as the variance due to drift has not been taken care of. Thus, the tests of significance based on these standard errors are only approximate.

7.3 Results

7.3.1 Body weight and measurements

Over the period of selection, a total of 159, 162, 70 and 50 female progeny were measured for body weight and various body measurements in the LGR, LFCR, control and open lines respectively at 12 months of age. A classification of the number of female calves by year and line is shown in Table 7.1. This classification and the total number of progeny recorded however vary from one age period to another. A similar classification of male progeny was presented in chapter four. Line means and standard deviations for body weight at approximately 6 and 12 months of age for male claves and 6, 12, 24, 36 and 48 months of age for females are presented in Table 7.2. Similar information for body measurements at 12 months of age is presented in Table 7.3.

(i) Body weight in male calves

The estimates of correlated annual genetic change for body weight at several ages for male calves are given in Table 7.4 and illustrated in Fig. 7.1. A negative but non-significant genetic trend was observed for male calves in the LFCR line over the age period of 2 to 13 months. In the LGR line, estimated genetic trends for body weight were generally positive but were significant only from about 9 to 13 months of age. Generally, estimates of correlated annual genetic change for body weight in the LGR line

TABLE 7.1

Classification of number of recorded female progeny at 12 months for body weight and measurements by year and line

Calf birth year	LGRL	LFCRL	CTL	OPL
1980	33	36	-	6
1981	28	30	11	4
1982	23	30	8	15
1983	30	24	15	10
1984	26	25	18	7
1985	19	17	18	8

TABLE 7.2

Line means and standard deviations for body weight (kg) for male (M) and female (F) calves at various ages

	LGRL		LFCRL		CTL		OPL		Standard deviation	
Trait	M	F	M	F	M	F	M	F	M	F
6 months body weight	160.2	144.2	155.4	144.0	151.5	132.7	158.0	141.7	32.57	26.18
12 months body weight	371.1	277.8	356.1	272.0	356.4	267.1	374.4	275.7	42.01	39.29
24 months body weight	-	401.6	-	391.2		384.8		397.6	-	49.25
36 months body weight	-	466.6		472.3		447.8		467.6	-	51.50
48 months body weight	-	465.18		487.8		456.4		521.69		56.43

TABLE 7.3

Line means and standard deviations for various body measurements (mm x 10) at 12 and 13 months of age respectively for male (M) and female (F) calves

	LGRL		LFCRL		CTL		OPL		Standard deviations	
Trait	M	F	M	F	M	F	M	F	M	F
Head length	454.7	390.7	454.9	393.6	452.5	383.5	459.0	388.4	19.23	17.90
First rib width	418.1	327.3	413.9	328.1	415.3	320.8	418.6	327.1	31.70	32.40
Hood width	456.9	390.9	446.2	390.4	446.5	382.2	453.6	390.0	25.25	28.19
Wither height	1073	985.6	1064	985.7	1063	982.3	1104	998.6	42.50	42.05
Body length	1307	1159	1290	1148	1292	1136	1326	1164	67.29	64.00
Rump height	1146	105.6	1131	1053	1130	1042	1173	1070	46.25	44.53
Scrotal circumference	354.3	-	352.3	-	350.0	-	358.0	-	25.30	

TABLE 7.4

Correlated responses per year in body weight (kg) in males at various ages

			OPL	
Age (months)	LGRL	LFCRL	INT	GC
2	-0.293 (0.23)	-0.318 (0.23)	1.530 (3.07)	-0.824 (0.70)
4	0.057 (0.35)	-0.328 (0.35)	2.930 (4.65)	-0.420 (1.07)
6	0.713 (0.57)	-0.297 (0.59)	2.650 (8.58)	-0.700 (1.94)
8	1.230 (0.715)	-0.774 (0.75)	-13.60 (10.8)	2.460 (2.41)
9	1.700* (0.78)	-0.794 (0.81)	-1.900 (10.3)	1.25 (2.43)
12	3.077** (0.91)	-0.197 (0.97)	4.500 (12.30)	2.250 (2.88)
13	3.315** (0.94)	-0.412 (1.00)	-1.100 (12.5)	4.37 (2.95)

INT = estimated difference between open line and control in the first year

GC = genetic change per year relative to the initial difference

* $P<0.05$
** $P<0.01$

increased with age (Fig. 7.1).

The correlated responses in body weight observed in the LGR line tended to be generally lower than estimates from most experiments involving direct selection for postweaning gain or yearling weight. The correlated annual genetic change expressed as a percentage of the mean reported for weaning weight at 205 days of age in Hereford cattle from direct selection for postweaning gain by Chevraux and Bailey (1977) was 1.9 percent. The estimate of annual rate of change reported by Aaron et al. (1986b) for weaning weight at 205 days in bulls was 0.93 percent in Angus cattle selected for yearling weight. The annual rate of change for body weight observed at a similar age in the LGR line was 0.51 percent. At about one year of age, the correlated annual percentage rate of change for body weight in males in the LGR line was about 74% of the direct rate of change for yearling weight for bulls observed by Newman et al. (1973) and Aaron et al. (1986b) respectively in Beef Shorthorn and Angus cattle.

None of the initial differences between the open and control lines or estimates of correlated genetic trend in body weight in males at the various ages were significant except at about 6 and 10 months of age. The estimated differences between the open and control lines in the first year at the two ages were 16.38 $\pm$ 6.69 and -26.1 $\pm$ 12.5 kg respectively. Corresponding estimates of genetic trend were -4.02 $\pm$ 1.61 and 5.76 $\pm$ 2.80 kg/year. Most estimates of the genetic trend in the open line had very large sampling error. This might be due to the few animals in the open line and differences between various bulls used within and across years. The estimates of correlated responses for body weight at any particular age showed

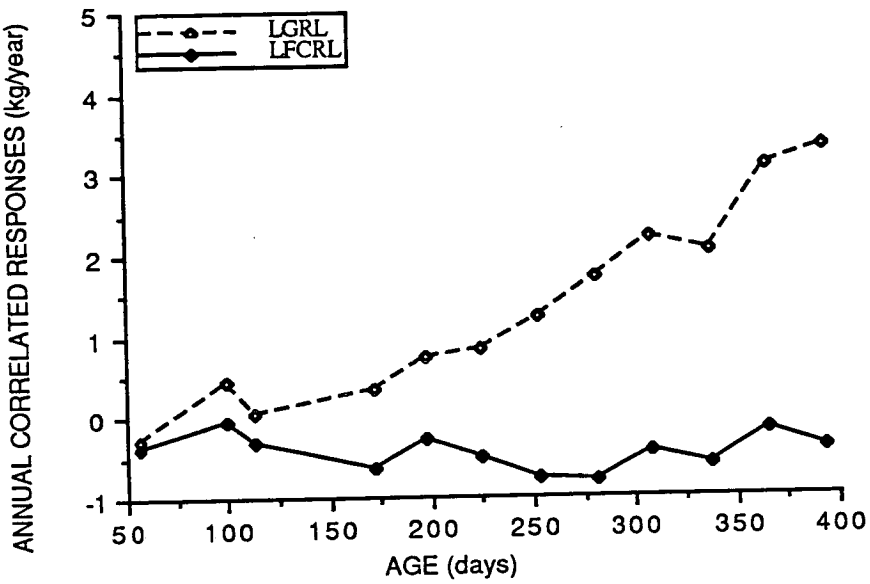

Fig. 7.1 Annual correlated responses for body weight in male calves at various ages.

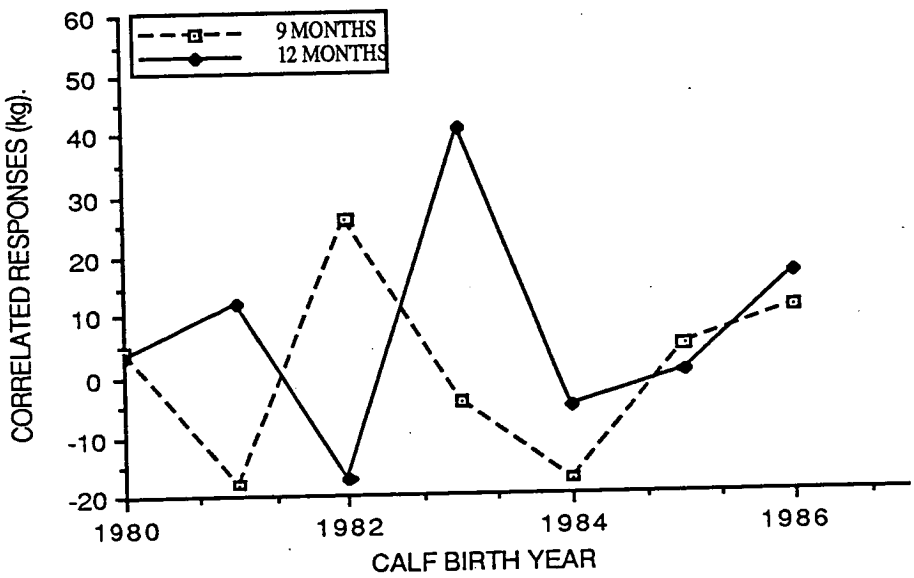

Fig 7.2 Correlated responses for body weight in male calves at 9 and 12 months of age in the open line

great variation (Fig. 7.2).

(ii) Body weight in female calves

The estimated correlated annual genetic change for body weight at several ages are presented in Table 7.5 and illustrated in Fig. 7.3. In contrast to males, positive and significant correlated responses in body weight were observed in the LFCR line. In general, annual correlated responses for body weight were significant in both selected lines from about 2 months of age to 24 months. Over the various ages, correlated responses were similar in magnitude and trend in both selected lines, although they tended to be slightly higher in the LGR line.

The correlated rate of change for weaning weight at 205 days reported for females from direct selection for yearling weight were 0.55 and 0.71 percent by Frahm et al. (1985b) and Aaron et al. (1986b) respectively in Hereford and Angus cattle. These are similar to the correlated rates of change of 0.56% observed in the LFCR line and 0.78% in the LGR line at approximately the same age. However, at one year of age the correlated rate of change in body weight in the LFCR line was only 55 and 66% of estimates reported by Newman et al. (1973) and Aaron et al. (1986b) respectively from direct selection for yearling weight. In the LGR line, the rate of change was similar to the estimate of Newman et al. (1973) but was only 80% of that of Aaron et al. (1986b).

From Figure 7.3, it seems that the reproductive cycle influenced magnitude of annual correlated responses for body weight in females. Annual correlated responses tended to increase up to 600 days (20 months) of age and declines gradually, which coincides

TABLE 7.5

Correlated responses per year in body weight (kg) in females at various ages

	Lines			
			OPL	
Age (months)	LGRL	LFCRL	INT	GC
0	0.079 (0.10)	0.048 (0.10)	-0.340 (1.07)	0.074 (0.35)
2	0.882** (0.32)	1.003** (0.33)	2.010 (3.42)	0.950 (1.13)
4	0.996* (0.46)	1.351** (0.48)	-0.030 (5.21)	0.400 (1.68)
6	1.096 (0.70)	0.781 (0.71)	-5.960 (7.87)	2.010 (2.54)
12	2.179** (0.77)	1.501 (0.79)	-3.4780 (8.47)	5.210 (2.76)
14	2.632** (0.85)	1.355** (0.88)	-8.02 (9.15)	7.46* (3.04)
24	4.210** (1.35)	3.050* (1.41)	-0.900 (13.6)	8.080 (4.48)
34	1.560 (2.09)	1.030 (2.23)	-15.00 (22.5)	8.340 (8.33)
48	1.870 (3.90)	3.19 (3.9)	34.90 (36.5)	6.600 (15.6)

INT, GC = see Table 7.4 for explanation

* P<0.05
** P<0.01

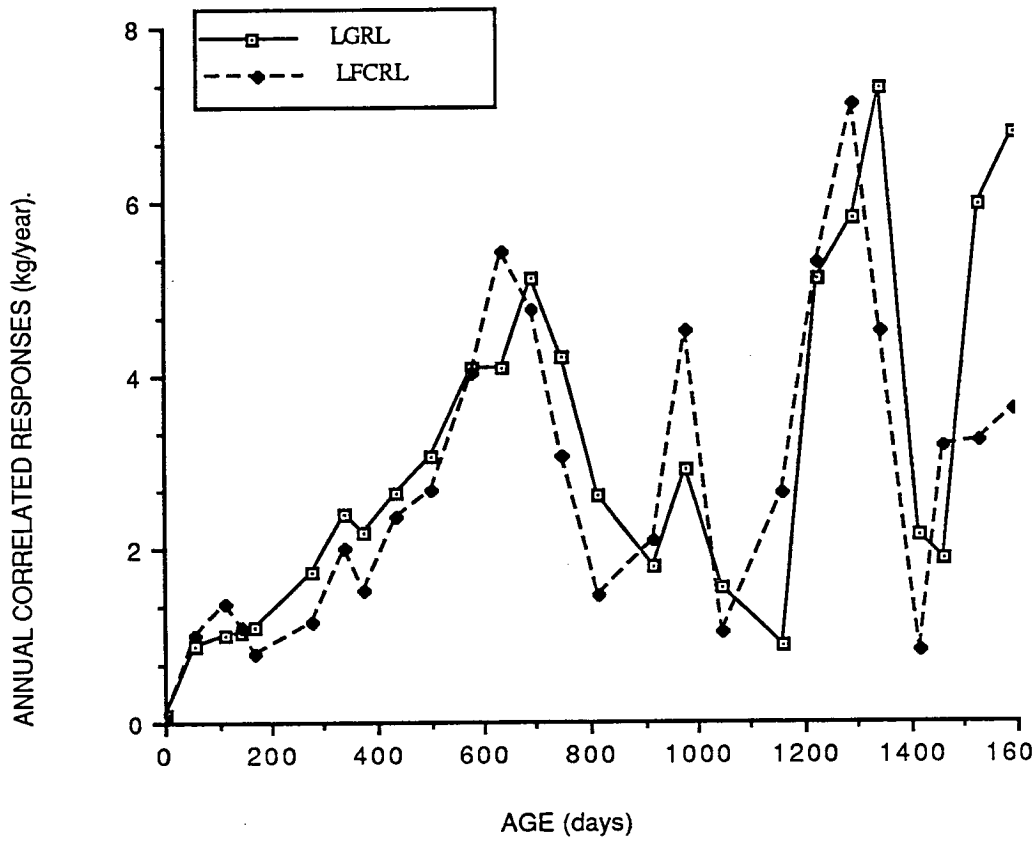

Fig. 7.3 Annual correlated responses for body weight in female calves at various ages.

with the period of late pregnancy in first parity, calving and weaning. There was again another increase as from 850 days (28 months) of age until about 977 days (32 months) followed by another decline, coinciding with the period of late pregnancy and calving in animals having their second parity. The next decline in correlated response seems again to coincide with calving at 4 years of age in animals having their third parity. The decline of correlated responses in body weight during the reproductive cycle in females, seems to suggest that body weight during reproductive and non-reproductive periods may not be influenced by the same genes to a very high degree. The phenotypic correlations between body weights during periods of high and low correlated annual genetic changes were fairly constant, about 0.50. This indicates that variation in body weight at the various periods may equally be due to permanent differences (both genetic and environmental) and special environmental variance between individuals.

As for males, estimates of the initial difference between the open and control lines in body weight were generally not significant. However estimates of genetic trend relative to the respective initial differences between the open and control line were positive and significant from 14 to 23 months of age. The estimates of genetic trends at 16 and 23 months were 12.98 $\pm$ 3.14 and 10.70 $\pm$ 3.94 kg/year respectively. Corresponding estimates for the initial difference between the two lines were -23.11 $\pm$ 9.72, and -7.00 $\pm$ 12.1 kg. There was great variation in estimates of correlated responses for body weight in any particular age as in males (Fig. 7.4).

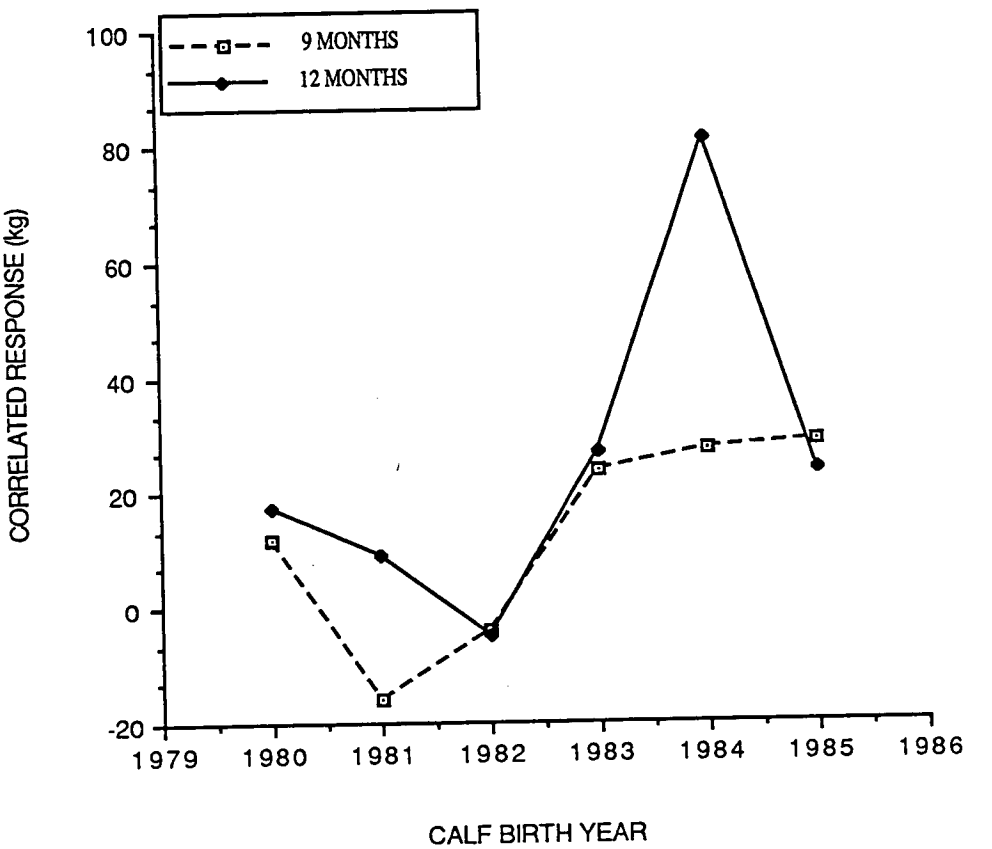

Fig. 7.4 Correlated responses for body weight in female calves at 9 and 12 months in the open line.

(iii) Body measurements in males

In the LFCR line, annual correlated responses for all body measurements were not significant (Table 7.6). All significant correlated responses for body measurements in the LGR occurred at the age of 9 months or/and 13 months of age (Table 7.6). The trend in terms of magnitude of correlated responses for wither height and body length over various ages are illustrated in Figures 7.5 to 7.6 respectively. Correlated responses for wither height and body length were only significant in the LGR line from 9 to 13 months of age and at 13 months of age for rump height and hook width. The significant correlated responses in the various body measurements in the LGR line occurred only over the same age period in which significant changes were observed for body weight. This coupled with the fact that insignificant correlated responses in body weight in the LFCR line were also associated with insignificant correlated changes in body measurements, seem to suggest that changes in body measurements might be dependent on changes in body weight.

In the open line, the only significant genetic trends were in body length at 9 and 13 months, wither height and rump height at 13 months of age (Table 7.6).

(iv) Body measurements in female calves

The results for correlated responses in females for body measurements are presented in Table 7.7 and illustrated for wither height and body length in Figures 7.7 and 7.8 respectively.

The most marked difference between both selected line in terms of correlated responses in body measurement in females was in body length. The estimates of annual correlated responses were

TABLE 7.6

Correlated responses per year for various body measurements (mm x 10) in males at different ages

Line	Age		Head length	First rib width	Head width	Wither height	Body length	Rump height	Scrotal[3] circumference
	6		-0.370 (0.44)	-0.721 (0.49)	0.962 (0.89)	1.036 (.131)	0.130 (0.93)	1.131	
LGRL	9		0.036 (0.45)	0.728 (.070)	-0.378 (0.54)	1.766* (0.90)	3.950** (.134)	-0.990 (1.02)	
	13		0.294 (0.41)	0.924 (0.75)	1.708* (0.57)	1.894* (0.90)	3.080* (1.51)	3.067* (0.99)	1.501 (0.56)
	6		-0.389 (0.38)	-0.744 (0.67)	0.596 (0.50)	-0.868 (0.93)	-0.764 (0.92)	-0.045 (0.97)	
LFCRL	9		-0.231 (0.48)	-0.957 (0.74)	-0.209 (0.45)	-0.563 (0.95)	-1.020 (1.18)	-0.431 (0.97)	
	13		-0.146 (0.43)	-0.126 (0.74)	-0.207 (0.61)	0.326 (0.95)	-0.280 (1.60)	0.502 (0.99)	0.642 (0.56)
	6	(1)	7.400 (4.63)	17.57 (8.06)	11.99 (6.10)	15.06 (11.2)	33.50 (15.8)	16.40 (14.2)	
		(2)	-1.850 (1.12)	-5.330 (1.95)	-2.270 (1.47)	-0.380 (2.70)	-5.420 (3.81)	-1.300 (3.27)	
OPL	9	(1)	-2.110 (6.04)	13.39 (9.48)	7.210 (6.89)	9.600 (12.1)	-33.50 (1.18)	-1.400 (14.6)	
		(2)	0.000 (1.43)	-2.680 (2.25)	-1.210 (1.64)	1.780 (2.87)	10.74* (4.27)	4.580 (3.36)	
	13	(1)	-1.110 (5.80)	1.230 (9.92)	6.330 (7.60)	10.00 (12.0)	-22.90 (1.60)	-5.200 (14.2)	-5.480 (8.35)
		(2)	1.350 (1.39)	0.480 (1.82)	-0.560 (1.82)	6.320* (2.87)	11.89 (4.79)	10.28** (3.30)	2.480 (1.94)

(1) Difference between open line and control in the first year
(2) Estimated genetic trend within the open line relative to the initial difference
(3) Available only at 13 months of age
*p< 0.05
**p< 0.01

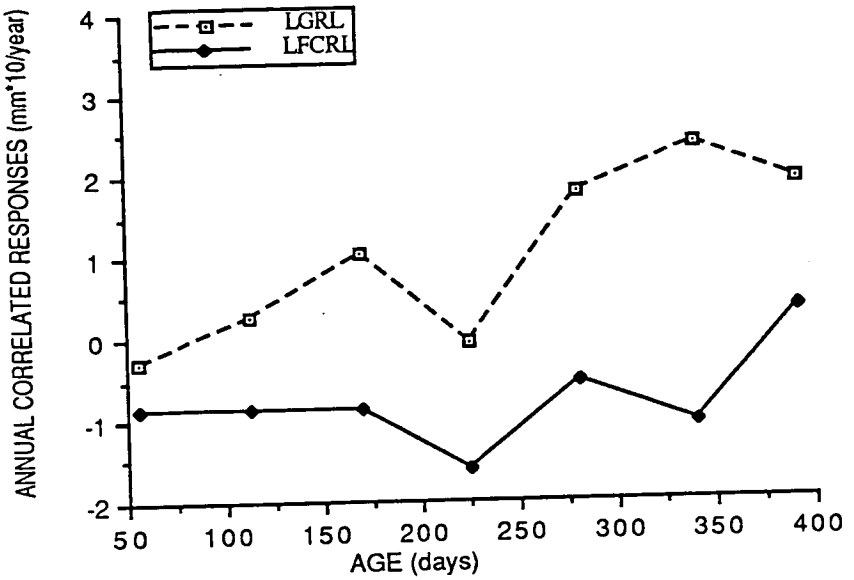

Fig. 7.5 Annual correlated responses for wither height in male calves at various ages.

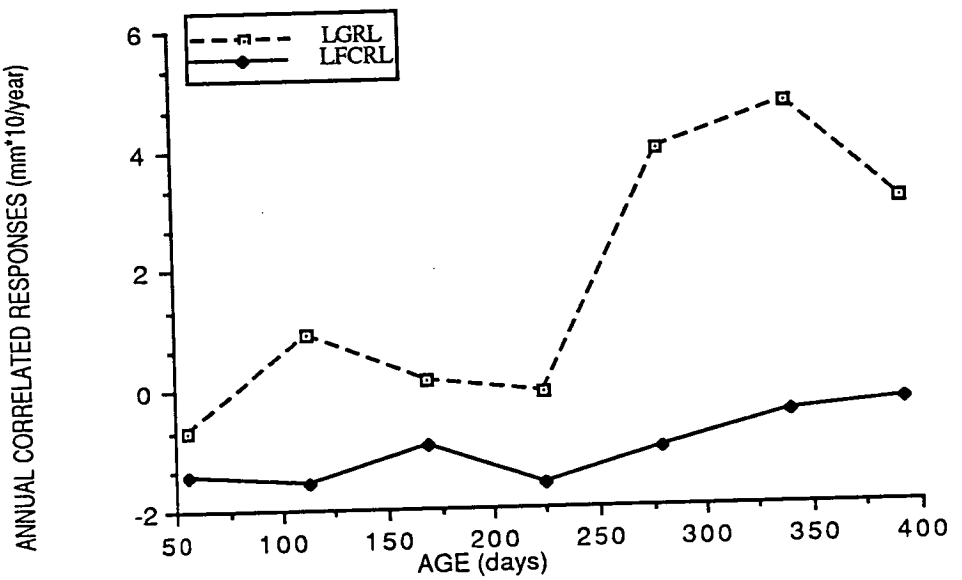

Fig. 7.6 Annual correlated responses for body length in male calves at various ages.

TABLE 7.7

Correlated responses per year for various body measurements in females at different ages

Body measurement (mm x 10)	Line	Ages (months) 6	12	24	36	46
Head length	LGRL	0.822 (0.49)	1.197* (0.69)	1.093* (0.50)	0.840 (0.74)	0.680 (1.06)
	LFCRL	1.041* (0.50)	1.687* (0.50)	1.804** (0.52)	1.093 (0.50)	0.85 (1.07)
	OPL(1)	-1.360 (4.34)	-3.130 (4.35)	-9.080 (4.95)	4.080 (9.90)	-2.530 (9.240)
	(2)	0.450 (1.41)	1.630 (1.42)	4.860** (1.66)	3.310 (3.68)	6.040 (4.13)
First rib width	LGRL	1.079 (0.83)	0.694 (1.00)	2.235* (0.91)	1.810 (1.48)	-0.110 (1.96)
	LFCRL	0.840 (0.85)	1.230 (1.02)	1.885* (0.94)	1.151 (1.61)	-0.22 (1.97)
	OPL(1)	-10.85 (7.34)	-2.700 (8.84)	-6.940 (8.96)	-11.200 (15.8)	-5.400 (17.2)
	(2)	1.810 (2.39)	2.760 (2.88)	7.290* (3.00)	2.910 (5.87)	0.440 (7.67)
Hook width	LGRL	0.722 (0.63)	1.330 (0.77)	2.282* (0.85)	1.240 (1.15)	2.390 (1.81)
	LFCRL	0.714 (0.65)	1.376 (0.79)	1.984* (0.81)	2.020 (1.25)	2.960 (1.82)
	OPL(1)	-9.480 (5.56)	-0.660 (6.82)	-5.640 (8.02)	-6.400 (12.2)	-1.700 (1.57)
	(2)	2.470 (1.81)	2.800 (2.22)	5.320* (2.69)	4.320 (4.55)	9.300 (7.30)

TABLE 7.7 (continued)

Body measurement (mm x 10)	Line	Ages (months) 6	12	24	36	46
Wither height	LGRL	1.450 (1.23)	1.230 (1.27)	3.170** (1.10)	2.000 (1.81)	3.170 (2.19)
	LFCRL	1.960 (1.26)	1.660 (1.30)	3.900** (1.14)	2.260 (1.96)	2.130 (2.20)
	OPL(1)	-17.70 (10.9)	-3.600 (11.2)	-2.800 (10.8)	9.100 (19.2)	18.300 (19.1)
	(2)	10.47** (3.55)	7.060 (3.65)	11.66** (3.62)	5.960 (7.15)	9.740 (8.51)
Body length	LGRL	4.410** (1.64)	6.740** (19.84)	5.020** (1.84)	6.120* (2.84)	12.28** (3.95)
	LFCRL	2.590 (1.68)	3.540 (1.89)	5.260** (1.92)	5.380 (3.09)	7.260 (3.96)
	OPL(1)	-12.50 (14.5)	4.500 (16.3)	-18.10 (18.1)	-34.50 (30.6)	-2.200 (34.4)
	(2)	8.460 (4.73)	8.810 (5.32)	19.97** (6.08)	27.70 (11.4)	30.40* (15.4)
[3]Rump height	LGRL	3.810* (1.58)	7.070 (3.65)			
	LFCRL	4.570** (1.62)	7.600* (3.74)			
	OPL(1)	-19.90 (15.1)	-13.20 (34.5)			
	(2)	11.47* (4.64)	8.800 (10.7)			

1 and 2 = As explained in Table 7.6.
3 = Rump height measurements were availale only up to 12 months of age
* P<0.05
** P<0.01

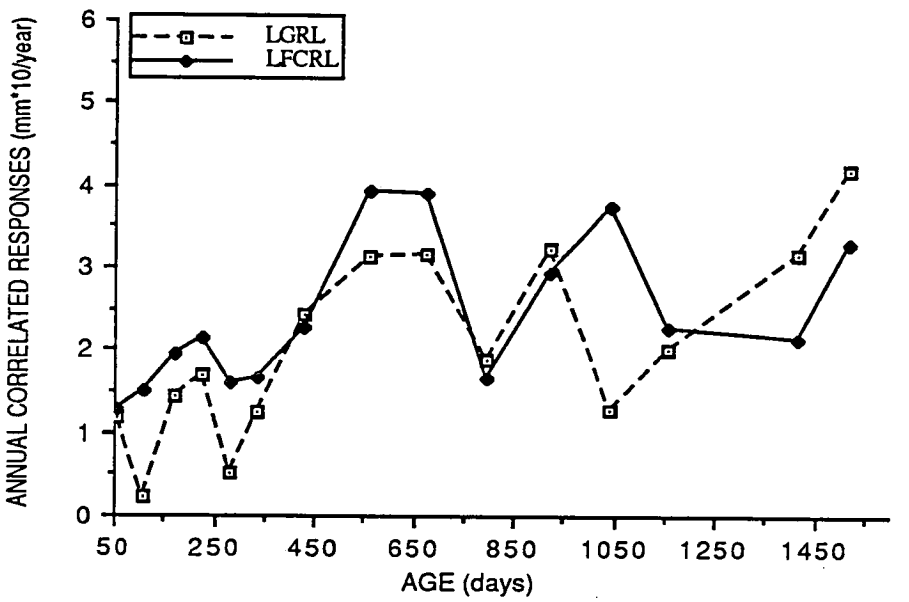

Fig. 7.7 Annual correlated responses for wither height in females at various ages.

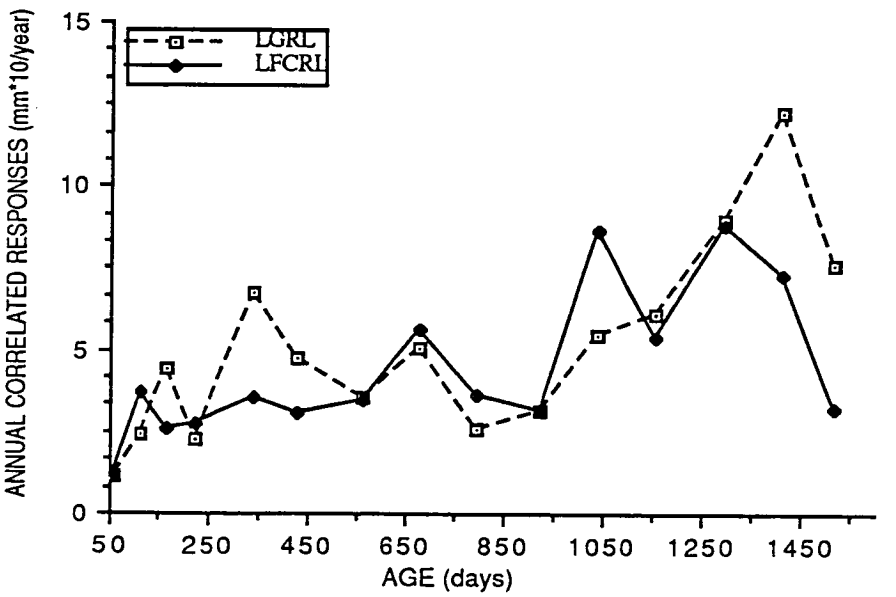

Fig. 7.8 Annual correlated responses for body length in females at various ages.

positive and generally significant in the LGR line from about 6 to 48 months of age. However in the LFCR line, correlated annual responses although positive were only significant at about 24 months of age.

Annual correlated responses for most other body measurements : first rib width, hook width and wither height were positive but only significant at about 24 months of age in both selected lines. Body measurements up to this age (24 months) were recorded in calves born in the project up to 1985 and therefore have the greatest amount of selection differential behind them.

Similar to the two selected lines, estimates of annual correlated responses for the 5 body measurements in females were generally positive in the open line but were only significant mainly at 24 months of age. Body length was however still significant at 36 and 48 months.

7.3.2. Reproductive traits

A possible source of bias in estimates of correlated responses in reproductive traits in both selected lines is the confounding effect of system of mating with lines. The LGR and LFCR lines were bred by natural mating while the control line was bred by artificial insemination. Thus estimates of correlated responses, which are deviations of each of the selected line from the control line, may be biased to the extent the system of mating influenced the reproductive traits studied. Line means and standard deviations for age at first calving, calving date, conception rate and calving interval are presented in Table 7.8.

TABLE 7.8

Line means and standard deviations for age at first calving, calving date and calving interval

Trait	Line means				Standard deviation
	LGRL	LFCRL	CTL	OPL	
Age at first calving (days)	750.0 (126)	743.6 (133)	776.6 (56)	819.4 (44)	103.2
Calving date (days in the year)	154.3 (287)	154.9 (316)	160.6 (106)	159.7 (88)	17.22
Calving interval (days)	373.1 (158)	381.9 (180)	377.4 (47)	382.0 (44)	63.65

Number of records shown in brackets

(i) Age at first calving (AFC)

The age at first calving was not significantly influenced by age of dam, calving date, sex of calf and calving difficulty score of the dam. The most significant source of variation in AFC was birth weight of the calf. The coefficient for the regression of AFC on birth weight of calf was 5.05 ± 1.09 days/kg. Estimated correlated annual genetic change in AFC were -4.930 ± 3.20 and -8.010 ± 3.31 days respectively in the LGR and LFCR lines; only the later was significant (Table 7.9).

(ii) Conception rate

Positive but insignificant genetic trends of 0.009 ± 0.01 and 0.001 ± 0.01 were observed in the LFCR and LGR lines respectively (Table 7.9). Similarly, the initial difference between the open and control lines in the first year and the estimated genetic trend for the open line were not significant.

(iii) Calving interval

None of the fitted fixed effects except year of calving had any significant effect on calving interval. Although estimates of genetic trend were negative in both selected lines, they were not significant (Table 7.9). However, the trend within the open line was positive but also not significant.

(iv) Calving date

The most significant ($P<0.01$) source of variation in calving date was birth weight of the calf both in parity one and over all parities. The regression coefficient for calving date on birth

TABLE 7.9

Correlated responses per year in conception rate, age at first calving and calving interval

Trait	Lines			
	LGRL	LFCRL	OPL	
			(1)	(2)
Conception rate	0.009	0.001	-0.045	0.035
	(0.01)	(0.01)	(0.10)	(0.03)
Age at first calving (days)	-4.930	-8.010*	89.10**	-18.90
	(3.20)	(3.31)	(33.70)	(10.9)
Calving interval (days)	-2.290	-1.03	10.80	-1.800
	(3.38)	(3.49)	(26.9)	(11.7)

(1) and (2) as explained in Table 7.6.

weight of calf was about 1.21 ± 0.19 days/kg both in parity one and overall parities. Other fixed effects considered such as sex of calf and age of dam had no signficant effect on calving date. Annual correlated responses in calving date were not significant in both selected lines (Table 7.10). However, over all parities a significant positive trend of 1.139 ± 0.47 days was observed in the LGR line. Neither the initial difference between the open and control lines in the first year nor the genetic trend within the open line were significant.

(v) Calving difficulty score

The percentage of calves in each class of calving difficulty score classified by line over all parities are shown in Table 7.11. The percentage of calves born unassisted (score = 1) was similar in all lines across all parities.

The sex and birth weight of calf constituted the most significant sources of variation ($P<0.01$) in calving difficulty both in parity one and over all parities. An increase of 1kg in birth weight increased calving difficulty score by 0.058 ± 0.009 and 0.027 ± 0.004 units respectively in parity one and over all parities. Male calves were associated with more calving difficulties. Age of dam at calving was only significant ($P<0.01$) over all parities with calving difficulty being higher in dams aged 2 to 3 years or more than 6 years old relative dams of 4 to 6 years of age. The estimates of annual correlated genetic change in calving difficulty in both selected lines were insignificant and of about the same magnitude in first parity and over all parities; but the trend was negative in the LGR line (Table 7.10). In the open line, estimated

TABLE 7.10

Correlated responses per year for calving date (days of the year), calving difficulty and calf mortality

Line	Parity	Calving date	Calving difficulty	Calving mortality	Preweaning mortality
LGRL	One	0.837 (0.59)	-0.108 (0.03)	0.023 (0.013)	0.110 (0.015)
	All	1.139* (0.147)	-0.015 (0.02)	0.009 (0.008)	0.005 (0.01)
LFCRL	One	-0.608 (0.61)	0.018 (0.03)	0.016 (0.014)	0.028 (0.016)
	All	0.883 (0.48)	0.016 (0.02)	0.008 (0.008)	0.019 (0.011)
OPL	One (1)	5.620 (6.34)	0.037 (0.31)	0.095 (0.115)	0.172 (0.130)
	(2)	-1.490 (4.27)	-0.080 (0.101)	-0.031 (0.037)	-0.052 (0.043)
	All (1)	-0.690 (2.04)	0.026 (0.16)	0.141* (0.060)	0.204 (0.07)
	(2)	0.180 (1.58)	-0.049 (0.058)	-0.049 (0.022)	-0.051 (0.028)

(1) and (2); see Table 7.6 for explanation of symbols
*P<0.05

TABLE 7.11

Percent proportion of calves in each calving score scale classified by line

Calving score	Percentage proportion in each line			
	LGRL	LFCRL	CTL	OPL
1	81	77	80	84
2	7	9	2	5
3	7	9	9	8
4	4	4	7	2
5	0.4	1	2	1

1 = no difficulty - calves unassisted

2 = little difficulty - assistance given by hand, but no jack or puller used

3 = moderate difficulty - assistance given with jack or calf puller

4 = major difficulty - calf jack used and major difficulty encountered

5 = caesarean birth - performed after determining that calf could not be delivered with a calf-puller

genetic trends in first parity and over all parities were similarly not significant but were negative (Table 7.10).

(vii) Calf mortality

The percent calf mortality at calving and before weaning observed in each line in parity one and over all parities are presented in Table 7.12. Estimated genetic trends for calving and preweaning mortality rates are given in Table 7.10. In parity one, calving mortality was 5.5 and 5.1% higher in the LGR and LFCR lines compared with the control; but over all parities, there were no differences between lines. Calving mortality was similar in both open and control lines in parity one and over all parities. In terms of estimated genetic trend, positive but insignificant trends of 0.023 $\pm$ 0.013 and 0.016 $\pm$ 0.014 were obtained respectively in the LGR and LFCR lines is parity one. Calving difficulty had a very significant ($P<0.01$) positive relationship with calving mortality. The coefficient for the regression of calving mortality on calving difficulty was 0.116 $\pm$ 0.01.

However over all parities estimated genetic trend were generally positive but insignificant for both selected lines. Most of the fixed effects were not significant except age of dam and birth weight which had a significant negative relationship (regression coefficient = -0.011 $\pm$ 0.001) with calving mortality. Calving difficulty also significantly influenced ($P<0.01$) calving mortality in over all parities; the regression coefficient of calving mortality on calving difficulty was 0.099 $\pm$ 0.01.

In parity one, the initial difference between the open line and the control in calving mortality was positive but the estimated

TABLE 7.12

Percent calf mortality at birth and before weaning

Lines	Calving mortality (%)		Preweaning calf mortality (%)	
	Parity one only	Over all parities	Parity one only	Over all parities
LGRL	19.05	11.15	20.63	14.98
LFCRL	18.69	11.04	27.07	18.61
CTL	13.56	11.21	18.64	15.89
OPL	13.64	11.36	25.00	21.59

genetic trend was negative, however, none of them were significant. Corresponding estimates over all parities were similar to those obtained in parity one in terms of direction of change but were significant.

Pre-weaning mortality was 2 and 8% higher respectively in the LGR and LFCR lines relative to the control line in one. Over all parities, the LGR line was 1% lower while the LFCR line was 3% higher than the control line in pre-weaning mortality (Table 7.12). Preweaning mortality was about 6% higher in the open line than in the control in parity one and over all parities. The estimates of genetic trend in parity one although positive in both selected lines, were insignificant (Table 7.10).

Over all parities, birth weight was the most significant ($P<0.01$) source of variation in preweaning mortality. The effects of sex of calf, age at calving, age at calving by sex interaction and calving date were not significant. There was a significant positive relationship between calving difficulty and preweaning mortality rate in parity one and over all parities (regression coefficient = 0.117 ± 0.015). The estimates of genetic trend were positive but insignificant in both selected lines (Table 7.10).

The initial difference between the open and control lines in preweaning mortality and the estimated genetic trend in the open line were not significant in parity one. However, the open line was initially slightly higher than the control line while the genetic trend was negative. Over all parities, the open line was significantly ($P<0.01$) higher than the control line in preweaning mortality but the estimated genetic trend though negative was not significant (Table 7.10).

7.4 Discussion

7.4.1 Body weight and measurements

The positive annual correlated responses in body weight at various ages observed for females in the LFCR line in contrast to the negative genetic trend in males was unexpected and is difficult to explain. Firstly the standard errors for the estimates of genetic change in females did not include the drift variance and are therefore biased. The estimates of change may therefore be confounded with the effects of genetic drift. Irgang et al. (1986b) reported different rates of response in replicate lines selected for weaning weight, the realised heritability estimates they obtained in two different replicates were -0.21 and 0.41. The differences in rates of response between replicates was attributed to the random effects of genetic drift on gene frequencies. The marked difference in the pattern of correlated response for body weight in females compared with male calves may also be confounded with such effects of genetic drift.

Secondly, differences in rate of genetic change between sexes have been reported by most workers (Frahm et al., 1985b; Aaron et al., 1986b) even under similar conditions of nutrition or management. In this experiment females were not recorded for LFCR and hence the rate of genetic change is unknown. It is therefore not possible to determine to what extent the differences in correlated responses in body weight between sexes could be due to differences in rates of direct response for LFCR in male and female calves.

And thirdly, male and female calves were reared on different

diets. Heifers were reared mainly on grass while bulls were performance tested on a pelleted diet consisting of grass and barley. The differences in genetic trend for body weight in bulls and heifers could partly be due to the difference in the type of diet fed. Pacer et al. (1986) reported that an Angus line selected for postweaning gain on a concentrate diet was signifciantly different from foundation animals in postweaning gain, weight per day of age and final weight. A similar line selected on a rouphage diet was not significantly different in any of the above traits from foundation animals. This seems to indicate the effect of genotype by feeding regime interaction on selection response. In this study the possible effects of genotype by feeding regime interaction on correlated responses in body weight are confounded by sex effects and cannot be estimated.

While it is difficult to attribute the differences in the pattern of correlated responses for body weight in bulls and heifers to any one of the factors discussed above, the differences however highlight the possible influence of genotype by feeding regime interaction in beef selection experiments and is one of the areas where further research is needed.

The positive and significant genetic trends obtained for males in body length and wither height at 9 and 13 months of age seem to indicate a positive genetic relationship between LGR and these body measurements. Growth rate being highly correlated with LGR, the above is consistent with the conclusion of Lush (1932) that the rate of gain is positively associated with body length and wither height. However, Black, Knapp and Cook (1938) reported a significant phenotypic correlation of -0.32 between gain and body

length and a non-significant correlation of -0.19 between wither height and gain working with dual purpose, beef, and dairy steers of unstated breeds. Kohli, Cook and Dawson (1951) obtained similar results with steers of Milking Shorthorn. Some of these inconsistent results may be differences in breeds and age at which measurements were taken.

The correlated rates of genetic change for wither height and body length were 23 and 30% of the change observed for body weight at one year of age in bulls. Corresponding estimates for female were 38 and 43%. In view of the high correlation between LGR and growth rate (or body weight), it seems the genetic correlation between LGR or growth rate and body measurements may not be very high. Selection for LGR or growth rate with some attention paid to physical appearances may reduce the maximum possible response. Estimates of genetic correlations between body measurements and production factors in beef cattle seem to be lacking in the literature.

7.4.2 Reproductive traits

The significant effects of age of dam and sex of calf on calving difficulty observed are similar to the reports of Brinks, Olson and Carroll, (1973). Male calves were associated with more calving difficulty. This has been attributed to higher differences in size, males having larger body dimensions (Philipsson, 1976) and higher average birth weight. In this study males were significantly ($P<0.01$) heavier than females at birth weight.

The significant role of birth weight in causing calving difficulty and calf mortality has been widely reported by several workers (Brinks *et al.*, 1973; Morris *et al.* 1986). Studying the

relationship between birth weight and dystocia incidence, Menissier (1975) reported that the frequency of dystocia rises sharply when birth weight exceeds a certain upper threshold value. However Morris et al. (1986) studying 3 herds of beef cattle in New Zealand did not observe any threshold but found a quadratic regression an adequate fit for their data. Fitting a quadratic regression for birth weight and calving difficulty did not improve the fit in this study. A similar result had been reported by Tong, Newman, Rahnefeld and Lawson (1988) for several breeds of cattle. Also a plot of the number of calves associated with of calving difficulty in each birth weight subclass as a percentage of total calves born in the herd against each birth weight subclass did not reveal any sharp increase in dystocia (Figure 7.9) but showed a gradual increase until about 30kg birth weight, peaked at 36kg birth weight and declined subsequently. Similarly, plotting the ratio of total dystocia score to total number of calves born within each birth weight (to account for severity of dystocia associated with each birth weight) against birth weight did not indicate any threshold. The highest incidence of dystocia occurred at 36kg, but this incidence was not subsequently sustained at higher birth weights (Figure 7.10).

In view of the positive relationship between birth weight and calving difficulty, and calving difficulty and calf mortality, a positive relationship was expected between calf mortality and birth weight. However, a significant negative relationship was obtained between calf mortality and birth weight. Similar relationships between birth weight and calving difficulty, calf mortality and birth weight were obtained by Morris et al. (1986). They attributed this phenomenon to high death rates of calves at heavier weights due to

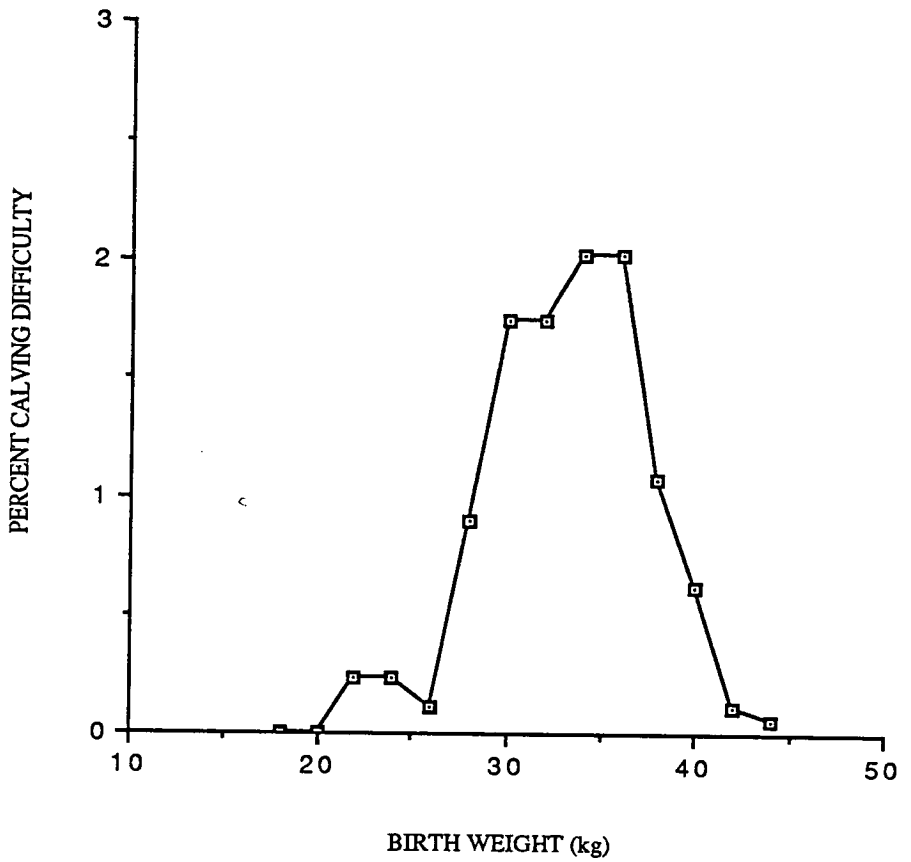

Fig. 7.9 Incidence of calving difficult within each birth weight as percentage of incidence in total number of calves born versus birth weight.

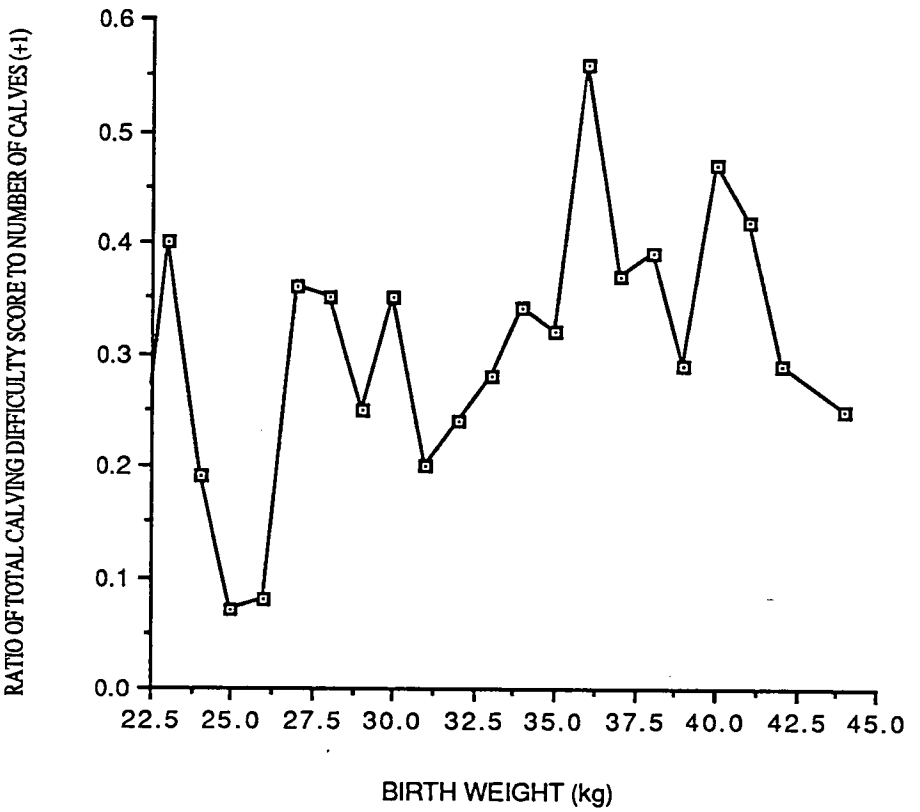

Fig. 7.10 Ratio of total calving difficulty score and number of calves born within each birth weight versus birth weight.

dystocia and a similar high death rate for calves of lighter weights. The net result is a decreasing linear response in mortality as birth weight increased. Other workers have similarly reported increased calf mortality when birth weight dropped below a minimum value (Notter et al., 1978), indicating an optimum birth weight range for calf viability. Plots of percentage calf mortality calculated within each birth weight subclass against birth weight subclasses in these data showed a similar trend with higher percentages of calf mortality at both extremes of birth weight (Figure 7.11). Almost all calves below 19kg at birth died at calving in this experiment. However, calf mortality expressed as a percentage of the total number of calves born across all birth weight subclasses, showed an increase up to 30kg birth weight and an eventual decline from 36kg afterwards (Figure 7.12).

The estimates of genetic trend obtained indicate that selection for LGR and LFCR was not accompanied by unfavourable correlated responses in the reproductive traits studied. Most of the genetic trends for reproductive traits were not significant. In a similar study on correlated responses in female reproductive traits resulting from direct selection for yearling weight in Angus cattle Luesakul-Roedech et al. (1986) concluded that selection for growth rate resulted in increased mature size, delayed sexual maturity and decreased dystocia. The negative genetic trend obtained for calving difficulty in the LGR line (though not significant) seems consistent with his conslusions but in the LFCR line, sexual maturity was enhanced.

In order of importance, birth weight of calf, age of dam and sex of calf seem to be the most important environmental factors

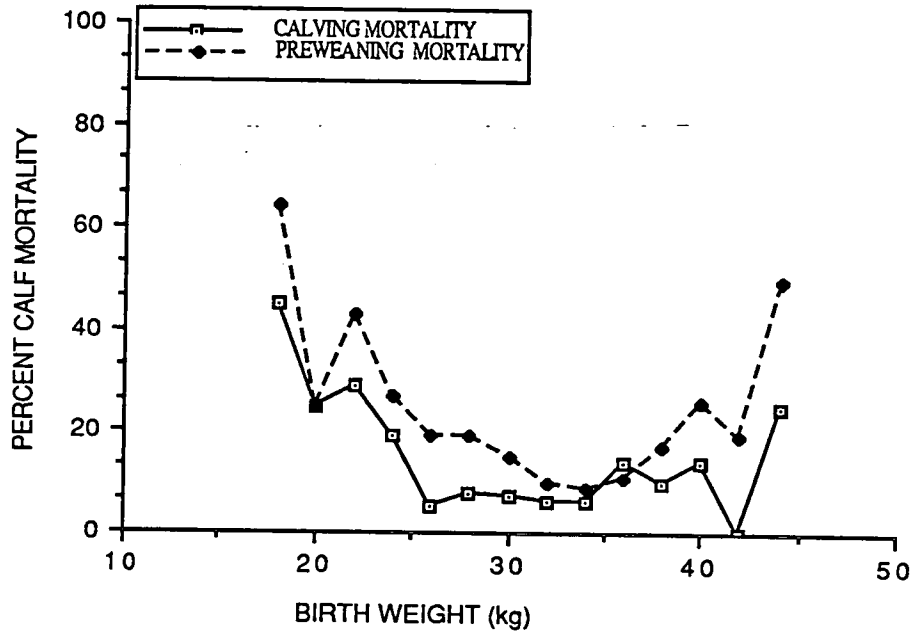

Fig. 7.11 Percentage calf mortality within each birth weight versus birth weight.

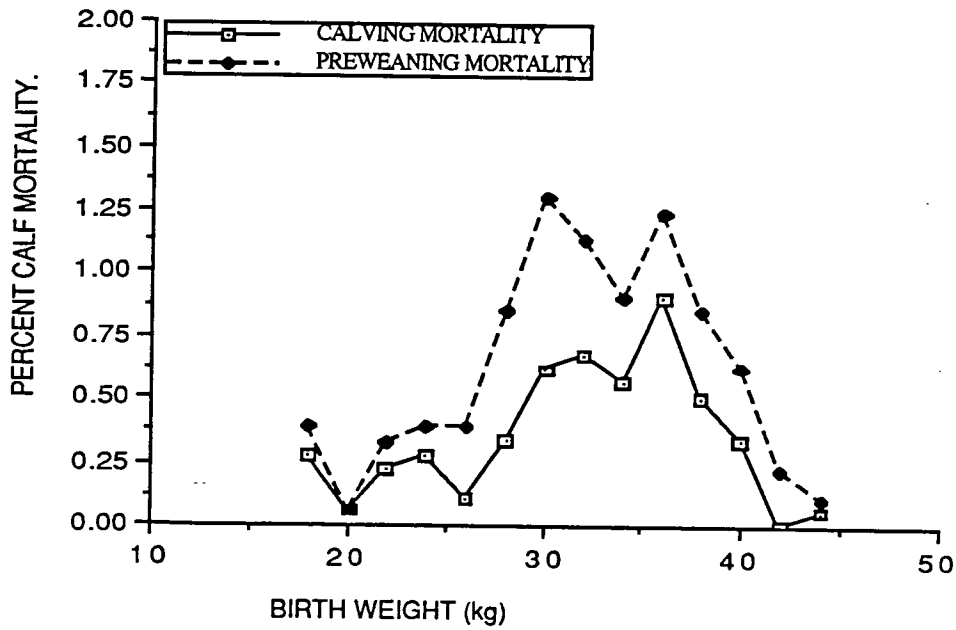

Fig. 7.12 Calf mortality within each birth weight as percentage of total number of calves born versus birth weight.

affecting reproductive traits. This is consistent with the conclusion of Tong et al. (1988) that birth weight seems a valuable trait for indirect selection to reduce calving problems.

CHAPTER 8

DIRECT AND CORRELATED RESPONSES TO SELECTION FOR LGR AND LFCR IN CROSSBREDS

8.1 Introduction

Comparison of crossbred progeny sired by bulls from selected and control lines provides an additional way of evaluating genetic change in the selection lines. This chapter is concerned with the evaluation of the first year's trial of a two-year planned comparison between crossbred offspring of bulls in the selected, control and open lines.

Some workers (Rowlands, Payne, Dew and Manston, 1974; Little, Kay, Manston, Rowlands and Start, 1977) have examined the possibility of using several blood metabolites measured early in life for predicting subsequent growth performance of calves. Finding a suitable predictor of subsequent calf performance would be of even greater importance for carcass traits, where one of the major problems associated with genetic improvement through selection is that of accurate assessment in live animals. While various *in vivo* carcass assessment techniques have been evolved, they suffer from a major limitation of not being able to give any indication of the potential of young animals for lean deposition a priori. Physiological predictors can have a major advantage over the other live animal techniques in that they may have the capacity to provide accurate estimates early in life of subsequent growth and carcass composition. Most previous studies on blood metabolites as possible predictors of subsequent calf performance have been in unselected populations and mainly involved trying to find significant correlations between growth rate or feed intake and various blood metabolites. These selected lines offer a unique opportunity to examine if there are marked differences in the concentration of metabolites between selected and control lines. In addition to

growth and feed data, various blood metabolites were sampled to examine any distinct line differences.

8.2 Materials and methods

8.2.1 Experimental plan and management procedure

From the 1983 calf crop, 5 high ranking bulls from the LGR and open lines, 4 and 8 respectively from the LFCR and control lines were randomly mated to Holstein/Friesian cows in several herds to produce calves in 1986. The mating plan was such as to ensure an equal representation of each line in each herd. The calves were contract reared to 12 weeks of age before transportation to the 3 trial locations : High Mowthorpe (HM), Drayton (DR) and Cold Norton (CN) for growing and finishing on an intensive silage beef system. The 80 calves performance tested in HM were group penned in two modules, by sex and within line with group feed recording. At DR and CN, calves were penned by sex across lines with individual feed recording. Across locations there were a total of 41, 43, 45 and 46 calves in the LGR, LFCR, control and open lines respectively. A classification of number of animals by line and location is shown in Table 8.1.

The steers were fed good quality grass silage ad libitum plus 2kg of concentrate consisting of rolled (or crushed) barley and white fishmeal in the ratio of 9 to 1, to a common age of 10 months. Thereafter the silage was supplemented with 2kg of mineralised rolled (or crushed) barley until slaughter. For heifers the silage was supplemented initially with 1.5kg of mineralised rolled barley which was adjusted as necessary depending on silage quality to achieve a daily live weight gain of at least 0.75kg/day. Steers and heifers

TABLE 8.1

Number of animals according to line and location

Station	LGRL	LFCRL	CTL	OPL
HM	18	20	20	20
DR	11	12	12	12
CN	12	11	13	14
Total	41	43	45	46

were sent for slaughter at a fixed age of about 400 and 420 days respectively at FRI, Bristol. A total of 40 animals were fully dissected while only sample joints were dissected for the remaining 135 animals. A regression equation was derived using the carcass information on the 40 fully dissected animals and on the carcass visual assessment of fatness and conformation based on the European Association for Animal Production (EAAP) system (De Boer et al., 1974) to predict weight of lean as follows:

Weight of lean in side (g) = 5799 + 4.46 ABDMUS -10.95 ABDMFOT + 0.533 SIDEWT1 - 345FSC

where

ABDMUS = weight of lean of lean in abdominal joint (g)

ABDMOT = weight of intermuscular fat and other tissues in abdominal joint (g)

SIDEWT1 = is the mean weight of the left and right sides for each carcass expressed in grams. It also includes the kidney knob and channel fat

FSC = EAAP fat score (1=minimum fatness and conformation and 15 = maximum)

Carcass lean percent was estimated by dividing the predicted lean weight by the sum of side weight 2 and cod fat weight. The sum of side weight 2 and cod fat weight approximates most closely to total tissue weight (total weight of items recovered from a full side dissection) obtained from full dissection (Fisher

and Bayntun, 1987). Side weight 2 is the same as side weight 1 but it does not include the kidney knob and channel fat.

8.2.2 Performance records

Full and 24 hour fasted liveweights at the start and the finish of the trial and full fed liveweight at 14 days intervals were recorded for each animal. The total amounts of feed consumed fortnightly were also recorded but these were on a pen basis for HM. The above information were used to calculate for each animal its daily gain (DG), daily feed intake (DFI) and food conversion ratio (FCR). Using the lean percent (LEAN) predicted for each animal and its killing out percent (KO), LGR and LFCR were estimated in the same manner as for the purebreds (see chapter three).

In addition to the growth and feed data, two blood samples were taken at the three locations (HM, DR and CN) at an average age of 20 and 32 weeks and analysed for protein, albumin, urea, B-OH-butyrate (Butyrate) and globulin concentrations. However at HM additional blood samples were taken at 22, 41 and 52 weeks of age and analysed for the same blood metabolites. All blood samples from HM were, in addition analysed for glucose and haemoglobin concentrations.

8.2.3 Statistical analysis

(i) Growth and feed data

The effects of age at start of test, days on test, sex of calf, location, line, sex by location and line by location interactions, pen and sires within lines were fitted for growth and feed variables. The line differences were tested using the sire

mean squares. The number of days animals were tested was omitted from the model in the analysis of initial weight at beginning of test. At HM, feed data were available on a pen basis, therefore pen means for DFI, LFCR and FCR were used in the analysis. Analyses were carried out for each location and combined over each location (a) giving equal weight to each observation and (b) for traits associated with feed (DFI, LFCR and FCR) and for traits in which the residual variance was not homogenous in the three locations (FWT, DG and LEAN) weighting each observation according to its variance found from the separate analysis.

(ii) Blood parameters

The same model used in the analysis of growth and feed data was fitted for blood metabolites except that age at beginning of test was replaced by age at blood sampling. The blood parameters sampled at about 20 and 32 weeks were analysed separately across all locations, followed by an analysis on the average of the two samples. A separate analysis was carried out for the blood data from HM as more blood samples and parameters were available. Correlations between blood parameters and DG and DFI at the age of blood sampling were estimated after adjusting all variations for important sources of variation using the models mentioned earlier.

8.3 Results

8.3.1 Growth and feed traits

The average age of animals at start of test across locations was 18.5 weeks, with the average starting age at HM, DR and CN being 16.1, 19.0 and 20.4 weeks respectively. The number of

days on test across locations averaged 273.1 days but it was 289, 267 and 255 days respectively for HM, DR and CN. A summary of growth and feed traits in terms of means and standard deviations are presented in Table 8.2.

Least square means for lines from the combined analysis across locations are given in Table 8.3 and for each location in Table A8.3 in appendix 1. There were no significant differences between progeny of both selected lines, the open line and the control in LGR. The same was applicable to LFCR both in the unweighted and weighted analysis. However progeny from both selected lines were about 10 $\pm$ 7g/day higher in LGR than progeny belonging to the control. This indicates that direct and correlated responses for LGR in the line LGR and LFCR lines respectively were of the same magnitude. The open line was about 4 $\pm$ 7g/day higher than the control in LGR.

Attempts were made to predict the expected direct and correlated responses in the crossbreds from the responses measured in the purebred progeny of 1985. The 1985 purebred progeny were sired by selected bulls from the 1983 bull calf crop out of which bulls used in the crossbred trial were also chosen. The expected responses in the crossbreds were predicted by multiplying the response measured in the 1985 purebred progeny by a proportion of the cumulative selection differential on these progeny that is accounted for by half of the individual selection differentials of their sires. These predictions are however only approximate because

(1) not all selected bulls which contributed progeny to the 1985 calf crop were used in the crossbred trial. On the other hand

TABLE 8.2

Means and standard deviations for growth, feed and carcass data across all locations

Trait		Means	Standard deviation
LGR (g/day)		314.6	53.9
LFCR (kg feed/kg lean gain)	(a)	17.18	1.19
	(b)	16.51	1.92
LEAN		57.92	3.63
KO		59.33	4.18
IWT (kg)		114.7	17.97
FWT (kg)		362.6	37.74
DG (g/day)		914.0	117.0
DFI (kg)	(a)	5.265	0.393
	(b)	5.131	0.047
FCR (kg feed/kg gain)	(a)	5.845	0.530
	(b)	5.632	0.124

(a) For only the two locations (DR and CN) where individual animal feed intake is recorded

(b) For HM, where feed intake was recorded on pen basis.

TABLE 8.3

Line effects for growth and feed variables from combined analysis of data from the three stations

Variable		Lines				
		LGRL	LFCRL	CTL	OPL	SED
LGR (g/day)		281.5	282.5	272.1	276.3	6.97
LFCR kg feed/kg gain		16.14	15.98	15.93	16.28	0.36
lean	(W)	16.23	16.08	15.89	16.27	0.51
LEAN		58.61	58.70	58.71	56.48**	0.68
	(W)	58.16	58.72	58.72	56.72	0.70
KO		57.45	57.26	56.83	58.57**	0.54
IWT (kg)		116.7**	109.2	109.2	117.0**	2.57
FWT (kg)		359.1**	351.8**	339.0	354.8**	4.87
	(W)	359.0**	352.6**	340.8	353.0**	3.84
DG (g/day)		850.8*	848.8*	817.2	839.8	13.6
	(W)	845.5**	847.8**	811.4	831.9	12.6
DFI (kg/day)		4.905**	4.891**	4.718	4.878**	0.050
	(W)	4.928**	4.807	4.680	4.788	0.078
FCR (kg feed/kg gain		5.518	5.493	5.500	5.540	0.082
	(W)	5.538	5.478	5.550	5.580	0.094

SED = standard error of difference between each selected line, open line and control line

(W) = weighted combined analysis

* = significantly different from the mean of the control ($P<0.05$)

** = significantly different from the mean of the control ($P<0.01$)

some bulls used in the crossbred trial did not contribute progeny to the 1985 calf crop as they were not selected. Therefore any within line variation in bulls' breeding values will bias the predicted responses.

(2) it is assumed that there are no differences in breeding values between the Hereford cows and Holstein/Friesian cows used to produce the purebreds and crossbred progeny respectively in the traits considered. Any difference in breeding values between the Hereford and Holstein/Friesian cows will bias the predicted responses and

(3) lean percent was predicted in different manners in the purebred and crossbreds. The predictions in the crossbred were based on actual dissected carcass lean in contrast to the purebreds and may be more accurate. This might cause differences between predicted and observed responses in the crossbred for traits in which lean percent is a component.

The predicted direct and correlated responses for the crossbreds are presented in Table 8.4. In the LGR line, the achieved and expected response in the crossbreds were not significantly different; the achieved response was about 66% of the expected. In terms of correlated response for LGR in the LFCR line, the positive genetic change observed was in sharp contrast to the expected negative change, however, both estimates were not significantly different. The negative direct response for LFCR in LFCR line observed in crossbred progeny is consistent with the expected value from the purebreds (Table 8.4).

Similarly, crossbreds of both selected lines were not significantly different from that of the control in terms of killing

TABLE 8.4

Predicted and observed direct correlated responses for the crossbreds from the purebreds

Trait	Predicted		Observed	
	LGRL	LFCRL	LGRL	LFCRL
LGR (g/day)	[a]14.25 (5.35)	-6.99 (9.05)	9.40 (6.97)	10.4 (6.97)
LFCR kg feed/kg lean gain	-0.281 (1.03)	1.32 (1.46)	0.40 (0.52)	0.100 (0.52)
LEAN	0.382 (0.73)	0.611 (2.52)	-0.56 (0.70)	0.00 (0.70)
DFI (kg/day)	0.064 (0.043)	0.023 (0.099)	0.248 (0.078)	0.127 (0.078)
GRT (g/day)	28.98 (8.48)	-15.87 (13.9)	34.10 (13.6)	36.40 (13.6)
FCR (kg feed/kg gain)	-0.150 (0.90)	0.089 (0.96)	-0.012 (0.94)	-0.072 (0.94)

[a] Standard error in brackets

out percent or lean percent. This is consistent with the predicted correlated responses from the purebred. The weighted and unweighted analysis for LEAN, FWT and DG yielded similar results in terms of line differences (Table 8.3). The LGR line was significantly ($P<0.05$) higher than the control in initial weight at beginning of test but the LFCR line was not different from the control. However both lines were significantly higher than the control in FW and DG. The observed correlated response for DG was very similar to the predicted value (34.1 ± 13.6 versus 28.98 ± 8.5) in the LGR line. In the LFCR line, the observed positive correlated response in DG was significantly different from a negative genetic change of -15.87 ± 13.9g/day predicted from the purebreds. The open line was significantly higher than the control in IWT, FWT and KO but lower in LEAN.

There were no line differences in FCR, both in the unweighted and the weighted analysis. The LGR line was significantly higher ($P<0.01$) than control in DFI both in the unweighted and weighted analysis but the open was not significantly higher in the unweighted analysis.

8.3.2 Blood parameters

A summary of blood parameters across locations in terms of means and standard deviations are presented in Table 8.5. Line effects on blood parameters at first and second samplings and averages of both samplings across locations are given in Table 8.6. No consistent and significant line differences were observed for any blood parameters at both samplings. The only significant line differences at the first sampling were : a lower urea concentration

TABLE 8.5

Mean and standard deviation for blood parameters across all locations

	Measurements			
	1	2	Average	SD[a]
Protein (g/l)	64.33	65.97	65.10	3.41
Albumin (g/l)	33.72	32.91	33.27	2.07
Urea (m.mol/l)	4.24	3.90	4.050	0.91
Butyrate (m.mol/l)	0.438	0.387	0.411	0.10
Globulin (g/l)	30.61	33.070	31.821	4.21
[b]Haemoglobin (g/l)	-	-	118.5	4.10
[b]Glucose (g/l)	-	-	3.016	0.13

[a] Standard deviation for the average of both measurements

[b] Data only from HM; average of five samples

TABLE 8.6

Line effects for blood parameters across all locations

Variable	Sampling	LGRL	LFCRL	CTL	OPL	SED[a]
Protein (g/l)	First	61.96	59.64	60.64	60.41	0.98
	Second	65.43	65.69	66.83	68.25	1.33
	Average	63.67	63.15	64.38	64.46	0.98
Albumin (g/l)	First	33.22	33.21	32.89	34.00**	0.33
	Second	28.83**	30.17	30.54	31.33	0.51
	Average	31.17	31.50	31.61	32.67**	0.34
Urea (m.mol/l)	First	3.176**	3.085**	3.863	3.489	0.22
	Second	3.012	2.790	2.830	2.805	0.27
	Average	2.980	2.810**	3.216	3.083	0.13
Butyrate (m.mol/l)	First	0.271*	0.304	0.333	0.336	0.023
	Second	0.363	0.378	0.370	0.309*	0.036
	Average	0.333	0.358	0.359	0.324	0.018
Globulin (g/l)	First	25.26	22.94	24.26	22.92	1.19
	Second	34.54	33.60	34.21	34.85	1.45
	Average	34.77	32.96	33.77	32.29	1.01

[a]Standard error of difference between each selected line, open line and control.

in both selected lines relative to the control line, a lower concentration of butyrate in the LGR line and a higher albumin concentration in the open line compared with the control. At the second sampling, the LGR and open lines had significantly lower albumin and butyrate concentrations compared with the control.

The results of the analysis of the blood data from HM are given in Table 8.7. The results presented are from the analysis of blood parameters averaged across the five samplings. The results were quite consistent with those from the combined analysis across the three locations except there were higher albumin concentrations for both selected lines relative to the control. For the two additional blood parameters considered in this location, no line differences were observed for haemoglobin but the LGR and open lines were significantly lower in glucose concentration relative to the control line. An examination of the results from the separate analyses of the blood samplings from HM indicated that the significant line differences for urea occurred only in the first blood sampling.

8.3.3 Correlations between blood parameters and growth rate and feed intake

A summary of the correlations between blood parameters and daily gain estimated within sires are presented in Table 8.8. Correlation estimates between blood parameters from the first and second blood samplings and growth rate using only the HM data were generally similar to results from a across the three locations and were therefore not presented. There was a significant positive correlation of 0.239 between albumin concentration and DG up to 20

TABLE 8.7

Effect of line on blood parameters (High Mowthorpe)

	LGR	LFCRL	CONTL	OPENL	SED[a]
Protein (g/l)	64.31	63.79	63.83	63.92	0.31
Albumin (g/l)	34.95**	34.87*	34.46	35.19*	0.18
Urea (m.mol.l)	3.485*	3.369**	3.652	3.537	0.08
Butyrate (m.mol/l)	0.324**	0.362	0.374	0.359*	0.007
Globulin (g/l)	27.40	27.00	27.38	26.70	0.34
Haemoglobin (g/l)	106.3	102.4	104.0	102.0	1.20
Glucose (g/l)	3.079*	3.101	3.149	3.063*	0.03

[a] Standard error of difference between each selected line, open line with control.

* $P < 0.05$

** $P < 0.01$

weeks of age (age at first blood sampling). However negative correlations of -0.369 and -0.191 were obtained between urea, globulin and DG respectively at 20 weeks of age. The significant relationships between albumin, urea and DG were maintained at subsequent ages with daily gain calculated at two week intervals up to 40 weeks. However the correlation between globulin and DG declined sharply at subsequent ages.

Rowlands et. al. (1974) and Little et al. (1977) have also reported positive correlation coefficients of 0.38 and 0.48 respectively between albumin and growth rate. The slightly larger correlation coefficients they obtained could be due to the fact they worked with relatively younger animals. These correlations seem to depend on the age at which blood constituents were sampled. This may partly account for the absence of significant correlations between daily gain and the blood parameters considered at 32 weeks of age. The same phenomenon was observed from the analysis of the HM blood data; most blood parameters from the second to the fifth sampling were not significantly correlated with daily gain. The two additional blood constituents considered in HM, glucose and haemoglobin, were not significantly related to daily gain. Adjusting daily gain of calves for differences in feed intake did not influence correlations in contrast with the observation of Little et al. (1977). They reported that adjusting weight gain for feed intake resulted in all correlations between weight gain and the blood parameters becoming insignificant.

Correlation estimates between blood parameters and feed intake across the three locations are given in Table 8.8. There were significant negative correlations of -0.252 and -0.201

TABLE 8.8

Correlations between blood parameters and daily gain and daily feed intake at 20 and 32 weeks of age (all locations)

	Daily gain		Daily feed intake	
Blood metabolites	20 wks	32 wks	20 wks	32 wks
Protein	0.137	-0.011	-0.122	0.002
Albumin	0.239**	0.051	0.009	0.182*
Urea	-0.368**	0.024	-0.252*	0.246**
Butyrate	-0.085	-0.036	-0.201*	0.080
Globulin	-0.191*	-0.017	-0.111	-0.060
[1]Glucose	-0.146	-0.035	-0.091	-0.183
[1]Haemoglobin	-0.086	0.050	0.032	0.402**

* $P<0.05$

** $P<0.01$

[1] Only from data from High Mowthorpe

respectively between urea, butyrate and daily feed intake at 20 weeks of age. In the second blood sampling at 32 weeks of age, the relationship between urea and DFI has become positive and albumin has become positively correlated with DFI. The positive correlation between feed intake and albumin agrees with the findings of Little et al. (1977). However, most of the studies have not reported any significant relationship between feed intake and urea (Rowlands et al., 1974; Little et al., 1977).

8.4 Discussion

In the LGR line, the observed direct and correlated responses in the crossbred progeny were in most cases consistent with expected values predicted from the purebred performance. Although direct response for LGR was not significant, which is similar to the results of the first crossbred trial of Frahm et al. (1986b) after six years of selecting for yearling weight, a high proportion of the response observed in the purebreds (66 percent) has been passed over to the crossbred progeny. After 14 years of selection, the response observed in the crossbred progeny by Aaron et al. (1986b) was about 60 percent of the cumulative direct response in the purebreds in two lines selected for weaning and yearling weight; although their estimates of responses were more precise.

In the LFCR line correlated responses in LGR and daily gain were in sharp contrast with expected results from the pure breeds. This difference in the pattern of response between the crossbreds and the purebreds might reflect differences in the type and quality of feed. Detail nutritional analysis of the diet fed to the

crossbreds was not available but it seems that a greater proportion of their diet consisted of grass silage. As in the case of correlated responses for body weight in females (chapter seven), the high correlated responses in LGR and DG in the crossbreds of the LFCR line seem indicative of the important role of genotype by feeding regime interaction on selection response.

A major limitation in this study with respect to using the various blood metabolites sampled to predict subsequent calf performance in carcass traits was the unavailability of carcass information at the ages in which blood metabolites were sampled across all locations. It was therefore not possible to relate line differences in blood metabolites to differences in carcass information or the two selection traits at exactly the same age.

Some of the blood metabolites measured are indicators of certain physiological processes in the body. Urea for instance is an indicator of amino acid metabolism (Davis, Carrigus and Hinds, 1970), and glucose an indicator of energy balance. A decrease in blood urea concentration may be a consequence of a reduced rate of amino acid degradation to urea (Davis et al., 1970). The significant decrease in urea concentration in both selected lines may be indicative of increased lean deposition in these lines relative to the control. Although the higher levels of LGR in both selected line were not significantly different from the control, a preliminary analysis of carcass data by Fisher and Bayntun (1987) showed the amount of carcass lean tissue to be significantly higher in both selected lines than in the control line. They reported lean tissue weights of 56.31, 55.26, 53.27 and 54.59kg respectively for the LGR, LFCR, control and open lines (with standard error of

the difference (SED) = 0.9). Angus (1987) working with three breeds of sheep, Oxford, East Friesian and Texel, reported that lambs of the leanest breed, Texel, had the lowest blood concentration of urea and the fattest breed, Oxford, had the highest amount of blood urea. Her results from the administration of recombinant bovine somatotropin (rBST) further confirmed this relationship between lean deposition and blood urea concentration. The administration with rBST, which increases lean deposition led to further reduction of urea concentration in the treated group relative to the control. Increased nitrogen retention from the treatment of animals with growth hormone has also been demonstrated in Holstein steers (Moseley, Krabill and Olsen, 1982). In addition, the significantly higher daily gain and lower urea concentrations in both selected lines are consistent with the negative phenotypic correlation observed between daily gain and urea concentration. The above evidence seems to implicate urea as a suitable candidate for a physiological predictor of lean growth. Certainly, urea concentration in relation to rate of lean deposition warrants further investigation.

The significantly lower concentrations of glucose in the LGR and open lines in the data from HM was associated with significantly higher daily gain in both lines at the same age. This might indicate a negative genetic relationship between daily gain and blood glucose level as the phenotypic correlation between both traits was not significant. Davis et al. (1970) reported an initial increase in blood level of glucose in lambs infused with growth hormone, reaching a peak in the first day but declined thereafter followed by another rise; which indicates a

non-consistent relationship between level of growth hormone and blood glucose. Angus (1987) did not observe any difference in blood glucose level between lambs administered with rBST and the control group. It may be inferred from the above that the relationship between growth rate and level of glucose observed in the LGR and open lines is not mediated through circulating levels of growth hormone but most probably through some other physiological processes or genetic factors.

The results do indicate that a substantial proportion of the responses achieved, especially in growth traits in the LGR line were expressed in the crossbreds. The positive responses in LGR and DG in crossbreds of the LFCR do indicate the possible important role of genotype by feeding regime interaction in beef cattle selection experiment. Urea seems to be the only likely suitable physiological predictor of lean deposition of all the various blood metabolites sampled.

Appendix 1

TABLE A8.3

Line effects for growth and feed variables in each station and in all stations combined

Variable	Station	Lines				
		LGRL	LFCRL	CTL	OPL	SED
LGR (g/day)	HM	292.9	305.7	281.2	288.0	10.3
	DR	303.3	273.4	283.0	281.1	15.58
	CN	274.48	282.5	277.8	283.1	16.17
	All	281.5	282.5	272.1	276.3	6.97
LFCR kg feed/ kg lean gain)	HM	15.30	4.93	16.09	16.19	0.53
	DR	15.32	16.20	15.01	15.52	1.09
	CN	18.52	17.66	16.84	17.44	1.03
	All	16.14	15.98	15.93	16.28	0.36
	All (W)	16.23	16.08	15.89	16.27	0.51
LEAN	HM	59.22	59.89	59.76	56.67	0.88
	DR	59.64	59.78	58.53	58.82	1.23
	CN	56.79	59.38	60.86	57.78	1.82
	All	58.61	58.70	58.71	56.48	0.68
	All (W)	58.16	58.72	58.72	56.72	0.70
KO	HM	57.99	58.47	57.21	59.92	1.05
	DR	58.60	56.06	59.32	58.86	1.41
	CN	57.92	58.65	56.80	58.63	0.87
	ALL	57.45	57.26	56.83	58.57	0.77
IWT (kg)	HM	113.2	111.1	108.8	116.1	4.63
	DR	128.3	110.3	120.6	121.5	4.14
	CN	108.6	100.3	96.26	111.8	4.60
	All	116.7	109.2	109.2	117.0	2.57
FWT (kg)	HM	357.0	354.5	345.5	361.5	5.06
	DR	359.6	330.1	334.0	333.9	5.53
	CN	324.0	310.6	294.0	325.7	10.5
	All	359.1	351.8	339.0	354.8	4.31
	All (W)	359.0	352.6	340.86	352.95	3.84

TABLE A8.3 (continued)

Variable	Station	Lines				
		LGRL	LFCRL	CTL	OPL	SED
DG (g/day)	HM	857.8	876.7	831.2	867.6	19.62
	DR	876.4	836.7	822.2	817.2	14.53
	CN	842.7	821.1	811.1	844.6	33.4
	All	850.8	848.8	817.2	839.8	13.58
	All (W)	845.5	847.8	811.4	831.9	12.6
DFI (kg/day)	HM	4.886	4.971	4.936	5.052	0.081
	DR	4.793	4.493	4.415	4.448	0.12
	CN	5.424	5.474	5.040	5.334	0.11
	All	4.905	4.891	4.718	4.878	0.050
	All (W)	4.923	4.807	4.680	4.788	0.078
FCR (kg feed/ kg gain)	HM	5.341	5.302	5.567	5.468	0.082
	DR	5.318	5.211	5.188	5.304	0.15
	CN	6.307	6.424	6.047	6.174	0.25
	All	5.518	5.493	5.500	5.510	0.082
	All (W)	5.538	5.478	5.550	5.580	0.094

CHAPTER 9

AN ALTERNATIVE ALGORITHM FOR INCORPORATING THE RELATIONSHIPS BETWEEN ANIMALS IN ESTIMATING VARIANCE COMPONENTS

9.1 Introduction

Linear models employed in the analysis of animal breeding data require the genetic relationships between animals to be incorporated. When data are available over several generations, the knowledge and the use of the relationships between animals can account for selection bias and result in more accurate estimates of variance components.

Meyer (1987) has recently shown how to derive transformed mixed model equations (MME) that use relationships. The modification depended on the proportions of genes in common between individuals and their descendants. An alternative algorithm is presented that depends on the number of parent-offspring relationships and not on the total number of related animals and has been found to be substantially faster than that of Meyer (1987) in deriving transformed MME with the relationship between animals incorporated.

9.2 THe model

Let us consider a univariate model with one random factor.

$$y = Xb + Zu + e \qquad (1.1)$$

where

y = vector of observations

b = vector of fixed effects

u = vector of random effects

e = vector of random residual error

X,Z = incidence matrices

Let

$$E\begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} Xb \\ o \\ o \end{bmatrix} \qquad V\begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & o \\ o & I\sigma_e^2 \end{bmatrix}$$

$$V(y) = ZAZ'\sigma_a^2 + I\sigma_e^2 \tag{1.2}$$

The MME equations on absorption of fixed effects pertaining to (1.1) are

$$(Z'SZ + \lambda A^{-1})\ u = Z'Sy \tag{1.3}$$

with

$$S = I - X\,(X'X)^{-1}X' \text{ and } \lambda = o_e^2/o_a^2$$

$$u = C^{-1}Z'SY \text{ where } C = (Z'SZ + \lambda A^{-1}) \tag{1.4}$$

The variance components to be estimated are σ_a^2 and σ_e^2 which represent variance between and within levels of random effects respectively. Restricted maximum likelihood (REML) equations to estimate σ_a^2 and σ_e^2 using an EM -algorithm and incorporating relationships are (Meyer, 1987).

$$\sigma^2_a = u\,A^{-1}\,u\,/\,[m - \lambda\,tr\,(A^{-1}C^{-1})] \tag{1.5}$$

$$\sigma^2_e = (y'Sy - y'SZu - \lambda u'A^{-1}u)/[N - r(X) - m + \lambda tr\,(A^{-1}C^{-1})] \tag{1.6}$$

where

m = number of levels of u

N = number of observations

r(X) = rank of X.

tr = trace

9.3 Equivalent model

Henderson (1976) and Thompson (1977) have shown that when ordered such that parents precede their progeny, A can be written as the product of a lower triangular matrix T and the square of a diagonal matrix D as follows

$$A = TDDT' \qquad (1.7)$$

Using (1.7), (1.2) can be expressed as

$$V(y) = ZTD^2T'Z'\sigma_a^2 + I\sigma_e^2$$

Thus if we define $Z_1 = ZTD$, an equivalent model to (1.1) is (Quaas, 1984)

$$y = Xb + Z_1u_1 + e \qquad (1.8)$$

where

$u_1 = (TD)^{-1}u$ and

$V(u_1) = I\sigma_a^2$

$$V(y) = Z_1 Z_1' \sigma_a^2 + I\sigma_e^2$$

MME equations and variance component estimates from (1.8) corresponding to (1.3) to (1.6) above are

$$[D'T'Z'SZTD + \lambda I]\, u_1 = D'T'Z'Sy \qquad (1.9)$$

$$C_1 u_1 = D'T'Z'Sy \qquad (1.10)$$

$$u_1 = C_1^{-1} D'T'Z'Sy \qquad (1.11)$$

$$\sigma_a^2 = u_1'u_1 \,/\, [m - \lambda \, tr\,(C_1^{-1})]$$

$$\sigma_e^2 = (y'Sy - y'SZTDu_1 - \lambda u_1'u_1) \,/\, [N - r(X) - m + \lambda\,(tr\, C_1^{-1})] \qquad (1.12)$$

By noting that L = TD and A = LL', where L is a lower triangular matrix, it can be seen that (1.9) can be expressed as (Meyer, 1987),

$$(L'Z'SZL + \lambda I)u_1 = L'Z'Sy \qquad (1.13)$$

Henderson (1976) gave rules for obtaining L = TD recursively and Meyer (1987) suggested forming the terms in (1.13) by calculating each column of L in turn. However the algorithm being described in this note is based on (1.9). The matrix T describes the contribution of ancestors to be genotypes of their parents in a pedigree assuming parents are coded before their progeny. The rules for T are

$T_{ii} = 1,$

$T_{im} = 1/2\ (T_{jm})$, if only one parent of i, namely j is known, i>m,

$T_{im} = 1/2\ (T_{jm} + T_{km})$; j and k, parents of i are known, i>m,

$T_{im} = 0,\ m>i.$

T can be thought of as the product of m matrices as

$$\prod_{i=1}^{m} T_{m+1-i}$$

with T_i having ones on the diagonals and 0.5 in the i,j and i,k elements where j and k are parents of i. The diagonal matrix D can be obtained by rules gives by Quaas (1976) which does not require L to be stored in the memory. Let $Z'SZ = C_{m+1}$. We require $T'C_{m+1}$ T, it is demonstrated below that this can be set up using

$$C_i = T_i' C_{i+1} T_i \quad , \quad i = m \text{ to } 1$$

with m being the number of individuals in the pedigree.

Let us consider as an example the pedigree used by Meyer (1987) where there were three animals whose progeny were measured for some trait.

Animal	300	400	500
Sire	?	222	222
Dam	111	111	300
No of progeny	10	18	12
Progeny Total	800	1000	600

From the above pedigree T and D are:

Identity of animals

$$111 \quad T= \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 1/2 & 0 & 1 & 0 & 0 \\ 1/2 & 1/2 & 0 & 1 & 0 \\ 1/4 & 1/2 & 1/2 & 0 & 1 \end{bmatrix} \quad \text{and } D = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0.866 & 0 & 0 \\ 0 & 0 & 0 & 0.707 & 0 \\ 0 & 0 & 0 & 0 & 0.707 \end{bmatrix}$$

T is the product of T_i, i = m to 1 ;

$$T_1 = T_2 = I$$

$$T_3 = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 1/2 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}, \quad T_4 = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 1/2 & 1/2 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix} \text{ and}$$

$$T_5 = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 1/2 & 1/2 & 0 & 1 \end{bmatrix}$$

To form $T'C_{m+1}$

form $E_{i-1} = T'_{i-1}C_i$ (1.15)

and $C_{i-1} = E_{i-1}\, T_{i-1}$, $i = m + 1$ to 2 (1.16)

Hence the j and k rows of E_{i-1} are the j and k rows plus half the $i-^{th}$ row of C_i.

Illustrating with the example given earlier, the coefficient matrix $Z'SZ$ (C_{m+1}) in the usual model (1.13) on absorbing overall mean as fixed effect, augmented to include ancestors is, C_6:

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 7.5 & -4.5 & -3.0 \\ 0 & 0 & -4.5 & 9.9 & -5.4 \\ 0 & 0 & -3.0 & -5.4 & 8.40 \end{bmatrix}$$

Applying (15) with i = 6 ;

$$E_5 = T_5'C_6 = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -1.5 & -2.7 & 4.2 \\ 0 & 0 & 6.0 & -7.2 & 1.2 \\ 0 & 0 & -4.5 & 9.9 & -5.4 \\ 0 & 0 & -3.0 & -5.4 & 8.4 \end{bmatrix} \qquad (1.17)$$

It can be seen that the 2nd and 3rd rows of E_5 are the 2nd and 3rd rows of C_6 plus half the 5th row of C_6. Similarly, applying (1.16).

$$T_5'C_6T_5 = E_5T_5 = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 2.10 & 0.6 & -2.7 & 4.2 \\ 0 & 0.6 & 6.6 & -7.2 & 1.2 \\ 0 & -2.7 & -7.2 & 9.9 & -5.4 \\ 0 & 4.2 & 1.2 & -5.4 & 8.4 \end{bmatrix} \qquad (1.18)$$

Again the 2nd and 3rd columns of (1.18) are the 2nd and 3rd columns of (1.17) plus half the 5th column of (1.17).

Applying the above principles, given any symmetric matrix C, $T'C_{m+1}T$ can be set up recursively from a list of pedigree and C_{m+1} without forming T or T'T by forming $C_n = T'_n C_{n+1} T_n$ ($n = m, \ldots 1$). As C_i is a symmetric matrix then only the lower triangle needs to be formed. If C is the matrix C_{n+1} then C_n can be formed and again stored in C, by the following rules where j and k are the parents of the n-th individual ($j < k$).

$$C_{ji} = C_{ji} + (1/2)\, C_{ni} \qquad (1 \leqslant i < j)$$

$$C_{jj} = C_{jj} + C_{nj} + (1/4)C_{nn}$$

$$C_{ij} = C_{ij} + (1/2)C_{ni} \qquad (j < i \leqslant m,\ i \neq k)$$

$$C_{ki} = C_{ki} + (1/2)C_{ni} \qquad (1 \leqslant i < k,\ i \neq j)$$

$$C_{kj} = C_{kj} + (1/2)C_{nj} + (1/2)C_{nk} + (1/4)C_{nn}$$

$$C_{kk} = C_{kk} + C_{nk} + (1/4)C_{nn}$$

$$C_{ik} = C_{ik} + (1/2)C_{nk} \qquad (k < i \leqslant m)$$

Concurrently if F = Z'Sy then T'Z'Sy can be found by at the n-th stage forming

$$F_j = F_j + (1/2)\, F_n$$
$$F_k = F_k + (1/2)\, F_n$$

Finally D'T'Z'SZTD of (9) is obtained by pre- and post- multiplying C set up above by D' and D respectively. And the transformation of the right hand side is completely achieved by pre-multiplying F by D'.

An example:

The example of Meyer (1987) stated earlier is used to illustrate the method. For ease of reference the pedigree could be

recoded as

Animal	3	4	5		1	0	0
					2	0	0
Sire	?	2	2	or	3	0	1
Dam	1	1	3		4	2	1
					5	2	3

The coefficient matrix has earlier been given and the corresponding right hand side is

$$\begin{bmatrix} 0 \\ 0 \\ 200 \\ -80 \\ -120 \end{bmatrix}$$

Commencing from the bottom of the pedigree and applying the rules stated above;

$C_{21} = C_{21} + (1/2)\, C_{51} = 0$.

$C_{22} = C_{22} + C_{52} + (1/4)C_{55} = 2.10$

$C_{42} = C_{42} + (1/2)C_{45} = -2.7$

$C_{52} = C_{52} + (1/2)C_{55} = 4.20$

$$C_{31} = C_{31} + (1/2)C_{51} = 0$$

$$C_{32} = C_{32} + (1/2)C_{52} + (1/2)C_{53} + (1/4)C_{55} = 0.60$$

$$C_{33} = C_{33} + C_{53} + (1/4)C_{55} = 6.60$$

$$C_{34} = C_{34} + (1/2)\, C_{45} = -7.20$$

$$C_{35} = C_{35} + (1/2)\, C_{55} = 1.2$$

The right hand side is correspondingly transformed as

$$F_2 = F_2 + 1/2\ (F_5) = -60.0$$
$$F_3 = F_3 + 1/2\ (F_5) = 140$$

The coefficient matrix and the right hand sides respectively are now

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ & 2.10 & 0.60 & -2.7 & 4.20 \\ & & 6.60 & -7.2 & 1.2 \\ & & & 9.90 & -5.4 \\ & & & & 8.4 \end{bmatrix} \quad \text{and} \quad \begin{bmatrix} 0 \\ -60 \\ 140 \\ -80 \\ -120 \end{bmatrix}$$

Note that the coefficient matrix above is exactly what was obtained in (1.8).

Similar steps are employed for progeny 3 and 4 and the base animals are not considered since their dams and sires are not known. After processing progeny 3 and 4, T'Z'SZT and TZ'SY becomes:

$$\begin{bmatrix} 0.525 & -0.375 & -0.30 & 1.35 & -2.10 \\ & 1.875 & -3.00 & 2.25 & 1.50 \\ & & 6.60 & -7.20 & 1.20 \\ & & & 9.90 & -5.40 \\ & & & & 8.40 \end{bmatrix} \quad \text{and} \quad \begin{bmatrix} 30 \\ -100 \\ 140 \\ -80 \\ -120 \end{bmatrix}$$

The diagonal matrix D for the pedigree has been given earlier. Pre multiplication of T'ZSZT and T'Z'SY with D' and post multiplication of the former with D yields D'T'Z'SZTD and D'T'Z'SY of (1.9) as

$$\begin{bmatrix} 0.525 & 0.375 & -0.260 & 0.955 & -1.485 \\ & 1.875 & -2.598 & 1.591 & 1.061 \\ & & 4.950 & -4.409 & 0.735 \\ & & & 4.950 & -2.70 \\ & & & & 4.20 \end{bmatrix} \quad \text{and} \quad \begin{bmatrix} 30.00 \\ -100.00 \\ 121.24 \\ -56.57 \\ -84.85 \end{bmatrix}$$

9.4 Comments

The algorithm is computationally easy and does not require T or T'T to be formed, thus an additional storage facility is not required. The algorithm is substantially faster than that described by MEYER (1987) as it depends on the number of parent offspring relationships. For example, in the analyses of the LGR line plus the control, the CPU time required to incorporate A consisting of 509

progeny and 126 base animals was about 8 minutes using the algorithm of Meyer (1987). Incorporating A by the algorthm described above needed only about 2 minutes.

CHAPTER 10

GENERAL DISCUSSSION AND CONCLUSIONS

The national average increase in carcass lean of beef cattle reported by Kempster and Solly (1988) was 0.4 percent from 1975 to 1986 in Britain. A corresponding estimate for pigs was 8 percent. Much of the improvement in carcass composition of pigs has been due to selection for reduced backfat thickness or increased lean growth rate and/or lean tissue conversion efficiency.

An apparent question is whether the rapid rate of genetic improvement in carcass lean in pigs is possible in beef cattle? Hitherto, there has not been experimental evidence to provide an adequate answer to the above question. Firstly, there has been the problem of assessing carcass traits in live animals in beef cattle and secondly, estimates of genetic parameters to base such improvement programme on carcass lean, and to determine its effects on other traits of economic importance have been lacking. This experiment is therefore unique in providing answers to some of the problems confronting improvement of the efficiency of lean meat production in beef cattle. The estimates of genetic parameters for LGR and LFCR indicate that these traits are associated with a high to moderate degree of additive genetic variation and selection for both traits should be effective. This has been confirmed by the positive rates of response observed for both traits.

Moreover this experiment has provided estimates of genetic parameters between LGR, LFCR and other economic traits in beef cattle. It has also been demonstrated that selection for LGR and LFCR has not be accompanied by undesirable correlated responses in reproductive traits. The estimates of genetic parameters would be useful in designing improvement programmes for beef cattle.

Smith (1984) reported rates of annual genetic change

theoretically possible in beef cattle by selection. For growth traits he reported a value of 1.4 percent. One of the usefulness of selection experiments is that they provide a check on the predicted theoretical rates of response. The annual rate of genetic of 1.5 percent achieved in this experiment for LGR shows that the possible rate of genetic change indicated for growth traits is attainable with proper design (an issue discussed below) and primary attention focussed on the trait of interest (97 percent of the maximum possible selection differential was achieved).

Compared with other experiments in beef cattle, the annual rate of genetic change for LGR is higher than reported for most selection experiments on body weight at weaning or yearling age, higher than the estimate for postweaning gain reported by Irgang et al. (1986b) in which only males were also selected, but lower than estimates of Bailey et al. (1971) and Chevraux and Bailey (1977) for postweaning gain. The percentage of the maximum possible selection differential achieved for LGR was slightly higher than estimates for most of the selection experiments on body weight. In addition, the low generation interval in this experiment (see Baker et al., 1980) and the slightly higher heritability estimate for LGR compared with that for weaning and yearling weight may be contributory factors to the high rate of annual change observed for LGR. It seems therefore that efficiency of selection in beef cattle for growth traits in terms of annual rate of change is influenced by the effectiveness of selection pressure applied, rate of generation turnover and the heritability of the trait on which selection is based.

Early selection experiments in beef cattle suffered from inadequate design and it was not possible to obtain precise estimates

of genetic change. The first experiment to feature a control line (Newman et al., (1973) demonstrated the usefulness of control populations. The variance of response using a control line is the sum of the variance of the means of both selected and control lines. Thus there is obvious advantages in designing both the control and selected lines as to minimise their variances, especially the drift variance. Smith (1977) ranked the use of control lines consisting of frozen semen as the most efficient in estimating genetic change compared with maintaining a natural mating control population or using a repeat mating, since there is no accumulation of drift variance over time. Also the effects of relaxed selection which may occur in natural mating controls through selection are avoided. Thus the establishment of a control line consisting of frozen semen in this experiment has been valuable in terms of obtaining precise estimates of genetic change. This is quite important as Smith (1988) mentioned poor methods of evaluation as one of the reasons why the predicted theoretical rates of genetic change are not realised in practice.

Secondly, the selected and control line were derived from the same base population. This implies that (1) it was not necessary to estimate the initial differences between the selected lines and the control and (2) the possible magnitude of genotype by environment interaction is reduced and hence the magnitude of the variance arising from such interaction. In general, when the selected and control lines are derived from the same base population, the regression of response on time can be forced through the origin, hence comparison between the selected line and the control may not be necessary in early generations, saving on test facilities and the

number of animals in the control line can be kept as low, with a saving on breeding facilities until required for the final evaluations (Smith, 1988).

The within sire family selection practised in the selection lines and the use of bulls for only one year in most cases may have helped in reducing the variance of family size and therefore the drift variance and the variance of response.

Replication is of obvious advantage in selection experiments in providing a direct measure of the variance structure of observed responses. However the low degree of replication in this experiment did not make it possible to obtain reliable estimates of the variance of response from the variance among the replicate lines (see Hill, 1980). Moreover the small size of the replicate lines resulted in slightly higher levels of inbreeding compared with estimates from recent beef selection experiments. In addition, the observed responses might have been influenced by the small size of the replicates. Nicholas (1981) showed that the expected response across a replicates is reduced from that expected in the total population as a single line because of the reduction in effective population size. Also in such small sized replicates, genetic drift could be of importance source of variation among the replicate lines, producing not only variation in mean response (Hill, 1971) and also variation in within-line additive genetic variance (Avery and Hill, 1977). In the LGR line the rate of annual genetic change in replicates 2 and 3 were 80 and 41 percent lower than in replicate 1. In the LFCR line, rate of annual response in replicates 1 and 3 were 60 and 50% lower than in replicate 2. Irgang et al. (1986b) have similarly reported different rates of response among replicate lines

selected for weaning weight and postweaning gain. It was attributed to the random influence of genetic drift on gene frequencies within the replicates.

Thus the replicates have been of little or no value in this study. Usually with limited facilities in beef cattle, the high degree of replication required to obtain reliable estimates of the variance of response from the variance among replicate lines might be difficult. When facilities are clearly inadequate it might be advisable to leave out replication to avoid the risk of inbreeding. Statistical methods such as REML might be used to estimate the variance of direct and correlated responses.

Biological indices such as LGR and LFCR do not involve economic calculations and are supposed to overcome some of the criticisms of economic indices (see Fowler et al., 1976). However they are still weighted according to the heritability, coefficient of variation (CV) of the component traits and the correlation between them (Smith, 1967). If there is a large imbalance in CV of component traits, the most variable trait will tend to dominate the biological index. From the estimates of cumulative selection differentials, direct and correlated responses and their pattern of accumulation for LGR, LFCR and their component traits, it seems much of the selection pressure and response accumulated through GRT and FCR respectively for LGR and LFCR, and little through LEAN. This indicates that more weight was given to GRT in LGR and FCR in LFCR compared with LEAN. Generally, GRT and FCR were more variable and higher in heritability than LEAN. The genetic correlation between GRT and LGR was 0.958 ± 0.03 and between LEAN and LGR was 0.369 ± 0.22. Corresponding estimates for FCR, LEAN and LFCR were 0.873 ± 0.07 and

-0.323±0.24 respectively.

Based on such similar estimates of phenotypic correlations from an analysis of data from initial stages of the experiment, Simm (1983) questioned the value of estimating carcass composition. He argued that there is little loss in expected response in LGR or LFCR from indirect selection on their most variable components, GRT and FCR. Under such situations, in vivo estimation of carcass composition may not be cost-effective. He concluded that selection for LGR and LFCR may lead to genetic increases in birth weight and mature size and proposed the use of economic indices as a better alternative means of improving efficiency of lean meat production.

Firstly, the observed correlated changes in birth weight (BW) were not as predicted by Simm (1983). In terms of standard deviation units, the secondary cumulative selection differentials for BW were about 80 and 35% lower in the LGR and LFCR lines respectively than estimates reported in most selection experiments in beef cattle on growth rate through sire selection. Correlated responses for BW in both lines were insignificant and generally lower compared with estimates reported from direct selection on growth rate. Although the correlated response in growth rate in the LGR line was similar to that of Aaron *et al*. (1986b) and even higher than that of Frahm *et al*. (1985b), these workers reported significant correlated responses for BW from selection on weaning and yearling weight. As mentioned in chapter six, it seems that the inclusion of LEAN as a component trait in LGR acted as a check to increased responses in BW. The genetic correlation between LEAN and BW is negative (-0.54±0.48) and the genetic correlation between LGR and BW (0.55±0.46) was lower between GRT and BW (0.78±0.34).

Secondly, with respect to mature size, not much data is yet available for females in the project. However the correlated responses in body weight for females at 3 and 4 years of age in both selected lines were insignificant. The number of records used were, however, somewhat limited and these were progeny of bulls born 1983 and have only about two cycles of selection behind them.

Thirdly, although Simm (1983) indicated that there is little loss in expected response in LGR or LFCR from indirect selection on GRT or FCR, much experimental evidence (see chapter two, section 2.3.1) seems to indicate little or no correlated responses in carcass traits due to direct selection for GRT. Although carcass evaluation for the purbred is not available, preliminary analysis of the carcass traits in progeny sired by 1983 bulls by Fisher and Bayntun (1987) showed the amount of carcass lean tissue to be significantly higher in both selected lines relative to the control. However the difference between the control and the open line was not significant. Moreover, it is worthwhile to note that the sires of these progeny had only two cycles of selection behind them. The on-going second phase of the crossbred trial involving progeny from sires with more selection pressure behind them might help in throwing more light on the effectiveness of selection for LGR and LFCR in changing carcass lean or composition. Although no cost-benefit analysis has been undertaken to determine if in vivo estimation of carcass lean is cost-effective, the above result is indicative that selection for LGR or LFCR is accompanied by some improvement in carcass lean.

Similar to the suggestion of Simm (1983), the Meat and Livestock Commission (MLC) (Allen and Steane, 1985) has recently proposed the introduction of a beef selection index into its breeding

services as a more efficient means of selecting for an overall breeding objective. The Commission identified the general objective of beef production in Britain as the ability of each cow to produce a calf each year, calved easily and which gives the highest possible yield of saleable meat at the lowest feed cost. On the basis of the above general objective, an index was constructed with a specific objective to "maximise the financial margin between the value of saleable meat and the cost of feed, taking into account the cost of difficult calvings". The traits included in the index were weights at birth, 200 and 400 days, calving difficulty and muscling scores, feed intake and fat thickness (estimated by scanogram). The index was constructed using genetic parameter estimates for the above traits summarised from the literature and estimated economic weights for feed intake, saleable meat and calving difficulty. Predicted genetic response to the index using data on British breeds such as the Angus and Hereford indicated that animals would produce a greater value of saleable meat at the expense of some increase in total feed intake, but with a marginal decrease in calving difficulty. The predicted responses in the composite traits in the index showed that the change was mainly due to increases in 200 and 400 days weight, decreased fatness with increased birth weight and daily feed intake as second order effects.

Notably, these responses are essentially the same as have been observed in the LGR line. There were significant positive correlated responses in growth rate up to 400 days and lean percent, positive correlated but insignificant response in feed intake and birth weight and a negative genetic trend in calving difficulty. Simm (1983) also constructed two economic selection indexes to

improve efficiency of lean meat production, with restriction placed on birth weight in one of the indices. The traits included in estimating the aggregate breeding value were birth weight, growth rate, feed conversion efficiency, killing out percent and carcass lean. The traits used in constructing indices were growth rate, feed conversion efficiency, ultrasonic fat and birth weight for the index in which it was restricted. The coefficients of the index indicated that much of the emphasis was on growth rate and feed conversion efficiency; removal of ultrasonic fats did not drastically affect the accuracy of the index. The correlations between the selection indices and the individual traits in the aggregate breeding value indicated that selection on these indices would actually lead to a little reduction in carcass lean but he argued that it would however increase the efficiency with which lean is deposited. The phenotypic correlations between LGR, LFCR and two of the indices were about 0.80. The observed direct and correlated responses in the LGR line were equally similar to the expected responses from the indices of Simm (1983).

The predicted responses from the indices constructed by Simm (1983) and Allen and Steane (1985) did not demonstrate any clear advantage of such indices over selecting for LGR. They were only superior in growth rate over the LFCR line. However, the negative genetic trends in growth rate and feed consumption in the LFCR line coupled with increased lean feed conversion ratio might be very useful under situations were feed availability constitutes a constraint such as in tropical conditions. Considering the problems of obtaining reliable genetic parameters and economic weights, selection for LGR seems adequate in improving efficiency of lean meat

production under conditions where feed availability is not a limiting factor. However, when feed availability is a constraint, LFCR seems an alternative selection criterion for improving efficiency of lean meat production. Slightly more weight can be applied on LEAN in LGR and LFCR by standardising the component traits.

In a review of correlated responses to direct selection for body weight in beef cattle, Baker and Morris (1984) identified the problem of genotype by environment interaction (gxe) as one of the areas to be emphasised in designing breeding programmes. The positive correlated responses for body weight in female calves on rouphage diet in the LFCR line, the similarity in correlated responses for growth rate in the crossbreds of the LGR and LFCR lines on a diet consisting mainly of silage in contrast to the purebred males on a diet high in concentrate, do highlight the possible influence of the type of diet on the pattern of response. This area needs further investigation to ascertain whether selection of stocks for improved growth rate should be carried out strictly under the same nutritional conditions in which they will be reared on commercial basis. This is quite important as contrasting results have been obtained for responses in birth weight as a result of selection for growth under temperate and tropical conditions (Baker and Morris, 1984).

Annual correlated responses in body weight in female calves declined significantly during reproduction. This suggests that the extent to which body weight during reproduction and non-reproductive periods are influenced by the same genes may not be very high. The ratio of birth weight to cow weight may be an important factor affecting calf mortality in 2-year old heifers (Morris et al., 1986).

Further studies are needed in this area to determine whether direct selection will be necessary if the intention is to improve body weight during reproduction and what is likely to be the consequence of such selection on calving performance and overall cow size.

Most of the correlated responses for the various body measurements were insignificant except for wither height and body length at some ages. The annual rates of genetic change for wither height and body length were much lower than observed for body weight (chapter seven). Considering all the various body measurements analysed and the low rates of annual genetic change for wither height and body length, the genetic correlations between LGR and the various body measurements are not likely to be very high. Selection experiments for LGR or growth rate (considering the high genetic correlation of 0.96 between the traits) with attention paid to physical appearances might result in not achieving the predicted theoretical rates of change for growth traits.

Finding a suitable predictor of subsequent calf performance in early life would be of primary importance in beef cattle especially in carcass traits. The results from the crossbred analysis indicate a negative genetic relationship between urea and lean growth and seem to implicate urea as a likely suitable physiological predictor of lean growth. Certainly further studies are required in this area. The second phase of the crossbred trait with progeny from bulls born 1985 and therefore much selection pressure behind them would throw more light on the suitability of urea as a predictor of lean deposition. It may also be necessary to analyse blood samples from the purebred bulls in the different lines early in life to determine any line differences and how these relate

to the lean growth rate estimated at this time and later in life at 400 days of age.

The small number of animals in the open line makes it difficult to draw conclusions about the rate of genetic change available to breeders who rely on the use of superior progeny tested Hereford bulls. However, these results indicate that much of the change is in growth rate and feed efficiency with little in carcass lean. This underscores the need to include carcass leanness in national improvement programmes of the Hereford cattle.

The results from this experiment indicate that although direct selection improved both LGR and LFCR, selection for LGR was more effective in increasing both traits. The design of the experiment was effective in providing precise estimates of realised genetic parameters.

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Vol. 56 February, 1988 No. 2

Animal Breeding Abstracts

Selection Experiments in Beef Cattle. Part 1. A Review of Design and Analysis

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Abstract

The design and analysis of selection experiments in beef cattle are reviewed in the light of current principles on the design of breeding programmes. It was shown that most early selection work in beef cattle suffered from several limitations arising from the small size of the selection herds and high levels of inbreeding. Most experiments had no effective means of measuring genetic response, and the drift variance was not accounted for in the estimation of the variance of response. These results were therefore biased in one respect or the other, and may not be very reliable. Recent selection work has shown much improvement in design in terms of increased population size, low levels of inbreeding by planned mating schemes, and the maintenance of control populations or divergent lines for the separation of genetic trends. However, the majority of current experiments are still deficient in replication, and most estimates of residual variance neglect the drift variance. While it may be difficult in beef cattle with limited facilities to achieve the degree of replication required to obtain reliable estimates of the variance of response, the need for replication is emphasised, since methods for estimating the drift variance in populations with overlapping generations have not been properly developed.

I. Introduction

Compared with laboratory species, relatively few cattle selection experiments have been undertaken, due to the high costs and the long generation interval. Most early studies were prompted by the effectiveness of selection experiments in laboratory animals and larger species, such as the pig, which checked the theoretical predictions of artificial selection. Many cattle experiments were limited to measuring phenotypic time trends, which could not be partitioned into the respective genetic and environmental components owing to lack of controls or proper design, and so had limitations. This is why Barlow (1978) observed that "the omission of control populations from most of the available experiments and the tendency towards multi-trait selection has resulted in genetic trends and realised parameters having to be recovered from the data, using varying techniques to measure environmental trends".

Most reviews on selection experiments in beef cattle were concerned mainly with growth rate of weight for age (Barlow, 1978; Koch, Gregory and Cundiff, 1982; Baker and Morris, 1984), and were therefore limited in scope. The review of Barlow (1978) was restricted to preweaning growth rate, while Koch *et al.* (1982) mainly summarised the results of North American selection experiments on growth rate.

In this review, selection experiments in beef cattle are examined in the light of current principles of design with a view to assessing their value, and to highlight the development trend in beef selection experiments. The results of selection experiments on growth rate and other traits are summarised in Part II of this paper.

II. Population Size

In a review of selection experiments in beef cattle, Dalton and Baker (1979) concluded that one of the major limitations associated with all work on cattle prior to 1970 was small population size. For example, Hoornbeck and Bogart (1966) selected in an Aberdeen-Angus line consisting of about 2

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sires and 20 females and 3 Hereford lines each consisting of 1 sire and 15 females on the basis of an index for preweaning gain, feed test gain, feed per unit of gain and conformation scores. Although selection differentials were positive, phenotypic trends were negative for all traits except score in the Hereford lines, but positive for all traits in the Angus line. The genetic trends were not estimated. In another case, Nelms and Stratton (1967) carried out selection for unadjusted weight at the end of a 268-day feed test in a line of about 30 Hereford cows, with response evaluated on 302 calves born during the selection period of 12 years. The design of the experiment did not permit the estimation of genetic trend. Similarly, Chevraux and Bailey (1977) carried out selection, in a line of Hereford cattle consisting of one or two sires and about 25-30 cows, for postweaning growth rate from 1956 to 1977, and phenotypic response was evaluated on 390 calves born during the selection period of 19 years.

Population size is important in artificial selection in two respects. First, from the work of Robertson (1960), selection in small populations increases the chance of loss of desirable alleles, and hence leads to a lower limit to selection. Second, in small populations, genetic drift is a important source of variation among selected lines, producing not only variation in mean responses (Hill, 1971) but also variation in within-line additive genetic variance (Bulmer, 1976; Avery and Hill, 1977). Thus, estimates of parameters from these early experiments with small size are likely to have large standard errors. However, most of the reports did not give any standard errors for the parameter estimates.

Hill(1980) showed how the variance of response can be reduced by increasing the total size of the selection experiment. Recent selection experiments in beef cattle have had larger population sizes. For instance, Koch, Gregory and Cundiff (1974) selected for weaning weight, yearling weight, and an index consisting of yearling weight and weaning weight in 3 lines, each consisting of 150 cows and 6 sires. Similarly, Pacer *el al.* (1986) reported response for yearling weight in 2 lines of Nelore and Guzerat cattle, each consisting of 120 cows and 6 sires.

III. Inbreeding

Closely associated with the problem of small population size in early experiments was that of high levels of inbreeding. Many of these trials were concerned with the effectiveness of selection in lines which were already inbred (Armstrong *et al.*, 1965; Hoornbeck and Bogart, 1966; Nwakalor, Brinks and Richardson, 1976), but in some cases, selection and inbreeding occurred concurrently (Brinks, Clark and Kieffer, 1965; Nelms and Stratton, 1967). In the inbred lines, the average inbreeding coefficient ranged from 19% (Hoornbeck and Bogart, 1966) to 33% (Armstrong *et al.*, 1965; Nwakalor *et al.*, 1976). Working with populations which were not initially inbred, Brinks *et al.* (1965) and Nelms and Stratton (1967) reported average inbreeding coefficients of 12 and 5% respectively for dams, and 16 and 11% respectively for calves.

The expected response from selection is likely to be reduced by inbreeding as a result of a proportionate decline in the additive genetic variance of the traits. In addition, traits associated with fitness may be directly depressed by moderate levels of inbreeding.

In recent selection experiments in beef cattle, the level of inbreeding has been effectively lowered by better design and increased population size. For example, the average inbreeding coefficients reported by Buchanan *et al.* (1982) and Irgang, *et al.* (1985*a*) were 0.03 and 2.0% respectively for dams, and 0.05 and 5.8% for calves.

IV. Genetic Change and Realised Heritabilities

Generally, selection experiments are concerned with the estimation of selection response (genetic change), realised heritability and their precision. The estimates of response should be unbiased by environmental fluctuations. Techniques used for evaluating genetic trends in beef cattle include maintaining a randombred control population, repeat mating schemes, intra-year comparison of sire or dam birth year progeny groups (that differ respectively in generations of selection or in birth year)l, and semen storage with subsequent evaluation on a common tested herd (Smith, 1962; Dickerson, 1969; Hill, 1972*a,b*, 1978; Koch *et al.*, 1982). Few divergent (high and low) selection experiments have been carried out (Seifert, 1975*a,b*; Barlow, 1980). Estimates of genetic change can be achieved by contemporary comparison of such two divergent selection lines.

Most early beef selection experiments relied on repeat matings for the estimation of genetic change (Hoornbeck and Bogart, 1966; Armstrong *et al.*, 1965; Benson *et al.*, 1972; Nwakalor *et al.*, 1976). In some cases, these repeat matings were not planned, but were found and used in an attempt to separate the genetic and environment changes (Flower *et al.*, 1964; Brinks *et al.*, 1965). Consequently, the number of repeat matings was small, and it was not possible to estimate genetic change for some years or traits due to inadequate number of repeat matings. Response was taken as zero in those years with no repeat matings; it is therefore likely that these estimates of genetic change were biased. Also, the sampling errors from the small number of repeat matings were large. Hill (1972*a*)

discussed the use of repeat matings in the estimation of genetic change. The possible sources of sampling error are drift variance, error of measurement, and genotype by environment interaction. If a repeat mating design is established in the population, the drift variance can be eliminated and the interaction variance is minimised, but there is a substantial contribution of the measurement error variance to the sampling error. The method has the particular advantage that few or no facilities are devoted to estimating the change. However, to some extent, some loss of genetic response will be associated with structuring the herd to permit repeat mating comparisons.

Bailey *et al.* (1971) and Chevraux and Bailey (1977) evaluated performance of progeny from different dam birth-year groups in estimating genetic change. Koch *et al.* (1982) found that estimates of genetic change from intra-year comparison of sire or dam birth year progeny groups are subject to large random errors because the number per group and the span of generations or birth years are usually small. Also, where comparison involves dams differing in age, genetic change is confounded with age-of-dam effects, and the validity of the differences is highly dependent on accurate estimates of age-of-dam correction factors. The data of Chevraux and Bailey (1977) were associated with a limited number of records in the younger dam-age subclass, and small variation in generation coefficients within years.

The difficulties involved in accurately estimating genetic change in experiments with no control populations were clearly demonstrated by Koch, *et al.* (1974*b*). They estimated response to selection for weaning weight, yearling weight, or an index of yearling weight and muscle score in Hereford cattle by the following 5 methods.

(1) From the selection differential of sire and dam indices, the genetic correlation between traits and their heritabilities, using the formula of Harvey and Bearden (1962). This was essentially evaluating the expected genetic change.

(2) Intra-year regression of offspring on generation coefficient, where generation coefficient refers to the average number of generations or segregations in the pedigree back to the foundation parents.

(3) Intra-year regression of offspring on midparent cumulative selection differential.

(4) Partial regression of offspring deviations on midparent cumulative selection differentials.

(5) Regression of offspring on midparent in an unselected population.

They indicated that none of the methods of estimation yielded a satisfactory result. Methods 1 and 2 did not include maternal effects, which, to the extent they are genetically determined, form a valid part of estimated response, and they were also subject to large sampling errors. The other methods did not actually give estimates of overall response; method 3 utilises information on only one of the observed selection differentials in estimating response, while methods 4 and 5 were restricted to an evaluation of offspring response in each line.

Stanforth and Frahm (1975) used semen from foundation and advanced generation sires on a common tester to estimate genetic trend. The use of semen storage for the estimation of response could be very efficient, since there is no accumulation of drift variance in the control. However, only the additive componment of change is estimated without bias (Hill, 1972*a*).

The first beef selection experiment to feature a control line was that of Newman, Rahnefeld and Fredeen (1973) in Canada on Shorthorn cattle. Their data demonstrated the usefulness of controls or other comparable methods of correcting for environment changes. Without the control, the effectiveness of selection would have been overestimated, since more than half of the increase obtained in yearling weight (about 60%) resulted from environmental changes. More recently, Barlow (1979), Frahm, Nichols and Buchanan (1985*a*) and Irgang *et al.* (1985*a*) also used control populations in their experiments. In the case of Frahm *et al.*, (1985), the original design did not include an unselected control line. An Angus line which had previously undergone one generation of selection for yearling weight was used to start the control line. The adequacy of this Angus population as a control line for the selected Hereford lines rested on the absence of breed by environment interactions. They indicated that analysis of data from early years of the study before selection showed that breed by year interactions were generally non-significant for the traits measured.

In experiments with control populations, response is measured as a deviation of the selected line from the control. The variance of response is the sum of the variances of the means of both selected and control lines, and the control might be set up to minimise its variance. This variance involves both variation of the selection differential and the drift variance. By ensuring a selection differential of zero or nearly zero, the drift variance can be reduced. Hill (1972*a*) showed how to construct a control such that the selection differentials are zero, and the drift variance reduced. It essentially involves choosing breeding individuals such that their mean performance for some particular trait is close to the mean performance of all recorded individuals in that generation. In some of the selection experiments, some unintentional selection was reported in the control lines (Newman *et al.*, 1973; Irgang *et al.*, 1985*a*). Frahm *et al.*, (1985*a*) observed slight increases in their control line, which were attributed to a small amount of selection that occurred during the early years in the population before conversion to a control line. Such directional change through natural or unintentional selection in the control would increase the variance of response (Hill, 1972*a*).

A well designed control population in beef cattle selection is that used by Irgang *et al.* (1985*a*). Attempts were made to minimise genetic change from selection and genetic drift by random

selection of replacement bulls within sire families and maintenance of low inbreeding levels by mating least-related individuals (see Hill, 1980).

If several selection lines and a control have been maintained contemporaneously, these animals could be used in the analysis of any trait, explaining the response or correlated response, in terms of cumulative selection differentials, genetic regressions and environmental effects. This could lead to more precise environmental estimates and hence more precise estimates of response than a comparison of each selected line with the control. This essentially is the multiple regression procedure (Richardson, Kojima and Lucas, 1968) which has been used in evaluating selection experiments in species with discrete generations (Leymaster, Swiger and Harvey, 1979; Quijandra, Zaldivar and Robinson, 1983). Recently, this technique has been used in estimating response in beef cattle by Frahm *et al.* (1985*b*) and Irgang *et al.* (1985*b*), and they indicated that it resulted in a more precise estimate of response compared with estimates from deviation of selected lines from the control. This was attributed to the fact that the method uses all available information to estimate simultaneously environmental effects and selection responses. In addition, correlations between genetic responses in selected lines due to use of a common control are avoided.

The procedure, however, assumes that the error variance structure in each generation is independent, but this is not so. Selection experiments are stochastic processes, and performance in a given generation is dependent on the genetic samples retained in previous generations (see Hill, 1972*b*).

More recently, the use of mixed model methodology (Henderson, 1973) for the separation of genetic and environmental trends has been used in the analysis of selection experiments. Sharma *et al.* (1985) estimated genetic trends in a beef synthetic and a Hereford control line using the mixed model method. The method yielded estimates of sampling variances which were smaller than those from repeat matings or control population analysis.

The use of mixed model analysis as a means of separating genetic trends from environmental trends was first suggested by Henderson *et al* (1959) in dairy cattle subject to culling. Blair and Pollack (1984) used this technique to evaluate response using an assumed estimate of heritability to predict genetic worth. The estimate of realised heritability was obtained by the regression of predicted yearly genetic means on cumulative selection differential. However Thompson (1986) has shown that the predicted yearly genetic means depends on the assumed value of heritability and not on the value of heritability in the population; in one example, the estimated heritability was approximately three-quarters of the assumed value. Hence the regression estimate is not an unbiased estimate of the population heritability. Utilising a different approach, Sorensen and Kennedy (1984) have shown that mixed model analysis could be used to estimate genetic trends even after several cycles of selection if certain conditions are met:

(1) the genetic and non-genetic variances, or their ratios, of the trait before selection are known;
(2) selection is a linear function of the records;
(3) the relationship matrix (A), is complete, that is, all animals involved in the selection decision, regardless of whether they contribute offspring, are used to derive A.

The use of A allows relationships between individuals to be used, and increases the accuracy of predictions of breeding values. The relationship matrix also circumvents the possible problems resulting from the reduction of genetic variance generated by gametic disequilibrium that builds up as a consequence of selection (Sorensen and Kennedy, 1984).

V. Precision of Estimates of Response

The precision of estimated response to selection is a function of the design of the selection experiment. Hill (1980) has reviewed the appropriate features for the design of selection experiments.

In most published early experiments in beef cattle, estimates of genetic changes and realised heritabilities were given without estimates of the variance of response (Flower *et al.*, 1954; Brinks *et al.*, 1965; Koch *et al.* 1974*b*). So the reliability of their estimates of response and the value of such experiments are greatly reduced. However, Newman *et al.* (1973) estimated variance of genetic response from the variance of the weighted regression of cumulative response on cumulative selected differential. Chevraux and Bailey (1977) estimated response by linear regression of trait on dam birth-year group, and the variance of the regression coefficient (also variance of response) was estimated by maximum likelihood. Frahm *et al.* (1985*b*) estimated variance of response from the variance of the regression of cumulated response on cumulative selection differential. Hill (1972*b*) has shown that the variance of the simple regression of cumulative response on cumulative selection differential is biased downwards because observations are assumed to have equal variance and to be uncorrelated, when in reality the variance of the population mean increases due to genetic drift as selection effects accumulate. Recently, Atkins (1985) confirmed these observations from the analysis of a selection experiment. Most analysis of selection experiments have neglected this component of the sampling variance. Irgang *et al.* (1985*b*), however, reported standard errors of realised heritabilities for weaning weight and postweaning gain which included the drift variance. Hill (1972*b*) and Sorensen and Kennedy (1983) have given formulae for estimating the drift variance.

However, Johnson (1977) has indicated that the usual expression for drift variance for overlapping generations is only asymptotically true. He has developed a more exact formula for this drift variance, and showed the true drift in the early years of an experiment to be much larger than the apparent drift from the approximate formula. Using the approach of Johnson (1977) and Hill (1972*b*) to estimate drift variance, Atkins (1985) found that the inclusion of the more appropriate formula of Johnson (1977) for overlapping generations had only a small influence on the variance of the regression in his 5-generation selection experiment.

VI. Replication

Only a few beef cattle selection experiments have included replication in their design (Newman *et al.*, 1973; Irgang *et al.*, 1985*b*). Actually, the latter workers did not include replication in their initial plan, but because selection was practised only in bulls, and sire families were confounded with years and repeated every third year, the data were grouped into three replicates within each line to evaluate empirical variation in selection response. The variance among replicates represents the sum of genetic drift and random error. Except in the case of weaning weight for bull calves, the variance of response from variance among replicates tended to be smaller than the variance from estimates of genetic drift and random error measurement.

The theoretical variance of response to selection represents variance between conceptual replicated lines. Thus, the obvious advantage of replication is that variance among lines can be estimated directly and independently of parameter estimates from the experiment (Hill, 1980). Unreplicated selection experiments do not provide an estimate of the true variance of response. Although it is possible to estimate the variance of response using formulae of Hill (1980) and Sorensen and Kennedy (1983), these are only approximate, and apply to populations with discrete generations. Moreover, while an estimate of drift variance can be made for directly selected traits, the drift variance of correlated traits cannot be estimated in this way (Hill, 1980). Thus, the need for adequate replication is emphasised in selection with overlapping generations.

However, the problem with the variance from replication is that it requires a high degree of replication before it can be reliable. For instance, with r replicates, this variance will be estimated with r-1 degrees of freedom. Such an estimate of between-line variance, while unbiased, is not reliable. With limited facilities in cattle, a very high degree of replication may not be possible, for the individual lines rapidly become inbred. The best compromise, as Hill (1980) suggested, may be to compute the total size of the experiment on the basis of the ratio of the coefficient of variation of response of the mean of the replicates, and then divide these facilities into as many replicates as inbreeding and practical consideration allow. Moreover, Muir (1986) has shown a precise method for estimating the variance about response, even with limited replication. The method is based on a Satterwaite approximation, which combines variance components estimated more precisely by other sources of variation in the analysis of variance. Using variance components estimated by this procedure, Muir (1986) markedly improved the precision of the estimates of realised heritability.

VII. Conclusions

Most early selection experiments suffered from inadequate designs in terms of small population size, high levels of inbreeding, and inadequate means of measuring genetic trend. Many reports were without estimates of error variance, and in the others the drift variance was not included. More recent experiments have shown improvements in design, with larger population sizes and lower inbreeding rates. In addition, control populations or divergent lines have been maintained to measure the genetic trends. However, there is still the need for replication, especially since methods for estimating the variance of correlated response are not yet available in populations with overlapping generations.

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Vol. 56 March, 1988 No. 3

Animal Breeding Abstracts

Selection Experiments in Beef Cattle. Part 2: A Review of Responses and Correlated Responses

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Abstract

The results of selection experiments on growth rate and other traits in beef cattle are reviewed. In experiments directly concerned with improvement of growth, generations of selection and average generation interval averaged 2.9 generations and 4.4 years respectively. About 0.20 standard deviations of selection per year (2% of the mean) had been achieved for single-trait selection on the basis of individual performance, with sire selection accounting for about 70-85% of the total selection pressure. The annual rate of genetic change, expressed as a percentage of the mean performance, averaged 0.63, 0.80 and 2.03 per year respectively for weaning weight, yearling weight and postweaning gain. Estimates of realised heritabilities were generally in agreement with those obtained by paternal half-sub analysis. Correlated responses were, on average, positive for birth weight, preweaning growth rate, milk yield and composition, but in most cases there were none for carcass traits. Little direct response has been achieved for twinning, but significant responses were obtained for tick resistance. There has been a higher response in growth traits in synthetic stocks compared with purebreds, because of their broader genetic base. The possibility of improving rate of genetic progress through multiple ovulation and embryo transfer and indirect selection are discussed.

I. Introduction

The primary aim of the beef industry is the efficient production of meat. This is greatly dependent on traits related to growth. Emphasis on growth has narrowed the experiences of selection in beef cattle compared with other species of farm livestock. Most selection experiments were directly concerned with improvement of growth rate, and share similar features. A review of these experiments is given, and a summary is presented in Table 1.

II. Selection Experiments on Growth Traits

This section examines selection experiments which have been primarily concerned with the improvement of growth traits. In order to have an understanding of what has been achieved, the experiments are discussed in several subsections.

1. Generations of selection and generation interval

The generations of selection are usually determined by the formula of Brinks, Clark and Rice (1961): $GC=(GC_s+GC_d)/2+1$, where GC is the generation coefficient of the calf and $GC(s)$ and GC_d are generation coefficients of the sire and dam respectively. Foundation animals are assigned a GC of zero. The GC of an animal after selection is the average number of Mendelian segregations in its

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pedigree, and measures one more than the number of generations of selection. The number of generations of selection for published beef cattle experiments is given in Table 1. The average over all experiments is 2.89 generations, with a range of 1.8 (Koch *et al.*, 1974*a*; Irgang *et al.*, 1985*a*) to 3.87 (Aaron, Frahm and Buchanan, 1986*a*). The range of generation coefficients among calves is about 1.7 generations (Koch *et al.*, 1974*a*; Chevraux and Bailey, 1977; Frahm *et al.*, 1985*a*). In short-term selection, response should be proportional to the generations of selection, assuming linearity of response.

Generation interval is the average age of the parents at the birth of their selected offspring. The generation intervals in the selection experiments reviewed are shown in Table 1. The overall average was 4.36 years. The average age for sires ranges from 2 years (Baker, Carter and Hunter, 1980) to 4.3 years (Koch *et al.*, 1982), and the average for dams from 4.0 to 6.6 years (Bailey *et al.*, 1971; Baker *et al.*, 1980). Most of these results were from natural-mating herds, and selection was on the basis of individual performance. The generation interval reported by Aaron *et al.* (1986*a*) when selection was based on combined individual and progeny performance in weaning weight was 5.6 years, compared with 4.1 years obtained in a similar line selected for the same trait using individual performance alone.

Koch *et al.* (1982) concluded that reducing average sire age from 3 to 2 years will improve annual selection differentials (accumulated selection differential/years) only marginally because of compensatory loss of selection intensity. However, preliminary results of the experiment of Baker *et al.* (1980) showed that mating of bulls selected on the basis of yearling weight (average age of sire about 2 years) doubled the rate of response compared with a scheme in which bulls are selected on 18-month weight (average age of sire 3 years) with the same selection pressure applied. They did not indicate what proportion of the difference in response could be attributed to reduction of generation interval or to the difference in genetic variance between yearly and 18-month weights. Koch *et al.* (1982) mention that the average age of dams could be significantly reduced by use of multiple ovulation and embryo transfer.

2. Selection differential

Midparent selection differentials, converted to standard deviation units and expressed on a annual basis to allow comparisons of selection intensities for different traits and between experiments, are given in Table 1. In most experiments, about 0.20 of a standard deviation of selection per year has been reported for single-trait selection on the basis of individual performance, which constitutes about 2% of the mean for traits with a coefficient of variation of 10%. Sire selection accounted for about 70-85% of the total selection intensity achieved (Chevraux and Bailey, 1977; Buchanan *et al.*, 1982*a*; Frahm *et al.*, 1985*a*; Aaron *et al.*, 1986*a*).

The comparison of actual and maximum potential selection differential provides an evaluation of the effectiveness of selection that actually occurred relative to the maximum potential, i.e. if the highest ranking individuals were used as replacements. In 23 experiments studied, about 80% of the maximum selection differential for sires and dams was achieved. This was about 90-100% in sires and 50-74% in dams. Inability to achieve the maximum possible selection differentials for performance has been attributed to unsoundness, selection on colour, death before production of any offspring, and failure of heifers to conceive.

Some of the effects of natural selection on artificial selection can be assessed by the ratio of the actual selection differential in parents leaving progeny to that expected from individuals chosen for breeding (Falconer, 1981). Irgang *et al.* (1985*a*), selecting for weaning and postweaning gain, did not observe any effects of natural selection.

Selection for growth at one stage of life, either for a single trait or an index, is usually accompanied by positive secondary selection differentials for growth at other stages of life (Table 2). From the reports of Koch *et al.* (1974*a*), Buchanan *et al.* (1982*a*), Frahm *et al.* (1985*a*) and Aaron *et al.* (1986*a*), the secondary selection differential obtained for weaning weight in lines selected for yearling weight was about 76% of the selection differential obtained by direct selection for weaning weight. On the other hand, the secondary selection differential for yearling weight in lines selected for weaning weight was about 80% of the selection differential for yearling weight from direct selection. These figures could be attributed to the strong genetic correlation between weaning and yearling weights. Frahm *et al.* (1985*b*) reported a realised genetic correlation of 0.69 between weaning and yearling weights. The secondary selection differential obtained by Irgang *et al.* (1985*a*) for weaning weight in the postweaning gain line was only 37% of the selection differential for weaning weight by direct selection. The realised genetic correlation for weaning and post weaning gain was 0.63 ± 0.16. The secondary annual selection differentials for birth weight resulting from selection on either weaning or yearling weights were of about the same magnitude, about 0.10 standard deviation (about 1% of the mean). Selecting on the basis of a yearling index composed of adjusted weaning and yearling weights, cow fertility and maternal weaning weight, Nicoll and Johnson (1986) reported that secondary selection differentials accumulated at the annual rates of 0.17 and 0.25 standard deviation per year for cow fertility and cow maternal weaning weight respectively, which they claim to be probably the first estimates for these 2 traits in beef cattle.

3. Genetic change and realised heritability

A summary of the various techniques used to evaluate genetic trends in beef cattle is given in Part 1 of this review. Data on selection experiments, including estimates of realised heritability (h^2_R), are presented in Table 1.

Koch *et al.* (1982), from a review of selection experiments in beef cattle, concluded that the unweighted averages for h^2_R were in good agreement with heritability (h^2) estimates from paternal half-sibs or offspring-sire regression. The average values of h^2_R they presented, and those from the summary of literature values reported by Woldehawariat *et al.* (1977), were respectively: birth weight 0.46 and 0.45, weaning weight 0.21 and 0.26, postweaning gain 0.36 and 0.34, final weight 0.36 and 0.46, and gain efficiency 0.23 and 0.38. Most subsequent reports in the literature have been in good agreement with these values. Frahm *et al.* (1985*b*) and Aaron *et al.* (1986*b*) obtained pooled h^2_R estimates of 0.24 ± 0.04 and 0.30 ± 0.03 respectively for weaning weight, and 0.14 ± 0.05 and 0.34 ± 0.03 for yearling weight. Irgang *et al.* (1985*b*) found a h^2_R of 0.25 ± 0.11 and 0.18 ± 0.09 for weaning weight and postweaning gain respectively by deviation from a control group. However, they obtained a very low estimate of 0.05 ± 0.05 for weaning weight using multiple regression procedures.

The average rate of genetic change computed from reports in the literature (see Table 1) were 2.65, 1.15 and 2.21 kg per year for yearling weight, weaning weight and postweaning gain respectively. The estimates were obtained from 9, 10 and 3 experiments respectively, where the traits were either selected on their own or in an index. Bailey *et al.* (1971) reported a rate of 0.17 kg per year for efficiency of gain. Following the example of Smith (1984), the annual genetic changes achieved by various workers were expressed as a percentage of the mean performance (Table 1). The average rate of genetic change was 0.63, 0.80 and 2.03% per year for weaning weight, yearling weight and postweaning gain respectively. Smith (1984) has indicated that the possible rate of genetic change in growth rate expressed as a percentage of the mean is 1.4% per year. Thus, the achieved responses are somewhat lower than the possible responses in weaning and yearling weight, but higher for postweaning gain. The rates of genetic change from selection experiments are higher than those that have been realised in the livestock industry (see Smith, 1984).

4. Correlated responses

There is a positive correlation between growth at one stage of life and growth and size at other stages. The estimates of genetic correlation among birth weight (BW), preweaning gain (WG) and postweaning gain (PG) reported by Koch *et al.* (1982) from the literature were: BW with WG, 0.34 to 0.36; BW with PG, 0.34 to 0.51; WG with PG, 0.16 to 0.22. Brinks *et al.* (1965) reported genetic correlations of 0.65, 0.55 and 0.79 between mature weight and weight at birth, weaning and 18 months. Thus, selection for body weight at any age usually results in correlated responses in body weight at all other ages. A summary of correlated responses resulting from selection on growth rate is presented in Table 2, and is discussed below.

(a) Birth weight, calving difficulty and calf mortality

One of the major criticisms of selection for growth rate is the associated problem of increased birth weight, and in some cases an increased incidence of calving problems and calf mortality (Barlow, 1978). It seems, however, that much criticism, especially concerning calving difficulty and calf mortality, has been based on reviews of correlations between growth rate and incidence of dystocia and not on empirical evidence from selection experiments. With the exceptions of Frisch (1981) and Bailey and Lawson (1986), positive correlated responses in birth weight were reported by all workers. The average rates of correlated response in birth weight from single-trait selection experiments for weaning weight and yearling weight were 0.17 and 0.21 respectively (about 0.38 and 0.47% of the mean). Thus, the correlated response in birth weight for yearling weight selection is slightly higher than for weaning weight selection. Buchanan *et al.* (1982*b*) reported genetic correlations of 0.56 and 0.63 between birth weight and weaning and yearling weights respectively.

In a trial to evaluate the effect of selection for growth rate on calving difficulty and calf mortality, Koch *et al.* (1982) found that birth weight, calving difficulty and calf mortality increased significantly in offspring of 2-year old heifers in a line of Herefords selected for growth rate. In older cows, there was little difference in calving difficulty (Baker and Morris, 1984). However, in the divergent lines of Angus cattle selected for growth rate at the Trangie Agricultural Research Station, Australia, there had not been any adverse effects on fertility or any calving problems in either heifers or cows in spite of the 20% difference in growth rate between the high and low lines (Baker and Morris, 1984). The high line was just as fertile as the control line, and had fewer heifer calving problems than the controls. The ratio of birth weight to pelvic area was identical in the 3 lines. Similar reproductive performance has been reported for the selection experiment for yearling or 18-month weight at Waikite, New Zealand (Baker *et al.*, 1980)

Frisch (1981), selecting a line of Hereford x Shorthorn cattle for higher growth rate under conditions of moderate to high environmental stress, reported that birth weight declined in the

Table 1. Summary of results from selection experiments on growth traits.

Author(s)	Duration of experiment	N	GI	GS	Inbreeding %		Selection criteria	Selection differential**					Annual genetic gain			
					Calf	Dam		Midparent	% realised through		% of potential maximum		Rate***	% of mean	Realised heritability	Method
									Sires	Dams	Sires	Dams				
Flower *et al.* (1964)	1954–59	392	4		18		WW + PG	0.15 0.25	81.4 1.00	18.6			2.07	1.14	0.77	Repeat matings
Brinks *et al.* (1965)	1934–59	1594	4.9		16.1	11.7	WW + WS + PG	0.13 0.10 0.22	84.6 80 100	15.4 20			0.56 0.14	0.29 0.18	0.23* 0.15*	Repeat matings
Nelms and Stratton (1967)	12 years	302	4.3		11.2	5.1	YW	0.19								
Bailey *et al.* (1971)	1955–69	1488	4.7				PG PG FE FE YS	0.22 0.13 0.17 0.20 0.20					1.49 2.17 0.18 0.17 −0.09	1.64 2.40 0.17 0.17 −0.11	0.57 1.0 0.60 0.44 0	Regression on dam's birth year
Chapman *et al.* (1972)	1963–69	765	4.3				PG WW YS	0.29 0.22 –	83 85 –	17 15 –					0.84 0.33 0.22	Deviation from AV herd
Newman *et al.* (1973)	1960–69	3577	3.2				YW	0.33	68.6	31.4			3.05 ± 1.12	0.77	0.45 ± 0.06	Control population
Gaskins (1974)	1947–69	1135	–				WW + WS + W/A						0.69 −0.02 0.00			Regression on dam birth year
Koch *et al.* (1974*a*,*b*)	1960–70	2956	4.6	2.0 1.8 1.9			WW YW YW+MS	0.19 0.21 0.18	79 88 84	21 12 16	77 94 97	52 50 71	1.06 3.05 2.34	0.53 0.74 –	0.27* 0.28*	Various regression methods
Nwakalor *et al.* (1976)	1946–71	3408		33.1	21.8		WW + FE+PG + YG						1.87			Repeat matings
Chevraux and Bailey (1977)	1955–74	390	4.7	3.2			PG	0.22	83	17	92	60	4.25 ± 2.05	3.65	0.35	Regression on dam birth year and generation coefficient

(Cont'd)

Table 1. (Cont'd)

Author(s)	Duration of experiment	N	GI	GS	Inbreeding %		Selection criteria	Selection differential**					Annual genetic gain			Method
					Calf	Dam		Midparent	% realised through		% of potential maximum		Rate***	% of mean	Realised heritability	
									Sires	Dams	Sires	Dams				
Marting and Alenda(1980)	21 years	2576	4.0				YW						4.06			Modified procedure of Smith (1962)
Buchanan *et al.* (1982a)	1963–77	2125	4.3	3.7	0.05	0.03	WW	0.23	79	21	86	66				
		2098	4.4	3.6			YW	0.24	84	16	95	62				
		2135	4.4	3.7			YW+MS	0.21	81	19	93	74				
Frahm *et al.* (1985*a*,*b*)	1964–78	627	4.7	3.2			WW	0.21	70	30	88	70	1.03	0.55	0.24±0.04	Control population and multiple regression
		605	4.7	3.1			YW	0.23	76	24	100	67	1.03	0.32	18.0±0.04	
Irgang *et al.* (1985*a*,*b*)	1970–81	2467	3.8	2.00	5.8	2.0	WW	0.19			82		0.77	0.51	0.25±0.11	Control population and multiple regression
			3.9	1.9			PG	0.14			89		0.48	0.43	0.18±0.09	
Nicoll and Johnson (1986)	1976–85	458	3.8	2.1			YI	0.28			86					
Aaron *et al.* (1986*a*,*b*)	1964–79	2249	4.1	3.9			WW	0.23	67	33	94	81	1.45	0.72	0.30±0.13	Same method as used by Frahm *et al.* (1985)
			5.6	2.7			IWW						2.10	1.04		
			4.7	3.7			YW	0.21	76	24	100	64	3.50	1.06	0.35±0.03	
Nwakalor *et al.* (1986)	1946–73	4833	4.1	5.5	36.3	25.5	WW + PG + FE + YG	0.33 / 0.69[m] / 0.10[m]	77	23			0.56[c] / – / −0.03[c]			Regression of offspring deviations on generation number
Pacer *et al.* (1986)	1980–84		4.8				YW	0.24	75	25			3.19	1.17	0.22*	Control population
								0.15	78	22			1.83	0.69		

N = Number of calves
I = Inbred line calves
M = Males only
C = Corrected for inbreeding effects
GS = Generations of selection
GI = Generation interval (years)
BW = Birth weight
WW = Weaning weight
IWW = Weaning weight (selection on the basis of individual and progeny performance)
PG = Postweaning gain
YW = Yearling weight
FE = Feed efficiency – kg gain/100 kg TDN (Bailey *et al.* 1971), Units (Nwakalor *et al.* 1986*a*,*b*).

WS = Weaning score
W/A = Weight per day of age
MS = Muscle score
YS = Yearling score
YG = Yearly grade
YI = Yearling index composed of adjusted weaning and yearling weight, cow fertility and maternal weaning weight
AV = Herd average performance (for PG, WW and YS)

* = Values were estimated
** = Selection differential in standard units per year
*** = Genetic change in kg/yr for growth traits

Table 2. Summary of correlated responses to selection on growth traits in beef cattle.

Author(s)	Selection criteria	Secondary selection differential								Correlated responses**									Realised genetic correlations								
		BW	WW	WG	PG	YW	MS	FE	YS	BW	WW	WG	PG	YW	MS	FE	YS	FAT	BW	WW	WG	WS	PG	YW	MS	YS	FE
Flower *et al.* (1969)	WW+PG	0.09				0.13				0.44																	
Brinks *et al.* (1965)	WW+WS +PG	0.08				0.16				0.17						0.20	−0.13										
Bailey *et al.* (1971)	PG							0.20	0.03							0.42			PG								0.98***
	PG							0.09									0.05		PG							−1.08**	
	FE				0.14				0.04				1.12														
	FE				0.17								0.92														
	YS				0.05			0.04					1.23	0.11													
Frahm and Lalande (1974)	PG									0.05	0.48																
Anderson *et al.* (1974)	YW									0.03	0.71																
Koch *et al.* (1974*a*,*b*)	WW	0.08		0.19	0.09	0.18	0.04			0.18		4.3	4.76	2.61	0.02				WW					0.34***			
	YW	0.08	0.14	0.13	0.18		0.10			0.22	0.77	2.76	7.82		0.01												
	YW+MS	0.08	0.11	0.10	0.15					0.22	0.68	2.54	7.48														
Chevraux and Bailey (1977)	PG			0.06							3.47																
Martin and Alenda (1980)	YW										0.14		14.0														
Buchanan *et al.* (1982*a*)	WW	0.13		0.22	0.08	0.20	0.15																				
	YW	0.11	0.17	0.16	0.20		0.10																				
	YW+MS	0.12	0.17	0.15	0.18																						
Frahm *et al.* (1985*a*,*b*)	WW	0.09		0.20	0.06	0.17				0.27		3.83	−1.51	1.55					WW					0.69			
	YW	0.11	0.85	0.17	0.17					0.24	0.91	3.38	0.80														
Irgang *et al.* (1985*c*)	WW									0.00		3.52		0.97	0.23			0.17	WW				0.63				
	PG									0.10		5.60		1.97	0.02			0.16									
Aaron *et al.* (1986*a*,*b*)	WW	0.10		0.23	0.03	0.16				0.24		5.56	3.52	2.10					WW					0.79			
	WW[c]	–	–	–	–	–					–	7.08	3.54	3.50													
	YW	0.10	0.16	0.15	0.18					0.45	1.52	4.76	10.72														

* = Secondary selection differentials in standard units per year
** = Correlated responses in kg/year for BW, WW, YW, grams per day per year for WG; PG, mm per year for fat, feed/gain/year for FE (Irgang *et al.*, 1985*c*) and kg gain/100 kg TDN (Bailey *et al.*, 1971)
*** = Realised genetic correlations estimated from data given in the papers
BW = Birth weight
WW = Weaning weight
WG = Preweaning gain
PG = Postweaning gain
YW = Yearling weight
MS = Muscle score
FE = Feed efficiency

selected line relative to the control, while live weight at all other ages increased significantly in the selected line. At the same time, calf mortality has been lower, with heifer calving rate higher in the selected line than in the control. These results were attributed to the effects of stress from the tropical climate. More recently, Bailey and Lawson (1986) reported a significant decline in birth weight in a line of Herefords selected for increased postweaning gain for 12 years, but no change in birth weight in an Angus line selected on the same criterion. Interestingly, Luesakul-Reodecha, Martin and Nelson (1986) obtained a significant trend of -0.4 for dystocia score in an Angus line selected for yearling weight for 19 years. These trends seem to disagree with the commonly held opinion that selection for growth is accompanied by increased birth weight and dystocia.

(b) Other growth traits

The correlated response in weaning weight obtained from direct selection for yearling weight by Koch *et al.* (1974*b*) and Frahm *et al.* (1985*b*) averaged about 81% of the direct response for weaning weight. The correlated response reported by Aaron *et al.* (1986*b*) for weaning weight from direct selection for yearling weight was greater than the response from direct selection (1.52 vs. 1.45 kg per year).

On the other hand, the corresponding correlated response for yearling weight as a result of selection for weaning weight was about 67% of the direct response for yearling weight. It seems, therefore, that selection for yearling weight had resulted in more improvement in weaning weight than the reverse. The above results were from single-trait selection experiments. Selecting for weaning weight on the basis of combined individual and progeny performance, Aaron *et al.* (1986*b*) reported that the correlated response for yearling weight was equal to the response from direct selection on individual performance.

The average annual correlated response for preweaning daily gain from reports in the literature were 4.30 and 3.63 g per day from selection for weaning weight and yearling weight respectively. Corresponding annual estimates for postweaning growth rate were 4.30 and 9.23 g per day.

There are not many reports on feed efficiency. Koch *et al.* (1982) reported that bulls from lines selected for growth rate had a significantly improved feed efficiency on test. The correlated responses in the weaning weight line and yearling weight line were 0.39 and 0.57 kg per Mcal of metabolisable energy respectively. Irgang *et al.* (1985*c*) did not observe any significant response for feed efficiency from selection for weaning weight of post weaning gain.

(c) Carcass traits

The genetic correlation estimates from the literature predict that selection for increased body weight should result in reduced fatness at constant age (Koch *et al.*, 1982). However, much experimental evidence seems to indicate no significant correlated response in carcass traits from selection for growth rate. Gallagher (1964) reported no significant differences between carcass traits for progeny of bulls selected for fast or slow growth. The only consistent and significant correlated response in carcass traits in the selection experiments for yearling weight in the Shorthorn reported by Anderson *et al.* (1974) was a higher percentage of bone and a lower lean to bone ratio. Almost similar results were reported by Martin and Alenda (1980) for Angus cattle. The data of Koch *et al.* (1982) indicated a correlated response of -0.19, -0.03 and 0.23 mm per year in fat thickness at 281 kg body weight from selection on weaning weight, yearling weight and an index combining yearling weight and muscle score respectively. Irgang *et al.* (1985*c*), however, reported significant positive correlated responses of 0.13 ± 0.04 and 0.16 ± 0.4 mm fat depth per year in lines selected for weaning weight and postweaning gain respectively.

Perhaps the level of feeding during the finishing phase may affect these correlated responses (Baker and Morris, 1984). For example, mice selected for high 6-week weight on a low plane of nutrition had a lower fat percentage at that age than mice selected on the same basis with adequate nutrition, when both lines were placed on the same nutritional plane (Falconer, 1960).

(d) Milk yield in beef cattle

From literature estimates of the genetic correlation between direct and maternal effects for weaning weight (r_g = -0.43), Barlow (1978) concluded that selection for weaning weight would reduce milk yield. However, as pointed out by Baker (1980) and discussed by Baker and Morris (1984), most of the estimates summarised by Barlow (1978) were from dam-offspring relationships, and they could be seriously biased by negative environmental covariance caused, for example, by levels of feeding for heifers. When this relationship is avoided, the genetic correlation between direct and maternal effects for weaning weight is lower, ranging from -0.05 to -0.28.

Frahm *et al.* (1985*b*) reported that milk yield was not significantly different between progeny sired by bulls selected either for weaning weight or yearling weight. However, milk fat percentage was 0.4 higher for progeny of bulls selected for high yearling weight. Aaron *et al.* (1986*b*) also obtained a similar result, but in addition, the daily milk yield of progeny sired by bulls selected for

weaning weight was significantly higher than that of the controls. Lawson (1978) indicated that selection on postweaning gain on a high plane (HP) or low plane (LP) of nutrition resulted in significantly higher solids-not-fat and protein percentages in animals on LP relative to the HP in Hereford cattle. Baker and Morris (1984) reported that preliminary results from the selection experiment of Carter (1971) indicated that cows in the yearling weight selection line have a higher milk yield than cows of the postweaning gain selection line, as assessed by calf weaning weight. Also, Angus cows from a line selected for postweaning gain on a roughage diet exceeded those of cows selected for the same criterion on a concentrate diet in respect of yields of milk, fat, solids-not-fat and protein by 5.1, 7.6, 7.8 and 12.5% respectively (Bailey and Lawson, 1986).

Another criticism against selection on growth rate is that it is usually accompanied by large mature cow size and increased fatness. Baker and Morris (1984) mentioned that evidence from experiments on correlated responses in cow weight is somewhat fragmentary. The only result they mentioned indicated that selection for early growth led to increased cow size. Luesakul-Reodecha *et al.* (1986) reported positive but non-significant trends of 0.35 and 4.12 kg per year for 205-day and 54-month weight in an Angus line selected for 365-day weight. However, Morris and Wilton (1978), in a review of the association between cow size and biological efficiency of reproduction, concluded that when all postweaning food requirements are added to the cow herd food costs, herd efficiency is little affected by cow size unless reproductive performance also changes. Experimental evidence indicating a major decline in fertility or increased fatness from selection for growth is rather limited.

III. Other Experiments

Other selection experiments not primarily concerned with growth may be grouped by their objectives.

1. Comparison of alternative selection schemes or methods

Carter (1971) investigated the effectiveness of sire selection on the basis of either corrected weaning weight, corrected final weight or postweaning gain, by evaluating the performance of progeny in a test herd for 10 years. The regression of the performance of progeny on the performance of sires indicated that selection on either weaning weight or yearling weight should result in appreciable genetic gains. On the other hand, sire's postweaning gain was a poor indicator of progeny performance for any trait.

Baker *et al.* (1980) compared the effectiveness of selection of Angus cattle for 13-month live weight (AS1), followed by first mating of selected animals at 14 months of age, with selection on 18-month live weight (AS2), with first mating as 2-year-olds. A yearling-mated Hereford herd selected on 13-month weight (HS1) and a control line of Angus with mating as 2-year-olds (ACO) were also kept. Relative to the control line, AS1 and HS1 improved in both 13-month and 18-month weights at about twice the rate at which AS2 improved. A summary of the preliminary results are presented in Table 3. The advantage of the selection scheme in AS1 and HS1 relative to that in AS2 is that it allows heifers to be mated at 2 years rather than the traditional 3 years in Australia, and this can result in increased calf production and permit early identification of less productive females. This, coupled with selection and mating of yearling bulls, should increase annual genetic progress through reduction of generation interval.

Table 3. Direct and correlated genetic responses to selection on either 13-month or 18-month body weight in cattle (kg per yr) (Baker *et al.*, 1980).

Line	Birth weight	Weaning weight	13-month weight	18-month weight
HS1	0.08 ± 0.04	0.88 ± 0.4	1.65 ± 0.56 (D)	3.10 ± 1.39
AS1	0.25 ± 0.05	0.98 ± 0.38	2.56 ± 0.55 (D)	2.71 ± 1.01
AS2	0.04 ± 0.06	0.34 ± 0.32	1.22 ± 0.65	1.48 ± 0.96 (D)

D – direct response
HS1 – Hereford line selected on 13-month live weight
AS1 – Angus line selected on 13-month live weight
AS2 – Angus line selected on 18-month live weight

2. Responses in synthetics and purebreds

Berg (1984) carried out selection on 2 synthetic cattle populations and a purebred Hereford line to identify any superiority in response of the synthetic lines over the pure Hereford line due to a broader genetic base. One of the synthetic lines was developed by crossing Charolais, Angus and Galloway (SY1), while the second consisted of 60% of large dairy breeds (Holstein, Brown Swiss and Simmental) with 40% of beef breeds (SD). The selection criteria were preweaning and postweaning gain

at one year of age in the synthetic lines, while industry bulls selected on the basis of superior performance or a progeny test were used by artificial insemination in the Hereford herd each year. A summary of results is present in Table 4. There were higher trends for the synthetic lines in cow productivity, birth weight and 365-day weight. However, industry bulls used in the Hereford line were not subjected to the same amount of selection pressure nor selected on the same criteria as those used in synthetic lines. These differences could have affected the results.

Table 4. Comparative performance of Hereford cattle and two synthetic lines selected for growth rate (1962–1982).

Trait	Cattle populations		
	HE[1]	SY	SD
Calf crop %	78	83	82
Phenotypic trend (1962–1982)			
Birth weight (kg per yr)	0.17	0.25	0.34
365-day weight (kg per yr in males)	2.02	4.36	5.18
Average performance (1977–1980)			
Feed efficiency (kg feed/gain)	5.17	5.37	5.76
Average daily gain (kg per day)	1.34	1.57	1.46
Dressing %	58.5	60.4	58.9
Fat cover (cm)	1.38	1.11	0.88
Loin-eye area (cm^2)	75.6	89.6	86.9

HE[1] = Hereford
SY = Synthetic line composed of Charolais, Angus and Galloway
SD = 60% dairy breeds and 40% beef cattle breeds

An experiment with a similar objective was initiated at Wokalup, Western Australia, in 1979 to compare the performance of purebred Hereford cattle with a synthetic (Wokalup Multibreed) line (Anonymous, 1985).

Similarly, Sharma *et al.* (1985) compared genetic response in a purebred Hereford and a multibreed synthetic line which were treated in the same way. The main selection criterion was weight for age in bulls at one year of age. Genetic trends were estimated by deviation from a control population, using best linear unbiased prediction (BLUP) and MIVQUE (minimum variance quadratic unbiased estimation) variance components estimated from the population. A summary of the results is presented in Table 5. Briefly, the mean selection differential was higher in the synthetics, which was attributed to the larger genetic base and greater variation in the synthetic line. Sire variance components were higher in synthetics than in Herefords, and non-genetic sources of variation seemed to be more important in the Hereford. The estimated genetic trends were similar in the 2 populations for preweaning traits, but slightly higher for postweaning traits in the synthetic population.

3. Selection for disease or parasite resistance

A few selection studies concerned disease resistance in beef cattle. Wharton, Utech and Turner (1970) reported heritability estimates of 39 and 49% for tick resistance from dam-calf and full-sib correlations respectively in Australian Illawara Shorthorn cattle, and proposed that selection for tick resistance might be effective. Utech, Seifert and Wharton (1978) carried out divergent selection for tick resistance in a population of Australian Illawara Shorthorns. All the cattle acquired their resistance by exposure to field infestation. Selection was based on the number of semi-engorged female ticks on animals grazing together in naturally infested pastures for a period of at least 3 weeks, and also on the number of female ticks maturing after artificial infestation with a known number of larvae.

The line selected for high resistance carried significantly fewer ticks than the low line at all times, on exposure to naturally or artifically infested pastures.

A similar, divergent selection experiment for high and low resistance lines to helminths, in particular *Cooperia* and *Haemonchus*, has also been initiated in Australia (Anonymous, 1985).

4. Effectiveness of selection for twinning

Heritability estimates for twinning, reviewed by Maijala and Syvajarvi (1977) were about 3%, with a repeatability of 6%. With such low values, most workers have dismissed selection for twinning as impracticable and undesirable (see Morris, 1984). Land and Hill (1975) have shown the importance of having a high initial herd average. They demonstrated theoretically that selection with the assistance of superovulation and embryo transfer should achieve genetic progress of 0.42 and 1.10% per year for initial herd twinning frequencies of 2 and 16% respectively. Mechling and Carter (1964)

Table 5. Estimated genetic response per year to selection in purebred Hereford and a synthetic population (1966–1978) (Sharma *et al.*, 1983).

Trait		Mean	MSD	Annual genetic change estimated by Control population	BLUP
Birth weight	HE	33.1	0.3	0.06±0.21	0.08± 0.06
(kg per yr)	SY	35.1	0.8	0.29±0.22	0.07± 0.06
Preweaning daily	HE	874	29.4	9.6 ± 5.4	4.2 ± 1.20
gain (g per day)	SY	1077	33.2	7.5 ± 4.9	4.8 ± 2.30
Weaning weight	HE	194	5.3	1.80± 0.03	1.10± 0.21
(kg per yr)	SY	233	7.2	1.64± 0.92	0.86± 0.43
+ Postweaning daily	HE	1297	33.9	13.72±44.3	17.93±11.32
gain (g per day)	SY	1399	46.7	48.12±49.4	31.25±11.15
+ Yearling weight	HE	418	12.2	5.81± 9.39	8.21± 6.00
(kg per yr)	SY	471	13.8	11.31±12.17	6.78± 2.15
++ 18-month weight	HE	376	0.3	7.54± 4.93	−6.10± 2.10
(kg per yr)	SY	408	0.2	7.52± 4.36	−11.90± 2.50

HE = Hereford line
SY = Synthetic line (composed of 35.7, 34.7, 21.7, 4.5 and 3.4% of Angus, Charolais, Galloway, Brown Swiss and others, respectively)
MSD = Mean selection differential
+ Males only
++ Females only

reported selection for twinning over 30 years in Aberdeen-Angus herds, but concluded that little real progress had been achieved.

In a recent review, Morris (1984) reported a series of selection experiments on twinning in Australia, USA, France and the German Federal Republic. The frequency of twinning for daughters from second or later calvings reported were: Australia, 8% from 76 calvings (controls, 0.6%); USA, 6.8% from 176 calvings (including first calving); France, 11% from 89 calvings.

In the German experiment, comparison of twin-born and control (single-born) females showed a difference of 0.94% in twinning.

5. Genotype x environment (GE) interaction

When GE interactions are important, response from selection in one environment is not likely to be fully transferred to other environments. Under such situations, genes governing performance in one environment are not all the same as those governing performance in another environment. It may be necessary to select stocks under the specific environment in which progeny of stocks will be reared (Falconer, 1981).

Beef selection experiments aimed at identifying important line by location interactions have been reported by Butts (1971), Koger (1979), Burns (1979) and Pahnish (1985) in Hereford cattle. Butts *et al.* (1971) investigated GE interaction in 2 herds of Hereford cattle, each consisting of 2 lines, one herd at Miles City, Montana, and one at Brooksville, Florida. A 7-year period of selection was followed by reciprocal exchange of animals. The primary selection criterion was an index with equal emphasis on preweaning and postweaning growth in bulls. They observed significant line by location interaction in birth weight, weaning weight, yearling weight, and pregnancy and weaning percentages.

Koger *et al.* (1979) and Burns *et al.* (1979) evaluated GE interaction in reproductive traits, birth weight and weaning weight in 4 lines of cattle which partly originated in the work of Butts *et al.* (1971). In addition to 2 lines which were developed independently in Montana and Florida (unrelated lines), they had another pair of lines which was developed from the same base populations in Montana, before undergoing subsequent selection in the two different locations (related lines). There was significant line x location interaction in preweaning rate, weaning rate, birth weight and daily gain in the unrelated and related lines. However, the line x location interaction was not significant for survival rate.

Pahnish *et al.* (1985) examined line x location interactions for postweaning traits in the same populations. Significant line by location interactions were observed in the unrelated line for postweaning daily gain, weight at end of test, and conformation score. The same result was obtained for the related lines. Investigations to understand the mechanism underlying these interactions identified differences in thyroid function of these animals. There were no differences in milk yield. However, the degree of GE interaction was not quantified in terms of the genetic correlation between the same traits in the different locations

Frisch (1981) investigated factors underlying GE interaction in growth rate under tropical conditions, by studying correlated response to selection for growth under stressful tropical conditions. A line of cattle selected for growth rate from 1970 to 1975 and a control line, with significant differences in live weight, were exposed to several levels of stress: plane of nutrition, high ambient temperature, infection with bovine infectious keratoconjunctivitis (BIK) or gastro-intestinal helminths (GIH). The selected line was shown to be more heat tolerant, to have a lower maintenance requirement, greater resistance to infection with BIK and GIH, and, consequently, higher growth rate in the presence of these stresses. However, cattle of the selected line did not have superior growth rate at low levels of stress. Thus, reversal of rank between selected and control lines for growth rate under conditions of high and low stress could be attributed to differences in resistance to environmental stress and not in growth potential.

The results of Pacer *et al.* (1986) seem to indicate some degree of interaction between line and plane of nutrition. While the Angus line selected for postweaning growth on a concentrate diet was significantly different from foundation animals in postweaning gain, weight per day of age and final weight, a similar line selected on a roughage diet did not differ significantly in any of above traits.

IV. Conclusions and Discussion

The positive genetic trends reported for growth traits indicate that selection for the improvement of growth traits is effective. Correlated responses in other growth traits from direct selection on yearling weight were generally larger than those from weaning weight selection. Thus, if the main objective is to increase weight in sire lines, selection on yearling weight is preferable. Experimental evidence seems to disagree with the commonly held opinion that selection for growth is necessarily accompanied by increased birth weight and dystocia. The literature reports show that improvement of growth traits still continues to be the main selection objective in beef cattle experiments, with very little emphasis on other traits.

The rates of genetic gain so far achieved in growth traits are somewhat lower than the possible rates indicated by Smith (1984). The lower rates of genetic change achieved in practice in beef cattle have been attributed by Smith (1986) to concern about other traits of uncertain economic importance, conservatism of breeders, and selection and generation turnover rates which are not optimal.

Land and Hill (1975), Smith (1984) and Land (1985) have discussed the possible ways by which the present rate of selection response could be improved. One of the major limitations to genetic improvement in beef cattle is the low female reproductive rate, which restricts selection intensity among females. Land and Hill (1975) and Land (1985) have shown that if female reproductive rate could be increased, it would be theoretically possible to double the rate of genetic change for traits which can be measured in both sexes before reproductive age, and the rate of genetic change could be increased by 1.6 times by using multiple ovulation and embryo transfer rather than normal reproduction.

Two other routes to faster improvement may be the use of major genes and indirect selection on physiological traits. An example of a major gene currently being exploited in breeding programmes in cattle is the double muscling gene, which results in a higher yield of lean meat. Hanset and Michaux (1985) reported about a 30% higher total muscle weight in Belgian White and Blue veal calves homozygous for the double muscling gene compared with normal homozygotes. Double muscling, however, is associated with calving difficulties.

Selection on physiological traits or biochemical factors indicating or controlling performance may allow indirect selection for commercial traits. This could offer great scope for reducing the generation interval, as animals could be selected early in life. It might also be useful in selecting young males for sex-limited traits. Presently, no such technique is available in beef cattle. However, the high and low growth rate lines of the Trangie Agricultural Research Station, Australia present a great opportunity to examine the biochemical and physiological components of response to selection for growth rate.

The increasing demand for lean meat also implies that selection objectives in beef cattle should be broadened to include carcass traits. Apart from the consumer's view, it has been suggested that the greatest scope for improving bio-economic efficiency in beef cattle, other than through reproduction, is by use of faster-growing, lean terminal sires (Dickerson, 1982; Barlow, 1984). Selection for leanness in live animals is possible by ultrasonic measurement of fat depth or area. Simm (1983) reported a correlation coefficient of about 0.70 between lean content estimated from ultrasonic measurements and by carcass analysis.

Acknowledgements

I wish to thank Dr. Charles Smith, Professor W.G. Hill and Mr. R. Thompson for their assistance.

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SELECTION FOR LEAN GROWTH RATE AND LEAN FOOD CONVERSION RATIO IN HEREFORD CATTLE

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RESUME

La réponse à la sélection est étudiée dans un troupeau Hereford comprenant deux lignées sélectionnées sur le taux de croissance de viande maigre (LGR) ou sur l'efficacité alimentaire pour la production de viande maigre (LFR), ainsi qu'une lignée témoin (CL). La sélection est faite de 1979 à 1986, seulement sur des mâles, et l'intervalle moyen entre les générations était de 2,4 ans dans les deux lignées sélectionnées. Les différentielles cumulatives de sélection étaient 59 g par jour et -3,2 kg de fourrage par gain de kg de viande maigre dans les lignées LGR et LFR respectivement. La réponse à la sélection a été estimée par deux méthodes : (1) la différence par rapport à la lignée témoin et (2) le maximum de vraisemblance restreint (REML). Selon la première méthode, l'héritabilité a été estimée à 0.53±0.14 pour LGR et à 0.38±0.13 pour LFR. Les estimations de gain génétique annuel étaient 5.0±1.6 g par jour pour la lignée LGR et -0.13±0.08 kg fourrage par kg de taux de croissance de muscle pour la lignée LFR. Les estimations de REML étaient à peu près les mêmes que celles de la première méthode, mais plus précises.

INTRODUCTION

The current trend in consumer's attitude for lean meat, is indicative that selection for efficiency of lean meat production is likely to be a long-term objective in beef cattle. This study is concerned with the evaluation of response in two lines of Hereford cattle selected for lean growth rate (LGR) and lean food conversion ratio (LFR) from 1979 to 1986.

MATERIALS AND METHODS

In 1977, a foundation herd of 227 Hereford cows was established to study the efficiency of lean meat production. During 1977-1978, the females were bred by artificial insemination (AI) to 48 bulls at AI stations and in private herds. Beginning with the 1978 calf crops, all bulls were ranked for LGR and LFR and the best 6 to 8 were selected and alloted to the LGR and LFR lines respectively. Each line consisted of three replicates with about 25 cows and 2 bulls per year. There was also a control line (CL) consisting of about 36 cows bred by frozen semen taken from some 25 bulls born in the foundation years.

Selection procedure and statistical methods

Bulls were selected on the basis of performance test up to 400 days of age for LGR and for 200-400 day LFR in the respective lines. The bulls were scanned ultrasonically towards the end of test on two occasions at three sites to estimate fat area. Lean percent (LP) was predicted from the fat areas. LGR was then estimated as the product of growth rate up to 400 days, LP and killing out percent (KO). LFR was estimated as food conversion ratio divided by LP and KO.

Response to selection was evaluated by 2 methods (1) Deviation from CL and (2) Restricted Maximum Likelihood (REML).

RESULTS AND DISCUSSION

Selection differential

The average age of parents was similar in both selected lines, about 2.4 years. The cumulative selection differential (CSD) in 1986 were 58.8g/day (2.0 standard deviation units(sdu)) for LGR in the LGR line and -3.2kg lean feed/kg gain (1.8 sdu) for LFR in the LFR line. The average sire selection differential per generation were 1.3 and 1.4 sdu for LGR and LFR in their respective lines.

Responses and genetic parameters

Realised heritabilities (h^2) from method (1) were estimated as the regression of response on CSD. Estimates of variance components and heritabilities from REML and genetic correlations (rg) are presented in Table 1. Heritabilities from method (1) were generally slightly higher than from REML. Inconsistent estimates of rg were obtained from the various lines (Table 1). Generally, precision of estimates from method (2) increased with population size. Comparing results for LGR on analyses based on LGR line alone, on the LGR and control and in all three lines (POP3), indicated a 123% gain in information from including the control and further 51% gain in information from including the LFR line.

Estimates of genetic change achieved (Table 2) from method (1) and REML were similar although the latter were more precise. Annual rates of change observed were 1.5 and 0.75% for LGR and LFR respectively.

TABLE 1. Heritabilities, variance components (with standard errors) for LGR and LFR and genetic correlations between LGR and LFR.

		Method (1)	Variance components (method 2)				
Trait	Population	h^2	rg	VA	VE	h^2	rg
LGR (g/day)	LGR + CL	0.53 ±0.14*	-0.76** ±0.14	460.84 ±122.4	518.79 ±99.7	0.47 ±0.11	-0.81 ±0.15
	POP3	±0.21	-0.23*** ±117.7	461.19 ± 92.7	538.10 ± 0.09	0.46 ±0.12	-0.70
LFR Kg feed/ kg lean	LFR+CL	0.38 ±0.13	-0.18 ±0.21	1.03 ± 0.6	2.61 ± 0.55	0.29 ±0.16	0.58 ±0.23
	POP3		±0.4	1.26 ± 0.3	2.75 ± 0.10	0.32	

* standard errors include drift variance
** rg = $(CR2/SD1)x01/h_1 xh_2 x02$; 1 = selected trait; 2 = correlated trait
SD=selection differential; 0 = standard phenotypic deviation
***rg = Square root of (CR1xCR2)/(R1xR2); CR=correlated response;
R=response

TABLE 2. Estimates of genetic change and standard errors for LGR and LFR per year

		Method 1	Method 2		
Trait	Line		LGR+CL	LFR+CL	POP3
LGR g/day	LGR	5.0 ±1.6	4.0 ±0.8		4.2 ±0.8
	LFR	0.2 ±1.5		1.0 ±0.8	1.1 ±0.9
LFR kg/feed kg lean gain	LGR	-0.17 ±0.08	-0.15 ±0.05		-0.14 +0.05
	LFR	-0.13 ±0.08		-0.12 ±0.05	-0.11 ±0.05

standard errors include drift variance