GENETIC EVALUATION OF THE REPRODUCTIVE PERFORMANCE OF LARGE WHITE PIGS SELECTED FOR COMPONENTS OF EFFICIENT LEAN GROWTH RATE

by

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Declaration

I hereby declare that this thesis is my own composition and is an account of the analyses performed by me whilst studying for the degree of Doctor of Philosophy at the University of Edinburgh, using data and facilities provided by the Roslin Institute (Edinburgh).

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October 1995

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Abstract

The reproductive performance of Large White pigs divergently selected for daily food intake (DFI), lean food conversion (LFC), lean growth rate on *ad-libitum* feeding (LGA), and lean growth rate on restricted feeding (LGS) was investigated in a series of four studies. Correlated responses to selection in litter traits and the genetic and phenotypic relationships between performance test and reproduction traits were estimated after five generations of selection. The effects of the alternative selection strategies on gilt liveweight and backfat depth measured at mating, farrowing and weaning and food intake during lactation were examined after seven generations of selection.

Responses in litter size and weight at birth and weaning were lower with selection for low DFI and high LFC than with selection for high DFI or low LFC. The average response in litter size at birth for the DFI and LFC selection groups was 1.5 pigs/litter. Responses in litter weights were a result of selection line differences in both litter sizes and piglet weights. The relationships between litter size, litter weights and piglet weights at birth and weaning were essentially linear. For *ad-libitum* fed pigs, genetic correlations between litter weights at birth and weaning with daily food intake and with growth rate on test were positive, but correlations with backfat depths were not significantly different from zero. For restricted fed pigs, litter birth weight was positively genetically correlated with growth rate and negatively correlated with backfat depth. Between selection line variation in backfat depth enabled detection of a non-linear relationship between predicted breeding values for litter weight at birth with predicted breeding values for average backfat depth of farrowing gilts performance tested on *ad-libitum* feeding.

At the start of the mating period, gilts selected for high DFI, LGA or LGS had similar liveweights, but different backfat depths, while the low DFI, LGA and LGS lines had different liveweights but similar backfat depths. Conception rates of gilts selected for low DFI or high LGS were similar and lower than for the alternative selection strategies, but the low DFI gilts were significantly older at farrowing than gilts selected for high LGS. At farrowing, backfat depth of gilts in the high DFI line was greater than in the gilts in the low selection lines of the LFC, LGA and LGS selection groups. Liveweight of the high LFC line was lower than with selection for high DFI, LGA or LGS. Reductions in liveweight (maternal and the products of conception) and backfat depth during lactation were similar for the high and low DFI selection lines, but pigs selected for low DFI consumed significantly less food. Reductions in liveweight and backfat depth were lower with selection for high LFC than with selection for low LFC and food intake during lactation was also lower. Pigs selected for high LGA had higher lactation food intake than pigs selected for low LGA but changes in liveweight and backfat depth were similar. Growth rates of piglets, from birth to 21 days of age, in the low DFI and high LFC selection lines were less than in the high DFI and low LFC lines. Responses in piglet pre-weaning growth in the LGA and LGS selection groups were not different from zero.

In conclusion, selection for LGA or LGS did not significantly affect reproductive performance, but selection for low DFI or high LFC impaired reproductive performance. Relationships between liveweight and backfat depth at the start of the mating period with conception rate were not consistent between selection groups, which suggested that reproductive development and conception rate may be determined by selection strategy dependent combinations of liveweight, backfat, age, and food intake. Piglet pre-weaning growth rates were negatively effected by selection strategies which resulted in a low voluntary food intake during lactation or low liveweight and backfat depth at farrowing.

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Chapter 1

Introduction

The favourable impact of improving reproductive performance in modern pig genotypes on the efficiency of pig production has long been recognised, but in commercial breeding schemes reproductive traits have been subject to less attention than growth and carcass traits (see review of Haley, Avalos and Smith, 1988). Responses in reproductive performance should be considered in the design of breeding programmes based on selection for growth and carcass traits. Reductions in reproduction traits, associated with selection for components of feed conversion efficiency, for example, would have substantial negative consequences to the pig breeding industry and would influence the choice of selection strategy.

Numerous experiments have established the effects of various selection strategies on growth and carcass traits. Pigs have been selected on the basis of performance in one trait, for example growth rate (Kuhlers and Jungst, 1991a and b) or backfat depth (Fredeen and Mikami, 1986a and b) or on an index combining growth rate and backfat depth (Jungst, Christian and Kuhlers, 1981; Cleveland, Cunningham and Peo, 1982; McPhee, Rathmell, Daniels and Cameron, 1988). Correlated responses in reproduction traits have been measured in several selection experiments for lean growth rate, (DeNise, Irvin, Swiger and Plimpton, 1983; Fredeen and Mikami, 1986c; Cleveland, Johnson and Cunningham, !988; Kuhlers and Jungst, 1992), but generally the responses have not been substantially different from zero, which suggests that selection for lean growth rate would have little effect on reproduction traits.

Increasingly, the emphasis of modern pig breeding programmes is on improving the efficiency of lean meat production, through improving feed efficiency and lean content at the expense of growth rate (Webb and Curran, 1986). The consequences of selection strategies for increased efficiency, or the correlated decline in voluntary feed intake (McPhee, 1981; Mitchell, Smith, Makower and Bird, 1982; Ellis, Smith, Henderson, Whittemore and Laird, 1983), on reproductive performance have seldom been considered.

It is likely that improving performance in growth and carcass traits and increasing efficiency of lean meat production, will continue to be a primary objective of modern pig breeding schemes. In order to maintain a satisfactory rate of genetic progress, a full understanding of the consequences of alternative selection strategies for efficient lean growth rate on other traits of economic importance, such as reproduction, is required. To optimise the efficiency of pig breeding programmes, the correct identification of animals of high genetic merit for both performance and reproduction traits is a fundamental requirement. Identification of performance test traits as predictors of genetic merit for reproduction traits, would be beneficial in increasing the rate of genetic improvement. Estimation of the genetic and phenotypic relationships between performance test and reproduction traits is therefore required, to provide the quantitative information necessary to evaluate alternative selection strategies.

Prediction of responses in reproduction traits requires unbiased estimates of the genetic and phenotypic relationships between performance test and reproduction traits. However, few studies have provided estimates of the genetic correlations between performance test and reproduction traits and estimates from different studies have not been consistent. Crump (1992) provided a comprehensive review of literature on the relationships between performance test and reproduction traits. Johansson and Kennedy (1983) reported negative genetic correlations between litter size and age to a fixed liveweight, indicative of a positive genetic correlation with growth rate. In contrast, the estimated genetic correlation of Merks and Molendijk (1995) for weight to a fixed age with litter size at birth was essentially equal to zero. Genetic correlation estimates of Short, Wilson and McLaren (1994) and Crump

(1992) for growth rate and daily food intake and litter size were small and not significantly different from zero. Vangen (1980a) provided positive estimates of genetic correlations between growth rate and litter size but estimates were smaller than their standard errors. Estimates of genetic correlations between backfat depth and litter traits have been similarly variable. Johansson and Kennedy (1983) presented positive estimates of the genetic correlations for backfat depth with litter size at birth and weaning. Estimates of Merks and Molendijk (1995), Short *et al* (1994) and Rydhmer, Lundeheim and Johansson (1995) were essentially equal to zero, while the estimates of Vangen (1980a) were negative with litter size at birth but zero for litter size at weaning. It is not possible to draw definitive conclusions regarding the genetic relationships between performance test and reproduction traits given the estimates of genetic correlations presented in the literature. However, one interpretation of the variation in between study estimates may be that genetic parameters are population specific. Therefore, for the inclusion of litter traits in selection indices estimation of the genetic parameters may require evaluation for each population under selection, since selection strategy, population and environment are confounded.

The Edinburgh - Wye lean growth selection experiment was set up, in 1984 (Webb and Curran, 1986) to increase the understanding of the genetic relationships of voluntary food intake with lean tissue growth rate and lean food conversion, so that the optimum system of performance testing could be recommended to the industry for any given production system. Two populations of pigs were established: a Large White population (at Edinburgh (Animal Breeding Research Organisation)) and a Landrace population (at Wye College, University of London). There were four divergent selection strategies and a control, in each population, with pigs selected for daily food intake, lean food conversion, lean growth rate on *ad-libitum* feeding and lean growth rate on restricted feeding. Although, evaluations of the correlated responses in reproduction traits were not defined in the original objectives for the study, Cameron (1994) noted that the cumulative selection differential of animals selected for low daily food intake was substantially lower than of animals selected for high daily food intake as a result of reduced reproductive performance. These results suggested that the correlated responses in reproduction traits would be substantially different from zero, and may influence the choice of selection strategy by the pig breeding industry.

Divergent selection strategies for daily food intake, lean food conversion, lean growth rate on *ad-libitum* feeding and lean growth rate on restricted feeding have resulted in pigs with dramatically different growth rates (to a fixed liveweight), backfat depths and food intakes during performance test (Cameron and Curran, 1994). The alternative selection strategies may have direct consequences on litter size and piglet weights, but pre-weaning litter and piglet traits may also be substantially influenced by the rearing ability of the farrowing gilts (for a review see Whittemore and Morgan, 1990). The effects of different liveweights levels of fatness and food intake on sow performance during lactation on piglet pre-weaning growth have been well documented (For example, Eastham, Smith, Whittemore and Phillips, 1988; Yang, Eastham, Phillips and Whittemore, 1989; Noblet, Dourmad and Etienne, 1990; Newton and Mahan, 1993). The differences in liveweight and backfat depth in the above studies have been achieved through an imposed nutritional treatment rather than by selection and the effect of genotype has not been considered. The effects of alternative selection strategies for efficient lean growth rate on liveweight and backfat depth of gilts at farrowing and at weaning on gilt performance during lactation and on pre-weaning piglet growth rate, require evaluation. The information provided will enable the responses in gilt post-farrowing traits and pre-weaning piglet traits to be determined and the genetic merit of alternative selection strategies for components of efficient lean growth rate to be comprehensively evaluated.

The chapters which follow report a series of studies which consider the consequences of four divergent selection strategies for efficient lean growth rate on subsequent reproductive performance in a population of Large White pigs. The experimental resource comprised the

Large White animals from the Edinburgh population of the Edinburgh-Wye lean growth selection experiment.

The main objectives of the studies were:

1. To determine the magnitude of correlated responses in litter and piglet traits resulting from the alternative selection strategies.
2. To provide estimates of the genetic and phenotypic parameters between performance test and reproduction traits for prediction of responses in reproduction traits in breeding programmes.
3. To determine the responses in liveweight and backfat depth (measured at the start of the mating period) and in conception rate, resulting from the alternative selection strategies. To estimate the contribution of liveweight and backfat depth (measured at the start of the mating period), to the accuracy of predicted genetic merit for litter traits at birth.
4. To determine the responses in gilt liveweight and backfat depth at farrowing and at weaning, and in pre-weaning piglet growth rate, resulting from the alternative selection strategies.

Chapter 2

Correlated responses in reproduction traits

Introduction

Selection for growth and efficiency in commercial pig breeding schemes has been based on performance test traits, such as growth rate, food intake and on predicted carcass traits. In several selection experiments, pigs have been selected on the basis of one trait, (e.g. growth or backfat; Kuhlers and Jungst, 1991 a and b; Fredeen and Mikami 1986 a and b) or on an index of growth rate and backfat depth, (Cleveland, Cunningham and Peo, 1982; Jungst, Christian and Kuhlers, 1981; McPhee, Rathmell, Daniels and Cameron, 1988). Although, selection on reproductive traits has been subject to less attention in commercial breeding programmes (see review of Haley, Avalos and Smith, 1988), the correlated responses in reproductive performance should be considered in the design of breeding programmes, based on selection for growth and carcass traits. Several studies have measured the responses in reproductive traits with selection on lean growth (Fredeen and Mikami, 1986c; Cleveland, Johnson and Cunningham, 1988; Kuhlers and Jungst, 1992), but in general, the responses have not been significantly different from zero. However, Cameron (1994) noted that the cumulative selection differential of animals selected for low daily food intake was substantially lower than with selection for high daily food intake, due to reduced reproductive performance. These results suggest that the choice of selection strategy will determine the magnitude of the correlated responses in reproductive traits and this has serious implications to the pig breeding industry.

The current chapter reports the correlated responses in reproductive performance after five generations of divergent selection for components of efficient lean growth rate in a Large

White population and to estimate the genetic and phenotypic parameters for reproductive traits.

Material and methods

Animals

Data were collected from five generations of Large White pigs divergently selected for daily food intake (DFI), lean food conversion (LFC), lean growth rate on *ad-libitum* feeding (LGA) and lean growth rate on restricted or scale feeding (LGS). Details on establishment of the selection lines are given by Cameron (1994) and Cameron, Curran and Kerr (1994). In each of the four selection groups, there were high, low and control lines and each line was designed to consist of 10 sires and 20 dams, with a generation interval of one year. Control lines were established to enable detection of asymmetric responses to selection and to provide genetic links between the four selection groups, as due to a batch farrowing management system, the selection groups farrowed at different times.

Pigs in the *ad-libitum* selection groups were performance tested over a fixed weight range with average start and finish weights of 30 and 85 kg. Pigs fed on restricted feeding were performance tested for a fixed time period of 84 days with an average start weight of 30 kg and food intake equal to 0.75 g/g of daily *ad-libitum* food intake. All animals were individually penned during the performance test. Animals were fed a high protein and high energy pelleted diet containing 224 g crude protein per kg dry matter (DM) and 15.9 MJ digestible energy (DE) per kg DM. At the end of test, ultrasonic measurements of backfat depth were taken at the shoulder, mid - back (analogous to P2 carcass measurement) and the loin on both sides of the pig.

The selection objectives were to obtain equal correlated responses, measured in phenotypic standard deviation units, in carcass lean content and growth rate (or food conversion ratio) in the LGA and LGS (or LFC) selection groups. In the DFI selection group, the objective was daily food intake. In the LGA, LGS and LFC selection groups animals were selected on indices combining measurements of performance test traits (Cameron, 1994; Cameron, Curran and Kerr, 1994). Selection in the high, low and control lines of each selection group was based on both the selection criterion value and the parentage of the animal, the latter to avoid increases in the rate of inbreeding, such that selection was partially on a within-sire basis rather than solely on mass selection. At generation four, the average inbreeding coefficient for the selection lines was 5.8%.

All animals were mated between nine and ten months of age, approximately eight weeks after the end of performance test. Matings were unsupervised and took place in outside paddocks. Individual boars were run with three gilts for six weeks and were inspected on a regular basis, so that inactive boars could be replaced. Pregnant gilts were fed 2.5 kg daily and farrowed sows up to 3.5 kg twice daily of a diet containing 184 g crude protein per kg dry matter (DM) and 15.2 MJ digestible energy (DE) per kg DM. All animals were farrowed in selection group batches at an average age of 414 (s.d. 19) days. The coefficient of variation for farrowing age was 0.05 due to the short mating period. No cross fostering was practised. Piglets were offered creep feed containing 264 g crude protein per kg DM and 18.0 MJ DE per kg DM from 14 days of age and were weaned at an average of 35 (s.d. 3) days.

Litter traits were measured on a total of 1220 Large White gilts, with 13030 records of piglet birth weights including stillborn piglets and 9951 records of piglet weaning weights. For each gilt, litter size and weight at birth and weaning were measured, with piglet weights at birth and weaning also recorded.

Statistical analysis

Additive genetic (co)variances for the gilt traits were estimated using an individual animal model. Full pedigree information was included in a multivariate residual maximum likelihood

(REML) analysis (Patterson and Thompson, 1971), using the REML algorithm of Meyer (1986). Additive genetic and common environmental (co)variances for individual piglet traits were estimated using an individual animal model in a multivariate derivative-free residual maximum likelihood (DFREML) analysis (Graser, Smith and Tier, 1987), adapted from the univariate DFREML algorithm of Meyer (1989), as proposed by Thompson and Hill (1990). For the estimation of variance components, fixed effects were not included in the analysis of gilt traits, as selection group-generation subclasses were confounded with months and years. Sex was included, as a fixed effect, in the analysis of piglet traits. Standard errors of heritabilities and common environmental effects were obtained using a similar procedure to Smith and Graser (1986). Standard errors of genetic correlations were estimated using the formulae of Robertson (1959).

The mortality of piglets, from birth to weaning, was not normally distributed and was analysed as a trait of the dam, using a generalised linear mixed model with binomial errors and a logistic link. The model was the marginal model of Breslow and Clayton (1993), fitted by the generalised linear mixed model procedure (Welham, 1994) for the GENSTAT statistical package (GENSTAT 5.3 Committee, 1993). Sires were included as random terms in the model with the selection group, line and generation subclass of each animal as fixed effects. The sire variance component was obtained from the generalised linear mixed model and the dam variance component was approximated from the estimate of the over-dispersion parameter, which was derived from the over-dispersed binomial variance using model III of Williams (1982). The residual variance on the logistic scale was equal to $p^2/3$ (Waddington, Welham, Gilmour and Thompson, 1994). The heritability of mortality, on the logistic scale, was calculated from estimates of the sire and dam variance components and the residual variance.

Maternal effects on litter size at birth were examined by daughter-dam regression, using a univariate DFREML (Meyer, 1989) analysis, including the litter size into which the dam was born as a linear covariate. Additive genetic effects, maternal genetic effects and the genetic covariance between the additive and maternal effects were estimated for the gilt traits using a univariate DFREML analysis as described by Meyer (1989).

A model including genetic group as a fixed effect was used to estimate the correlated responses at generation five, where genetic group corresponded to the selection group, line and generation subclass of each individual. Relationships between litter and piglet weights at birth and weaning with litter size at birth and weaning were examined to determine the relationship between litter size and weight and the existence of uterine constraints on pre-natal piglet growth and litter size.

Results

Correlated responses to selection

Means and phenotypic standard deviations for each trait are presented in Table 2.1. The observed mortality rate from birth to weaning included stillborn piglets and was comparable to the Meat and Livestock Commission (MLC) 1995 average (23.1 *v.* 20.4) (MLC, 1995). The total number of gilts farrowing and the number of piglets born and weaned by selection group are given in Table 2.2. The number of gilts farrowing in the LFC selection group was substantially less than in the other selection groups and consequently there were fewer piglets born and weaned. There were on average 20 fewer gilts farrowing in the LFC selection group in generations 2, 4 and 5, than in the DFI, LGS and LGA selection groups. In particular, in generations 4 and 5 the lower number of farrowing gilts was restricted to the LFC high line, the reasons for this are not yet apparent.

Litter size and weight at birth and weaning showed slight negative skewness (average -0.46 and -0.63, s.e. 0.14). When litters of less than four piglets at birth and less than two piglets at weaning were removed from the data set, the skewness coefficients were reduced (average

-0.05 and -0.16). It was not considered appropriate to transform the data to correct for skewness or to delete the small number of records contributing to the effect, as they proportionately comprised only 0.06 of the data. Individual piglet weights were normally distributed.

Table 2.1 *Means and phenotypic standard deviations of measured reproductive traits*

Trait		Mean	s.d.
Litter size at birth		10.3	2.9
Litter size at weaning		7.9	3.1
Mortality †	Observed (%)	23.1	-
	Logistic ‡	-1.2	0.5
Litter birth weight (kg)		12.9	3.6
Litter weaning weight (kg)		63.5	24.8
Piglet birth weight (kg)		1.3	0.3
Piglet weaning weight (kg)		8.1	2.0

† Mortality rate of piglets from birth to weaning x100 on the observed and logistic scale
‡ Mortality rate on the logistic scale equalled ln p(/1-p)

Table 2.2 *Total number of gilts farrowing, number of piglets born and weaned by selection group*

Selection group	Gilts farrowing	Piglets born	Piglets weaned
Daily food intake	330	3471	2580
Lean food conversion	246	2678	1980
Lean growth (*ad-lib*)	308	3146	2449
Lean growth (scale)	336	3735	2942

Table 2.3 *Estimates of selection line effects, within each selection group, for reproductive traits after five generations of selection for each selection group*

Selection		Litter size		Mortality †		Litter weight (kg)		Piglet weight (kg)	
group	line	Birth	Weaning	Obs	Logit	Birth	Weaning	Birth	Weaning
Daily	High	11.5	7.5	33	-0.7	13.2	63.5	1.10	8.5
food	Cont	11.1	8.9	19	-1.5	13.7	76.4	1.23	8.6
intake	Low	9.6	6.6	30	-0.9	10.2	46.0	1.05	7.2
Lean	High	9.1	7.1	21	-1.3	10.7	57.0	1.18	8.4
food	Cont	10.7	9.0	14	-1.8	13.7	68.5	1.31	7.9
conversion	Low	10.4	8.9	14	-1.8	13.5	74.3	1.26	8.4
Lean	High	10.9	8.6	20	-1.4	12.6	67.6	1.13	8.2
growth	Cont	10.8	9.2	13	-1.9	13.9	72.7	1.28	8.2
(*ad-lib*)	Low	9.9	8.4	15	-1.8	12.7	68.1	1.33	8.5
Lean	High	10.2	7.3	29	-0.9	14.0	56.6	1.38	7.9
growth	Cont	11.0	8.4	23	-1.2	13.8	67.8	1.25	8.0
(scale)	Low	9.6	8.1	15	-1.8	11.0	61.0	1.16	8.1
	s.e.d ‡	1.1	1.2	§	0.4	1.4	10.1	0.13	0.5

† Mortality rate from birth to weaning x 100 on the observed (Obs) and logistic (logit) scale

‡ Average standard error of the difference between the high and low selection lines at generation 5

§ Standard error not estimated as observations on a 0,1 scale

Correlated responses in reproductive performance after five generations of divergent selection for components of efficient lean growth are presented in Table 2.3. Differences between the high and low lines in litter size at birth and weaning were not statistically significant in the four selection groups (Table 2.3), although the low DFI and high LFC lines had lower litter sizes than the alternative lines. Although, average s.e.d. are presented in the

Tables, the significance of responses to selection were tested using the appropriate s.e.d. for each comparison. Mortality rate between birth and weaning was statistically significantly higher in the high LGS line than in the corresponding low line.

The highest incidence of postnatal death occurred when litter size at birth was low. There was a proportional reduction of 0.12 in mortality for every piglet increase in litter size at birth until litter size equalled 5 (Figure 2.1), after which there was a proportionate increase in mortality of 0.01 per unit increase in litter size. Piglet pre-weaning mortality decreased rapidly with increasing piglet birth weight, with mortality less than 0.10 for piglets with a birth weight greater than 1.5 kg (Figure 2.2).

The low DFI, high LFC and low LGS lines had significantly lower litter weights at birth, than the complementary selection lines and the control lines, but there were no responses in piglet birth weights. The high and low line differences in litter and piglet weaning weight were not statistically significant, except for the low DFI line, which had lighter piglets at weaning than in the high DFI and control lines (Table 2.3), with no difference in weaning age (1.5 days, s.e.d. 2.5).

Relationships between litter and individual piglet weights with litter size at birth and weaning

The essentially linear relationships between litter and piglet weights at birth and weaning with corresponding litter sizes are illustrated in Figures 2.3 and 2.4, respectively. At extreme litter sizes, variation in mean piglet weights, about the regression line, was a result of comparatively few observations at these points. The linear regression coefficients indicated a 1.0 kg (s.e. 0.02) increase in litter birth weight and a 6.9 kg (s.e. 0.1) increase in litter weaning weight for every piglet increase in litter size at birth and weaning, respectively. Conversely, with increased litter size, piglet birth and weaning weights decreased by 0.03 kg (s.e. 0.003) and 0.19 kg (s.e. 0.02) respectively. Within-selection group regression coefficients were not statistically different from each other or from the overall coefficients.

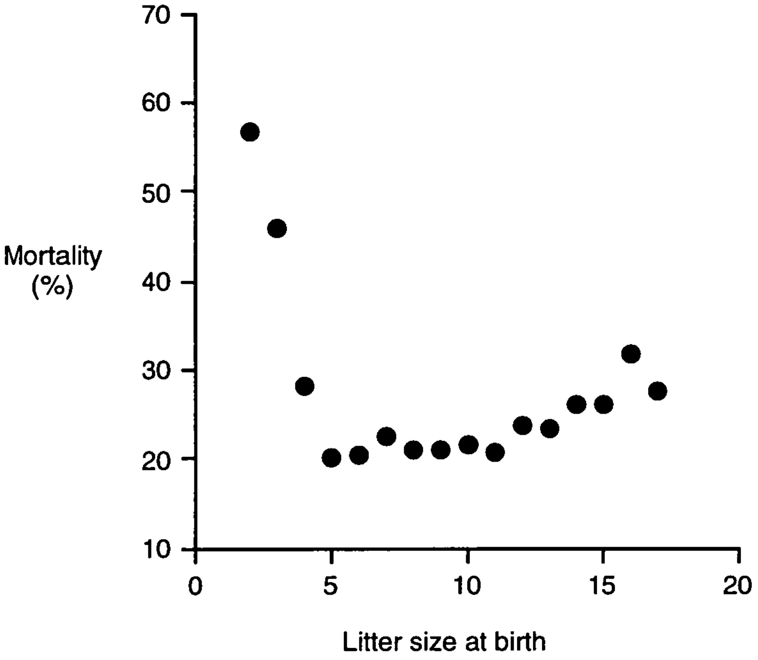

Figure 2.1. Pre-weaning mortality at a given litter size

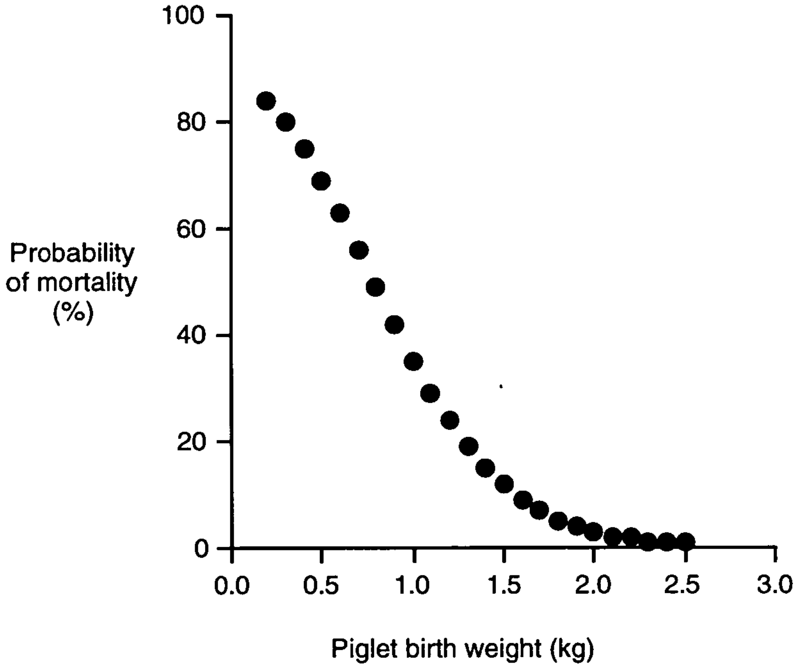

Figure 2.2. Pre-weaning mortality at a given birth weight

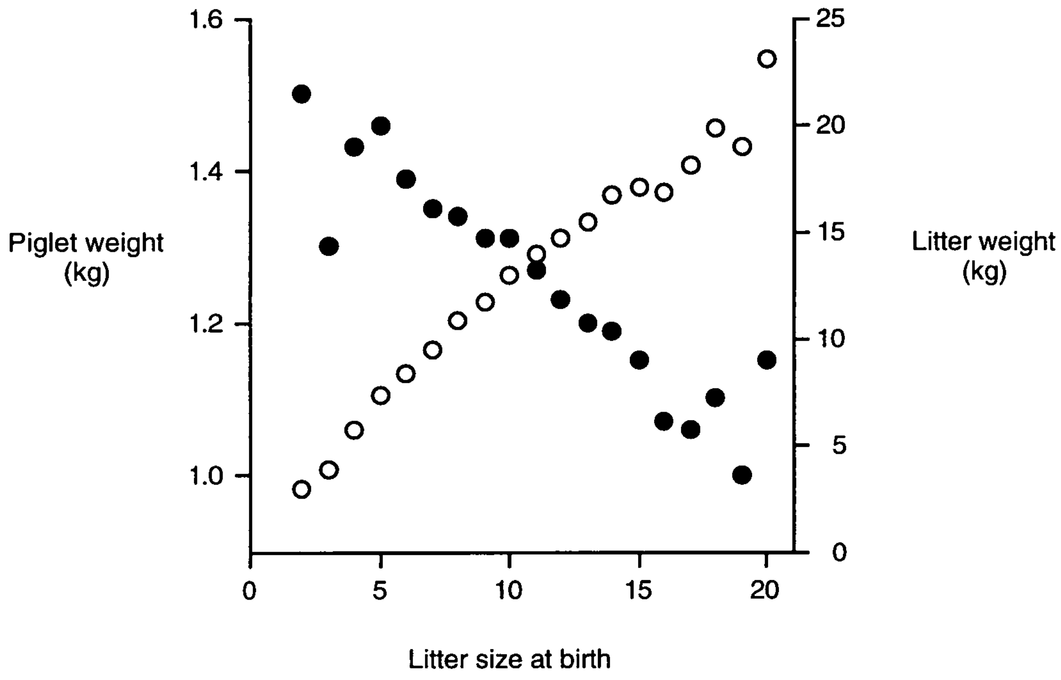

Figure 2.3. Average litter weight (○) and piglet weight at birth (●) with litter size at birth

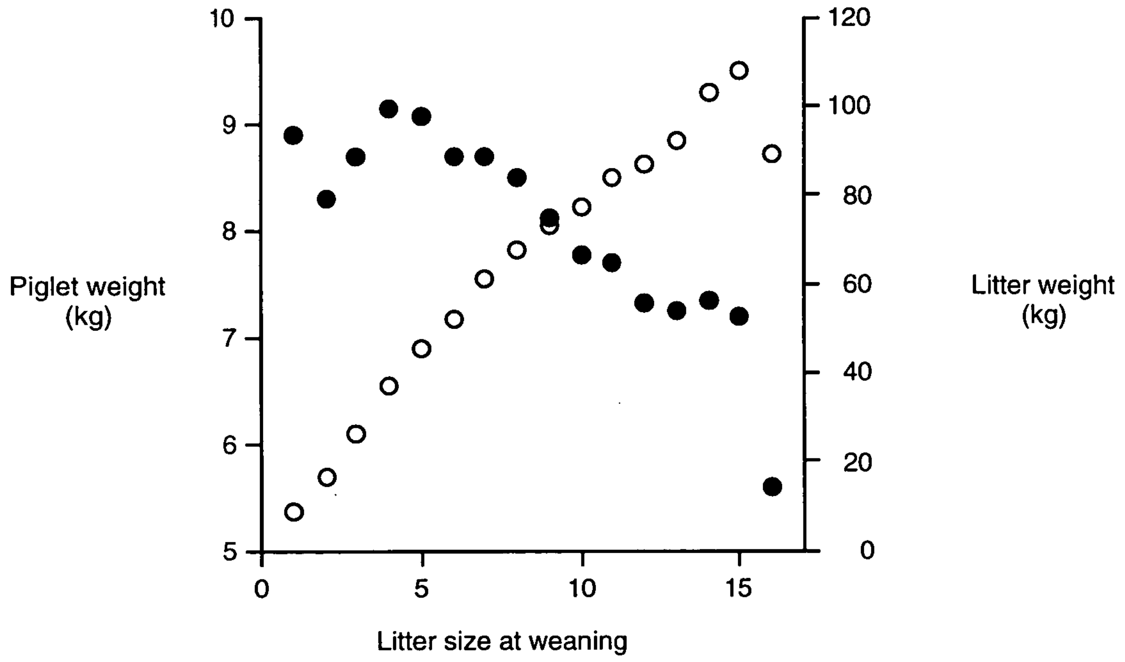

Figure 2.4. Average litter weight (O) and piglet weight at weaning ( ) with litter size at weaning

Table 2.4 *Comparison of linear and quadratic models including litter size at birth or weaning for litter weights*

Dependant trait	Covariate in Model	Variance components Genetic	Variance components Residual	R^2 †
Litter birth weight (kg)	-	1.47	11.8	11
	Linear	1.65	2.4	82
	Quadratic	1.66	2.2	84
Litter weaning weight (kg)	-	87.5	525.0	14
	Linear	22.4	113.1	82
	Quadratic	23.7	102.0	83

† R^2 = (Model sums of squares / total sums of squares) x 100

Incorporation of litter size as a covariate substantially increased the proportion of variation in litter weights at birth and weaning, which was accounted for by the model (Table 2.4). Linear adjustment of litter weight for litter size at birth and weaning markedly reduced residual variances of both traits and the genetic variance of litter weight at weaning, but there was little change in the genetic variance of litter weight at birth (Table 2.4). Estimates of variance components of piglet weights at birth and weaning were not changed by inclusion of a linear or quadratic term for litter size.

Adjustment of litter birth and weaning weights to constant litter sizes diminished the differences between the high and low selection lines in litter weight traits, except in the LGA selection group, while responses in the LGS and DFI groups for litter birth and weaning weights, respectively, remained (Table 2.5). Adjustment of piglet birth weight to constant litter size did not significantly change the magnitude of responses in any of the selection groups. Selection line differences in piglet weaning weights were unchanged when adjusted to constant litter size.

Table 2.5 *Comparison of high - low line differences in litter and piglet weights at birth and weaning when litter size at birth or weaning was included or not included as a covariate in the model*

Selection group	Litter wt (kg)				Piglet wt (kg)			
	Birth		Weaning		Birth		Weaning	
Litter size †	Includ	-	Includ	-	Includ	-	Includ	-
Daily food intake	0.8	3.0	11.3	17.5	0.14	-0.05	1.4	1.3
Lean food conversion	-1.3	-2.8	-3.9	-17.3	-0.13	-0.08	-0.3	0.0
Lean growth (*ad-lib*)	-1.1	-0.1	-1.8	-0.5	-0.08	-0.20	-0.2	-0.3
Lean growth (scale)	2.1	3.0	0.8	-4.4	0.27	0.22	-0.2	-0.2
s.e.d ‡	0.9	1.4	4.6	0.1	0.06	0.13	0.3	0.5

† Litter size included (includ) or not included (-) as a covariate in the model

‡ Average standard error of the difference between the high and low selection lines at generation 5

Genetic parameters

Heritabilities, genetic and phenotypic correlations for litter size and weights at birth and weaning are given in Table 2.6. Heritability estimates for litter size and weight were of similar magnitude at birth and at weaning. Phenotypic correlations between traits were high and positive. Genetic correlations were marginally lower than the phenotypic correlations, except for the genetic correlations between litter size at birth and litter weights.

Piglet birth and weaning weights had high positive phenotypic and genetic correlations (Table 2.7). Residual and common environmental correlations were of the same order of magnitude, with common environmental effects being substantially greater than the heritability estimates, especially for piglet weaning weights. Estimates of heritability and the common environmental effect from a univariate analysis of piglet birth weight were similar to estimates from a multivariate analysis (0.14, s.e. 0.02 and 0.37, s.e. 0.01). The heritability of mortality was estimated as 0.04 on the logistic scale.

Table 2.6 *Genetic and phenotypic parameter estimates for litter sizes and weights at birth and weaning*

Trait	NBORN	NWEAN	LBWt	LWWt
Litter size at birth (NBORN)	**0.06** †	0.69	0.84	0.55
Litter size at weaning (NWEAN)	0.53	**0.08**	0.72	0.88
Litter weight at birth (LBWt)	0.25	0.46	**0.11**	0.69
Litter weight at weaning (LWWt)	0.21	0.87	0.61	**0.14**

† Heritability estimates (in bold) on diagonal with phenotypic correlations (r_P) in upper triangle and genetic correlations (r_A) in lower triangle
s.e.(h^2) = 0.04, s.e. (r_P) = 0.02, average s.e. (r_A) = 0.24, except s.e. (r_A = 0.87) = 0.06

Table 2.7 *Genetic, phenotypic and common environmental parameters estimates for individual piglet weights at birth and weaning*

	Piglet weight (kg)	
Trait	Birth	Weaning
Genetic and Phenotypic		
Piglet birth weight (kg)	**0.16** †	0.46
Piglet weaning weight (kg)	0.67	**0.08**
Common environmental		
Piglet birth weight (kg)	**0.38** ‡	0.45
Piglet weaning weight (kg)	0.42	**0.45**

† Heritability estimates (in bold) on diagonal with phenotypic correlation (r_P) in upper triangle and genetic correlations (r_A) in lower triangle s.e. (h^2) = 0.02, s.e. (r_P) = 0.01, s.e. (r_A) = 0.09
‡ Common environmental effects (in bold) on diagonal with residual correlation (r_E) in upper triangle and common environmental correlation (r_C) in lower triangle s.e. (c^2) = 0.01, s.e. (r_E and r_C) = 0.01

Maternal effects, as estimated from daughter-dam regression coefficients (Table 2.8) on litter size at birth, were not significantly different from zero in any of the selection groups, although all estimates were non-positive. Similarly, estimates of maternal genetic effects of the dam for litter size and weights at birth and weaning were not significantly different from zero, as the difference between log likelihoods from models which included or did not include a maternal genetic effect were less than 1.0 for each trait.

Table 2.8 *Daughter-dam regression coefficients and maternal effects for litter size at birth, within each selection group*

Selection group	Regression coefficient	s.e.	Maternal effect
Daily food intake	-0.11	0.06	-0.14
Lean food conversion	-0.10	0.07	-0.13
Lean growth (*ad-lib*)	-0.10	0.07	-0.13
Lean growth (scale)	-0.01	0.07	-0.04

Discussion

Correlated responses to selection

Correlated responses in reproductive performance to divergent selection for components of efficient lean growth rate in Large White pigs have demonstrated that selection for particular aspects of efficient lean growth adversely affects reproductive performance. Litter size at birth and weaning were reduced with selection for low DFI or high LFC, but not in the complementary selection lines. Selection for low DFI also resulted in decreased piglet weaning weight. The asymmetric responses to selection, primarily in lines which have reduced daily food intake, suggest that low daily food intake during performance test is maintained during pregnancy, such that pre-natal piglet development is impaired. There were no significant responses in reproductive traits with divergent selection for LGA or LGS, except for decreased litter birth weight with selection for low LGS. Vangen (1980a) also found no difference in litter size and piglet weight at birth when pigs were divergently selected on an index based on growth and backfat, which was similar to the LGA selection criterion.

In several studies, it has been proposed that body composition is closely related to reproductive development and performance in pigs. For example, a negative genetic correlation between backfat and age at puberty was reported (Eliasson, Rydhmer, Einarsson and Andersson, 1991), while the estimated correlation between backfat and litter size was positive (Johansson and Kennedy, 1983). Similarly, Rydhmer, Johansson, Stern and Eliasson (1992) reported a positive and negative genetic correlation for pubertal age with leanness and growth rate, respectively. Results from the above studies support the suggestion of Kirkwood and Aherne (1985) that selection for carcass lean content may be indicative of selection for increased mature size, which, at a given age, produces a physiologically younger animal with a later onset of puberty, implying reduced reproductive performance compared to fatter animals at the same age. Therefore, an experiment has now been established to specifically examine the relationships between sow body composition at mating with subsequent litter size and piglet performance, in each of the four selection groups. The results from this experiment will be reported in a subsequent paper.

Vangen (1972) and Mersmann, Pond, Stone, Yen and Lindvall (1984) reported that the pre-weaning mortality rate was greater in piglets born to leaner rather than fatter dams. Mersmann *et al* (1984) suggested that fatter sows may provide more energy or critical nutrients to new born pigs, through a greater concentration of lipid in milk, which may influence their survivability. Increased pre-weaning mortality may also be attributed to higher restlessness observed in leaner sows (Vangen, 1980b; McKay, 1993). Results from the current study were similar to those of Vangen (1972), that a higher rate of pre-weaning mortality was associated with low piglet birth weight and high litter size. In contrast, the high mortality in litters of less than five piglets was not closely related to birth weight.

Adjustment of litter and piglet weights for litter size at birth and weaning

Inclusion of litter size as a covariate in the model for litter and piglet weight at birth and weaning indicated that the relationships between these traits were essentially linear. Similar results have been reported by Crump (1992). Between-litter variation in piglet weights was larger when litters were small, but there were comparatively fewer records at extreme litter sizes. A substantial amount of variation in litter weights at birth and weaning was attributed to litter size. For example, responses in litter weights at birth in the DFI and LFC selection groups were mainly due to changes in litter size. However, in the LGS selection group, heavier litter weights at birth were primarily due to heavier piglets at birth, while the response in litter weight at weaning in the DFI selection group was attributable to both differences in litter size and piglet weight.

The negative relationship between piglet weight and litter size at birth implies a uterine constraint on pre-natal piglet growth, due to increased competition among embryos/foetuses for uterine resources (Christenson, Leymaster and Young, 1987). The positive linear relationship between litter weight and litter size at birth, with litter size ranging from one to 20 piglets, does not support the suggestion of an upper limit to uterine capacity, defined as the maximum number of foetuses that an individual can carry to term (Bennett and Leymaster, 1989). However, the existence of uterine constraints on pre-natal piglet growth may be implied by the magnitude of the regression coefficient, which was significantly less than the average piglet weight at birth.

Genetic parameters

The parameter estimates may be biased as reproductive traits were measured on selected females only and that selection was based on their performance in non-reproductive traits. The effect of selection on genetic parameter estimates for correlated traits has been well documented (Meyer and Thompson, 1984; Sorensen and Kennedy, 1984). In a univariate situation, inclusion of a complete relationship matrix in a REML analysis can take account of the effect of selection (Sorensen and Kennedy, 1986; Kennedy, 1990). Although all pedigree information was included in the model, selection on several traits may induce bias in genetic parameter estimates (Sorensen and Johansson, 1992). Therefore, genetic and phenotypic relationships between performance test and reproductive traits will be estimated in a multivariate analysis, in a subsequent study.

The reported selection line differences in reproductive traits were estimated from measurements on selected gilts within each selection line, rather than from all gilts within a line, such that the selection line differences may be overestimated. The extent of overestimation is a function of the selection differential in the last generation and the phenotypic regression of the reproductive trait on the selection criterion. In the experimental design, 20 out of 50 gilts were selected from the high and low lines each generation, such that the maximum selection differential was 1.9 σ_P. Therefore, the maximum value for the over-estimate of the response, as a result of only measuring selected females, will be 1.9 r_p σ_P, where r_p and σ_P are the phenotypic correlation and standard deviation respectively. For example, in the DFI selection group, given a preliminary estimate of the phenotypic correlation between daily food intake and litter weight at weaning of 0.07, the lower limit for the response would be 14.2 kg compared with the measured response in litter weaning weight of 17.5 kg.

Heritability estimates for litter size were similar to those of previous studies (see review of Haley *et al*, 1988). Similarly, heritability estimates for litter and piglet weights at birth and weaning were consistent with estimates of Vangen (1980b) and Crump (1992). Common environmental effects for piglet weights were substantially larger than heritability estimates, which indicated a high intraclass correlation between litter mates. The similarity between litter mates is expected as birth weights are influenced by uterine constraints and litter size, while weaning weights will be limited by nutrient supply from the dam. The low heritability estimate, on the logistic scale, for pre-weaning mortality suggests that there is little potential for genetic improvement in pre-weaning mortality with either direct or indirect selection. It may be more effective to select for reduced variation in litter size, rather than selecting for increased litter size, given that mortality increases with litter size and that the genetic effect on mortality is negligible.

Regression coefficients of the litter size an animal produced on the litter size into which it was born, from the current study were similar within each *ad-libitum* fed selection group and to those of Rutledge (1980). The regression coefficient is equal to $[h^2/(2-m)]+m$, where h^2 is the heritability of litter size and m is the maternal effect (Falconer, 1965). The average maternal effect for the three *ad-libitum* fed selection groups was equal to -0.13, such that an increase of one pig in the litter of the dam would result in a reduction of 0.13 pigs in her daughters' litters. The estimate of the maternal effect from the current study was of the same order of magnitude as that of Van der Steen (1985). Standardisation of litters at birth, through cross fostering, was suggested by Van der Steen (1985) to reduce the negative maternal influence on an animal's subsequent litter size. Given the negative relationship of litter size with piglet birth and weaning weights it may be necessary to take account of the post-natal maternal effect when selecting for piglet growth traits. However, selection line differences in piglet weights and estimates of genetic and residual variances at both birth and weaning were unchanged, when adjusted to constant litter size, which is analogous to standardisation of litter size at birth as suggested by Van der Steen (1985). The adjusted selection line differences provide little evidence to suggest that selection for piglet growth will be adversely affected by maternal effects.

There was no evidence of maternal genetic effects for litter size and weights at birth and weaning in the present study, which was consistent with results of Haley and Lee (1992). However, Southwood and Kennedy (1990) reported significant maternal genetic effects for litter size at birth and weaning, although the magnitude of the effects was dependent on the dam's genotype. There are few estimates of maternal genetic effects, but the above studies suggest that the relative importance of maternal genetic effects may be population specific and dependent on both the data structure and the method of analysis.

The study has indicated that selection for lean growth on either an *ad-libitum* or restricted feeding regime did not significantly affect reproductive performance, while animals in the high lean food conversion ratio or low daily food intake lines had reduced reproductive performance. However, to understand the biological basis for responses in litter size, measurements of additional traits are necessary. Weight and ultrasonic backfat depth at mating need to be measured to establish the relationship between body composition of the sow with conception rate, litter size and piglet growth. Laparoscopic measurement of ovulation rate is required to assess potential litter size and embryo survival. The responses in reproductive performance have implications for the design of breeding programmes. Genetic and phenotypic relationships between performance test and reproductive traits will be estimated in a subsequent study, as prediction of responses in reproductive traits is required for the design of breeding programmes based on selection for growth and carcass traits.

Chapter 3

Genetic and phenotypic relationships between performance test and reproduction traits

Introduction

Evaluation of selection programmes for improvement in components of efficient lean growth in pigs should be based on both the correlated responses in growth and carcass traits and the responses in reproductive performance. Results from selection experiments for increased growth rate and reduced backfat depth have indicated either small positive (Vangen, 1980a; Fredeen and Mikami, 1986c) or negligible responses (DeNise, Irvin, Swiger and Plimpton, 1983; Cleveland, Johnson and Cunningham, 1988) in reproduction traits.

Estimates of genetic correlations between performance test and reproduction traits from different studies have been variable in both sign and magnitude. For example, genetic correlation estimates for backfat depth with litter size at birth have been positive (0.24, Johansson and Kennedy, 1983), negative (-0.32, Vangen, 1980a) or zero (0.07, Crump, 1992). The estimates from each of the studies however, were not significantly different from zero and differences between studies were not significant.

In chapter 2 it was reported that selection of pigs for low daily food intake or high lean food conversion had impaired reproductive performance after five generations of selection, through different combinations of reduced litter size and weight. The correlated responses to selection provided qualitative information on the effect of alternative selection strategies, but not the quantitative information that is required to evaluate selection strategies. In chapter 2 it was concluded that precise estimates of the genetic and phenotypic relationships between performance test and reproduction traits were required for reliable evaluation of alternative selection strategies, to take account of responses in both growth and reproduction traits.

In the current chapter the genetic and phenotypic relationships between performance test and reproduction traits were estimated in a population of Large White pigs after five generations of divergent selection for components of efficient lean growth rate.

Material and methods

Animals

Performance test and reproduction data were collected from five generations of pigs, divergently selected for daily food intake (DFI), lean food conversion (LFC) and lean growth rate (LGA) on an *ad-libitum* feeding regime and for lean growth rate on a restricted feeding regime (LGS). Details of the establishment of the selection lines are given in chapter 2.

After five generations of selection, 4334 *ad-libitum* fed and 1558 restricted fed pigs had been performance tested. In each selection group, animals were selected on the basis of performance test traits and therefore only a subset of performance tested gilts had measurements on reproduction traits. In total, 884 gilts tested in the *ad-libitum* fed selection groups and 336 gilts tested in the restricted fed selection group had farrowing information.

Selection objectives and criteria

The selection objectives were to obtain equal correlated responses, measured in phenotypic standard deviation units, in carcass lean content and growth rate (or food conversion ratio) in the LGA and LGS (or LFC) selection groups. In the DFI selection group, the selection objective was daily food intake. In the LGA, LGS and LFC selection groups, animals were selected on indices combining measurements of performance test traits

(Cameron, 1994; Cameron, Curran and Kerr, 1994). Selection in the high, low and control lines of each selection group was based on both the selection criterion value and on the parentage of the animal, the latter to reduce variation in inbreeding coefficients, such that selection was partially on a within-sire basis rather than solely on mass selection.

Performance test

During the performance test, animals were individually penned and fed a pelleted diet consisting of 224g crude protein per kg dry matter (DM) and 159 MJ digestible energy (DE) per kg DM. Pigs on both feeding regimes started test at 30±3 kg. *Ad-libitum* fed pigs finished test at 85±5 kg and restricted fed pigs were tested for 84 days. The food intake of the restricted fed pigs was determined by the time on test and was intended to be 0.75 g/g of the daily food intake of *ad-libitum* fed pigs. At the end of test, ultrasonic measurements of backfat depth were taken 6.5 cm off the mid-line at the shoulder, mid-back (analogous to P2 carcass measurement) and loin on both sides of the pig.

Reproduction traits

Selected gilts were mated between 9 and 10 months of age, approximately four months after the end of the performance test. Matings were unsupervised and took place in outside paddocks. Individual boars were run with three gilts for six weeks and were inspected on a regular basis, so that inactive boars could be replaced. Pregnant gilts were fed 2.5 kg daily and farrowed sows were fed to appetite a ration consisting of 184 g crude protein per kg DM and 15.2 MJ DE per kg DM. Sows were farrowed in selection group batches at an average of 414 (s.d. 19) days of age. No cross fostering was practised. Piglets were offered creep feed containing 264 g crude protein per kg DM and 18.0 MJ DE/ per kg DM from 14 days of age and were weaned at an average of 35 (s.d. 3) days. For each gilt, litter size and weight at both birth and weaning were measured.

Statistical analysis

Genetic (co)variances and environmental (co)variances for performance test and reproduction traits, were estimated using a modification (Juga and Thompson, 1993; Thompson, Crump, Juga and Visscher, 1995) of the bivariate derivative free residual maximum likelihood (DFREML) (Graser, Smith and Tier, 1987) algorithm. Within each pair of traits, the method of Thompson *et al* (1995) enabled inclusion of different fixed and random effect structures in the model for each trait. Data from the three selection groups with *ad-libitum* feeding, DFI, LFC and LGA, were combined and analyses of data for the two feeding regimes were carried out separately. In each analysis, data from all performance tested boars and gilts was combined with the reproduction data of farrowing gilts with the full relationship matrix for all animals, including the base population, incorporated in the analyses.

For *ad-libitum* fed pigs, the maximum of the log likelihood (log L) was evaluated using the Simplex method and iterations were assumed to have converged when the variance of the values of -2 log L, which were stored in the Simplex, was less than 10^{-8}. Standard errors of heritabilities and genetic correlations were obtained using a similar procedure to that of Smith and Graser (1986).

For restricted fed pigs, performance test and litter traits at birth were analysed using the same method as for *ad-libitum* fed pigs. Estimation of genetic and phenotypic (co)variances between performance test and litter traits at weaning was problematic using the DFREML methodology, as on several iterative steps, the genetic variance-covariance matrix on the canonical scale was not positive-definite. Therefore, heritabilities of performance test traits were estimated using multivariate DFREML and the remaining parameters were estimated using a grid search procedure, with log L evaluated over a grid of values, defined by values for the heritability of the reproduction trait and the coheritability of the performance test and reproduction trait, to identify the parameters which maximised log L, with the heritability of the performance test trait fixed.

Sex, testing shed and month of performance test were included as fixed effects for performance test traits. In the analysis of reproduction traits, no fixed effects were included, as selection group-generation subclasses were confounded with month and year of farrowing. For the *ad-libitum* fed pigs, end of test weight was included as a covariate in the analyses of backfat traits with weights at the start and end of test included as covariates for total food intake and days on test. For restricted fed pigs, weight at the start of test was included as a covariate in the analyses of weight off test and backfat depths. Common environmental effects were included in the models for performance test traits. The environmental covariance between performance test and reproduction traits was included in the model, as an additional random effect, since farrowing gilts had measurements on both performance test and reproduction traits.

Effect of selection on bias and precision of parameter estimates

Analysis of data collected only from selected gilts would result in biased estimates of the genetic parameters (Meyer and Thompson, 1984; Sorensen and Johansson, 1992), as selection was based on performance test traits, only a subset of animals had measurements on reproduction traits. Genetic (co)variances and environmental (co)variances for performance test and reproduction traits were therefore estimated in two subsets of the data from the *ad-libitum* fed selection groups : (1) all 2170 performance tested gilts, such that only a subset of animals had records on both performance test and reproduction traits and (2) the 884 selected gilts with measurements on both performance test and reproduction traits. In the complete data set, containing all performance tested boars and gilts from the *ad-libitum* fed selection groups, the full relationship matrix for all animals, including the base population, was incorporated in the analysis. In the analyses of the two data subsets, the relationship matrix was reduced to consist only of pedigree information for the animals with records. Standard errors of genetic correlations were obtained using a similar procedure to that of Smith and Graser (1986).

Results

For *ad-libitum* fed pigs, the number of animals performance tested in each selection group was similar (Table 3.1).

Table 3.1 *Number of animals with performance test and reproduction records in each selection group*

	Performance test			Reproduction
Selection group	Boars	Gilts	Total	
Daily food intake	740	723	1463	330
Lean food conversion	736	721	1457	246
Lean growth (*ad-libitum*)	688	726	1414	308
Lean growth (restricted)	771	787	1558	336

However, the number of litter records in the LFC selection group was lower than in the DFI and LGA groups, due to fewer farrowing gilts in the high LFC line. The means and phenotypic s.d. of performance test and reproduction traits for *ad-libitum* and restricted fed pigs are presented in Tables 3.2 and 3.3, respectively. Restricted fed pigs had lower growth rate, higher total food intake, but similar backfat depths to *ad-libitum* fed pigs, but there were no substantial differences between *ad-libitum* and restricted fed pigs in reproduction traits. After five generations of selection, the mean inbreeding coefficients of 7.6% and 7.3% for the high and low selection lines were similar both within and between-selection groups, but higher than the mean inbreeding coefficient of 3.1% for the control lines, as a consequence of the experimental design (The s.d. for the inbreeding coefficients of the high, low and controls were similar, 2.4, 2.6 and 2.7 respectively).

Table 3.2 *Means and phenotypic standard deviations of performance test traits for the ad-libitum and restricted fed pigs by selection group*

Feeding regime	Ad-libitum						Restricted	
Selection group	Daily food intake (DFI)		Lean food conversion (LFC)		Lean growth (LGA)		Lean growth (LGS)	
	Mean	s.d.	Mean	s.d	Mean	s.d	Mean	s.d.
Daily food (kg)	1.94	0.27	1.91	0.25	1.93	0.26		
Ave daily gain (g/day)	835	124	824	118	811	118	709	77
Food conversion	2.35	0.29	2.34	0.30	2.40	0.31		
Weight off test (kg)							88.8	6.6
Total food (kg)	124	16.2	124	16.5	126	17.5	134	
Days on test	64.6	10.6	65.8	10.3	66.3	10.7	84	
Shldr backfat (mm)	27.3	2.2	26.8	4.5	26.9	4.3	26.0	4.1
Mid backfat (mm)	13.7	2.6	13.5	2.7	13.4	2.6	12.8	2.2
Loin backfat (mm)	14.4	3.1	14.3	3.3	14.1	3.0	12.8	2.6
Ave backfat (mm)	18.5	3.1	18.2	3.3	18.1	3.0	17.2	2.7

Table 3.3 *Means and phenotypic standard deviations of reproduction traits for ad-libitum and restricted fed pigs by selection group*

Feeding regime	Ad-libitum						Restricted	
Selection group	Daily food intake (DFI)		Lean food conversion (LFC)		Lean growth (LGA)		Lean growth (LGS)	
	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
Litter size birth	10.6	2.8	10.1	3.2	10.2	2.9	10.4	2.8
Litter size weaning	7.9	3.2	7.5	3.3	8.0	3.0	8.2	3.0
Litter birth wt (kg)	12.6	3.5	12.4	3.9	12.8	3.5	13.8	3.5
Litter weaning wt (kg)	60.6	24.5	60.2	26.1	64.7	23.7	67.7	24.1

Table 3.4 *Heritability (h^2) and common environmental effect (c^2) estimates (x 100) of performance test traits for ad-libitum and restricted fed pigs*

Feeding regime	*Ad-libitum*		Restricted	
	h^2	c^2	h^2	c^2
Daily food intake (kg)	24	9		
Average daily gain (kg)	31	12	23	1
Food conversion ratio	17	6		
Weight off test (kg)			22	4
Total food intake (kg)	16	6		
Days on test	26	11		
Shoulder backfat (mm)	48	9	31	1
Mid backfat (mm)	44	10	41	6
Loin backfat (mm)	39	10	35	8
Average backfat (mm)	46	10	34	9
Average s.e.	3	1	4	2

Growth rate and backfat depths were qualitatively similar traits on the two feeding regimes, but the heritability estimates of growth rate and shoulder backfat depth were lower on restricted feeding than on *ad-libitum* feeding (Table 3.4). The heritability estimates for mid-back and loin fat depth were similar for the two feeding regimes. Common environmental effects for performance test traits of *ad-libitum* and restricted fed pigs were of similar magnitude, except for the low value for growth rate of restricted fed pigs (Table 3.4). Heritability estimates of reproduction traits for *ad-libitum* fed pigs were similar (Table 3.5). For restricted fed pigs, the heritability estimates of litter traits at weaning were significantly lower than those at birth.

Table 3.5 *Heritability estimates (x 100) for reproduction traits in the ad-libitum and restricted fed pigs*

Feeding regime	*Ad-libitum*	Restricted
Litter size at birth	10	21
Litter size at weaning	13	2
Litter weight at birth (kg)	9	23
Litter weight at weaning (kg)	16	4
Average s.e.	5	8

Estimates of the genetic, environmental and phenotypic correlations for performance test and reproduction traits of *ad-libitum* fed pigs are given in Table 3.6. Genetic correlations for reproduction traits with daily food intake and growth rate were positive, but were negative with days on test. The genetic correlations for reproduction traits with days on test were similar in magnitude but of opposite sign to the correlations with growth rate, as the performance test was on a fixed weight basis. Food conversion ratio was negatively correlated with reproduction traits, but the estimates were not significantly different from zero.

Litter weight traits were generally more highly correlated with performance test traits, than were litter size at birth and weaning, although the differences were not significant. Genetic correlations between backfat depths and reproduction traits were also not significantly different from zero. Environmental and phenotypic correlations were all less than 0.10 in magnitude and were substantially lower than the estimates of the genetic correlations.

Table 3.6 *Correlations (x 100) between performance test traits and reproduction traits for the ad-libitum fed selection groups*

	Litter size at birth			Litter size at weaning			Litter weight at birth			Litter weight at weaning		
	r_A †	r_E	r_P	r_A	r_E	r_P	r_A	r_E	r_P	r_A	r_E	r_P
Daily food intake	23	3	6	21	3	6	48	-4	4	42	-2	7
Average daily gain	44	7	-1	31	1	7	65	-8	6	52	-4	10
Food conversion ratio	-19	3	0	-7	3	1	-23	3	0	-11	1	-1
s.e.	19			18			18			15		
Total food intake	18	3	5	-10	3	1	18	4	6	-13	1	-1
Days on test	-48	-3	-5	-40	3	-5	-65	9	-4	-56	6	-8
s.e.	18			18			15			14		
Shoulder backfat	4	2	2	20	4	1	-8	7	-2	21	4	7
Mid backfat	-18	6	0	-6	4	7	-29	3	1	0	3	2
Loin backfat	-12	4	1	4	0	1	-20	4	-1	7	1	2
Average backfat	-8	4	1	9	2	4	-18	5	0	11	3	5
s.e.	14			13			15			12		

† : r_A, r_E and r_P are the genetic, environmental and phenotypic correlations

For restricted fed pigs, litter weight at birth was positively genetically correlated with growth rate and negatively correlated with backfat depths (Table 3.7), but correlations for litter size at birth were not significantly different from zero. Phenotypic correlations were generally of the same sign as the genetic correlations, but the environmental and phenotypic correlations were less than 0.15 in magnitude.

Table 3.7 *Correlations (x 100) between performance test and reproduction traits at birth for restricted fed pigs*

	Litter size at birth			Litter weight at birth		
	r_A †	r_E	r_P	r_A	r_E	r_P
Average daily gain	20	5	8	50	4	14
s.e.	20			18		
Shoulder backfat	8	7	7	-42	1	-10
Mid backfat	-1	6	3	-41	9	-6
Loin backfat	4	3	1	-42	11	-5
Average backfat	5	5	5	-48	0	-14
s.e.	18			16		

‡ r_A, r_E and r_P are the genetic, environmental and phenotypic correlations

Bivariate DFREML analyses of performance test traits with litter size or weight at weaning was problematic, for restricted fed pigs, with genetic correlation estimates essentially equal to one. Reanalysis of litter traits at weaning, using the grid search procedure, resulted in the log likelihoods being maximised when the heritability estimates were negative. However, in univariate analyses of litter traits at weaning, the heritability estimates were 0.02 and 0.04 (Table 3.5), respectively, and the standard errors of the estimates, determined using a quadratic regression of the log likelihood on the heritability estimate, were 0.20. Assuming the estimated heritability of litter size at weaning was normally distributed with a mean of 0.02

and standard error of 0.20, then the probability of obtaining a negative heritability estimate would be 0.46. Since the log likelihoods were maximised with negative heritabilities for litter traits at weaning, the estimated genetic correlations between performance test and litter weaning traits were unreliable and, therefore, they have not been presented.

Relationships between performance test and reproduction traits

Estimation of genetic correlations between traits measures the linear relationship between the traits. The relationship between performance test and reproduction traits was examined to test the validity of the assumption. Predicted breeding values of performance test and reproduction traits were estimated, for 884 selected gilts, using the genetic and phenotypic parameters estimated in univariate analyses of the traits. The proportional reductions in the variance of predicted breeding values for reproduction traits attributable to linear and non-linear regressions on predicted breeding values for the performance test trait were used to quantify the extent of the linear and non-linear relationships. There was no evidence to reject the assumption that the relationship between predicted breeding values of daily food intake (Figure 3.1) and growth rate (Figure 3.2) with reproduction traits were linear. For example, the proportional reductions in the variance of predicted breeding values for reproduction traits due to linear and non-linear regressions on growth rate were 0.15 and 0.16, respectively. However, the between-selection line variation in backfat depth enabled detection of a non-linear relationship between average backfat depth and litter weight at birth, for farrowing gilts tested on *ad-libitum* feeding. Figure 3.3 clearly shows a non-linear relationship between the selection line means for average backfat depth and the selection line means for litter weight at birth. The relationship between the predicted breeding values for average backfat depth and the predicted breeding values for litter weight at birth was also non-linear. In Figure 3.4, the predicted breeding values for backfat depth have been grouped into categories with intervals of 0.5 mm and each point represents the average predicted breeding value for litter birth weight corresponding to each of the backfat categories. The proportion of variation in litter weight attributable to linear and non-linear

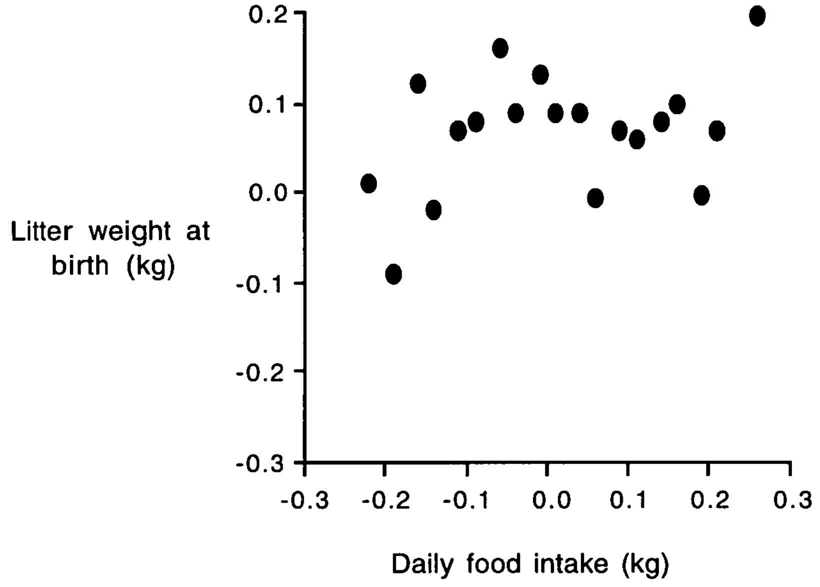

Figure 3.1. Estimated breeding values for daily food intake with estimated breeding values for litter weight at birth for the ad-libitum selection groups

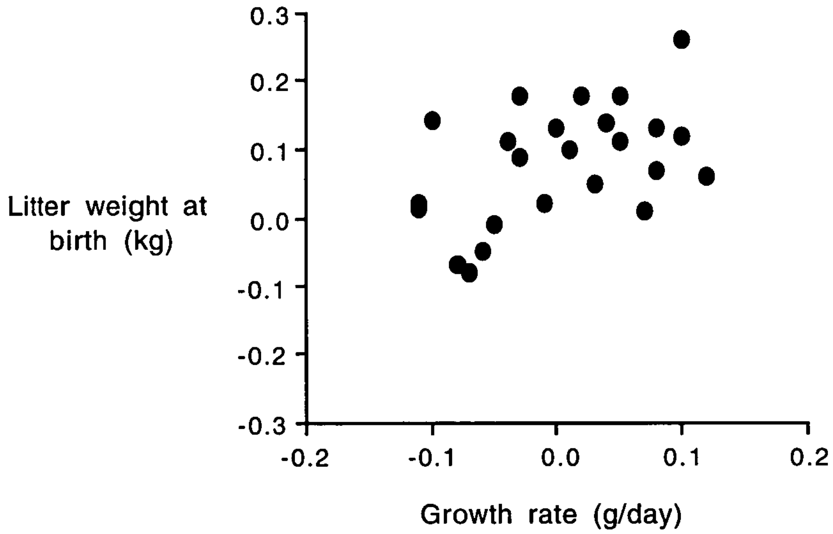

Figure 3.2. Estimated breeding values for growth rate with estimated breeding values for litter weight at birth for the ad-libitum selection groups

The estimated breeding values for daily food intake and growth rate have been grouped into categories with intervals of 250g and 100g for daily food intake and growth rate respectivey and each point on the graphs represent the average litter weights in each of the categories

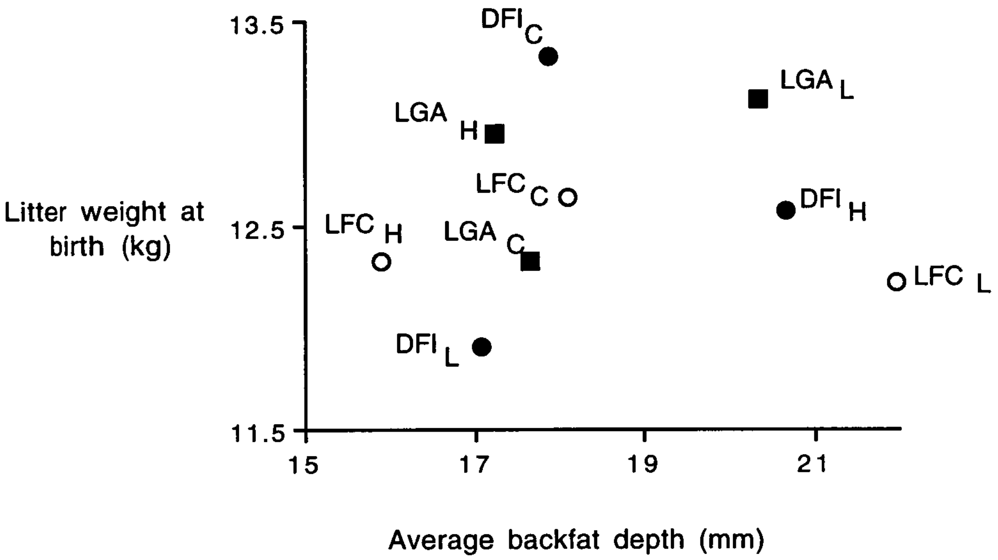

Figure 3.3 Selection line means for average backfat depth and litter weight at birth for the high (H), low (L) and control (C) lines of the daily food intake (DFI), lean food conversion (LFC) and lean growth (LGA) on ad-libitum feeding selection groups

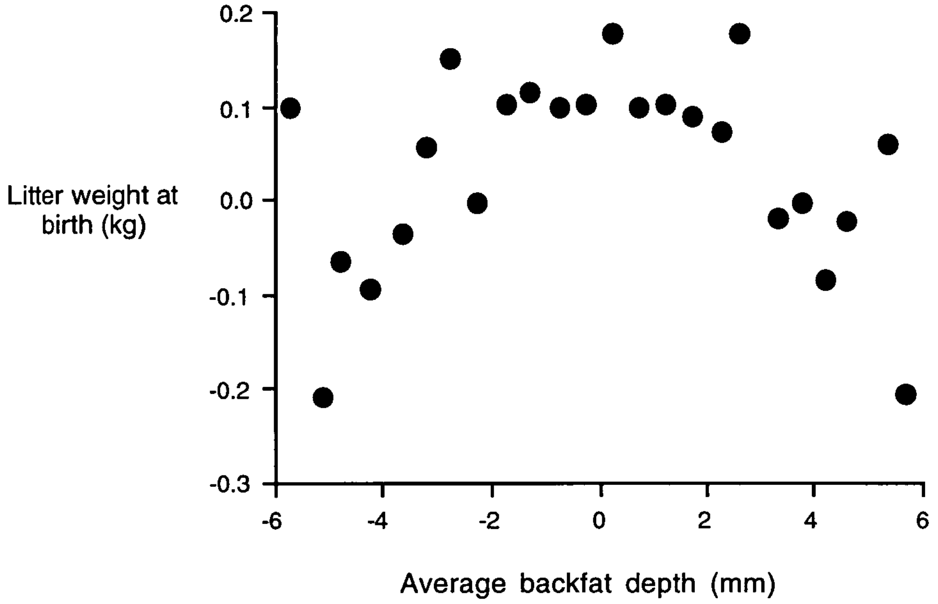

Figure 3.4 Estimated breeding values for average backfat depth with estimated breeding values for litter weight at birth for the ad-libitum selection groups

regressions was 0.00 and 0.42, respectively. In contrast, the linear and non-linear regressions of litter weight at birth on average backfat depth for restricted fed pigs accounted for similar proportions of variation, 0.10 and 0.13.

Table 3.8 *Genetic correlations between performance test traits with litter size and weight at birth estimated from the complete data and two subsets of the data*

	Litter size at birth			Litter weight at birth		
Data set	Boars and gilts	All gilts	Farrowing gilts only	Boars and gilts	All gilts	Farrowing gilts only
Daily food intake	0.23	0.15	-0.07	0.48	0.34	0.00
Average daily gain	0.44	0.20	0.17	0.65	0.56	0.33
Food conversion	-0.19	-0.08	-0.34	-0.23	-0.30	-0.46
Mid-back fat depth	-0.18	-0.12	-0.21	-0.29	-0.30	-0.33
	s.e.(r_A) †	relative s.e. ‡		s.e.(r_A) †	relative s.e. ‡	
Daily food intake	0.20	1.19	1.34	0.18	0.98	1.07
Average daily gain	0.19	1.17	1.36	0.15	0.89	0.97
Food conversion	0.19	1.13	1.18	0.20	1.10	1.15
Mid-back fat depth	0.13	1.06	1.14	0.14	1.02	1.06

† s.e. of genetic correlation (r_A)estimate

‡ s.e.(r_A) data on boars and gilts / s.e.(r_A) for subset of data

Effect of selection on bias and precision of parameter estimates

Genetic correlations for performance test traits with litter size and weight at birth estimated from the three data sets are given in Table 3.8. Assuming that analysis of the complete data set, with records on all performance tested boars and gilts, resulted in unbiased estimates of the genetic correlations, then exclusion from the analyses of boars or gilts with no reproduction records, resulted in negatively biased genetic correlation estimates. There was substantial negative bias in the correlation estimates for daily food intake and average daily gain with reproduction traits and to a lesser extent for food conversion ratio. In contrast, the precision of estimated genetic correlations for performance test traits with litter size and weight at birth was indirectly related to the number of animals, with only performance test records, since the genetic covariance estimate was a function of the predicted breeding values for both traits.

Discussion

For *ad-libitum* fed pigs, the genetic correlation estimates for growth rate and daily food intake with litter traits at birth and weaning were positive, while those with food conversion ratio were negative, but not significantly different from zero. Litter weights at birth and weaning were more highly correlated with growth rate and daily food intake than the corresponding litter sizes. Heritability estimates of litter size and weight at birth and weaning were of similar order of magnitude. The positive association between growth rate and daily food intake with litter traits and the relatively similar heritabilities for litter sizes and weights, suggested that selection strategies which change growth and daily food intake may result in relatively greater genetic changes in piglet growth rate than in litter size.

Genetic and phenotypic parameters

Comparison of the results from the current study with those from previous experiments is difficult as there are few estimates of genetic correlations between performance test and reproduction traits, particularly for gilts, and estimates from different studies have not been consistent (Table 3.9). Johansson and Kennedy (1983) reported negative genetic correlations, between gilt litter size at birth and age to a fixed weight, which was indicative of a positive correlation with growth rate. In contrast, the average of the within-line estimates of the genetic correlations for growth rate and daily food intake with number born, for first parity sows, reported by Short, Wilson and McLaren (1994), were less than 0.1 in magnitude. Crump (1992) reported small genetic correlations for growth and daily food intake with number of piglets born alive. The estimated genetic correlations for growth rate and litter size of Vangen (1980) were positive, for first and second parity sows, but the estimates were smaller than the standard errors. Similarly, estimates of genetic correlations between backfat depth and the reproductive performance of gilts have varied substantially between studies. Johansson and Kennedy (1983) reported positive correlations with litter size at birth and weaning, while the estimates of Short *et al* (1994) and Rydhmer, Lundeheim and Johansson (1995) were not different from zero. The estimates of Vangen (1980a) were negative for backfat with litter size at birth, but were essentially zero for litter size at weaning.

Table 3.9 *Summary of the genetic correlation estimates (x100) between performance test traits and litter size at birth and weaning (standard errors in parenthesis)*

	Growth rate		Backfat depth		Daily food intake
Study	Litter size birth	Litter size weaning	Litter size birth	Litter size weaning	Litter size birth
Vangen (1980a)	11 (42)	36 (36)	-32 (30)	-6 (31)	
Johansson and Kennedy (1983)			24	21	
Crump (1992)	-2.9 (14)		7 (12)		7 (15)
Short *et al* (1994)	5 (3)		3 (3)		-1 (3)
Rydhmer *et al* (1995)	-1 (10)		-11 (10)		

One interpretation of the between-study variation in the sign and magnitude of the genetic correlations between growth rate and daily food intake on test with reproductive performance is that the parameter estimates are population specific, due to the confounding of selection strategy, population and environment within experiments. A comparison of between-study estimates may, therefore, not be appropriate.

Relationships between backfat depth and reproduction performance

The between-selection line variation in backfat depth was sufficient to detect a non-linear relationship between predicted breeding values for backfat depth and predicted breeding values for litter birth weight, which indicated that extreme genotypes for backfat depth may have lower reproductive performance than average. The study of Vangen (1980a) provided some support for the non-linear relationship between backfat depth and reproductive performance. Vangen (1980a) reported positive, non-significant regression coefficients for the cumulative responses in litter size at birth and weaning to selection for high lean growth rate, but significantly negative regression coefficients for the cumulative responses to selection for low lean growth. Observed responses in backfat depths (Cameron and Curran, 1994) and litter birth weight (chapter 2) of the selection lines in the current study also suggested a non-linear relationship between backfat depth and reproduction. Litter birth weights of the control lines were similar to those of the high daily food intake and low lean food conversion lines, which were fatter than the control line by 2.8 mm. Both litter birth weights and backfat depths of the complementary selection lines were lower than the controls by 3.2 kg and 1.2 mm, respectively. The presence of a non-linear relationship between the predicted breeding values for backfat depth and litter birth weight raise questions regarding the assumptions of the linear models used to predict responses to selection. The precision of predicted responses in reproduction traits to selection on an index including backfat depth will be low, if the non-linear relationship between traits is not accounted for, as the estimated genetic correlation may not be significantly different from zero.

Higher inbreeding coefficients in the high and low selection lines than in the control lines may have contributed to the non-linear relationship between predicted breeding values for backfat depth and predicted breeding values for litter birth weight. Recent estimates of the regression coefficients for ultrasonic backfat depth and litter size at birth on inbreeding coefficient were -0.017 mm (Takahashi, Christian, Rothschild, Harville and Sugimoto, 1991) and -0.015 (Rodriguez, Rodriganez and Silio, 1994). Given that the mean inbreeding coefficients of the high and low lines were 4% greater than in the control lines, the expected inbreeding depression of the selection lines relative to the control lines for ultrasonic backfat depth was -0.07 mm, given the regression coefficient of Takahashi *et al* (1991). Similarly, the expected inbreeding depression of the selection lines for litter birth weight was equal to -0.08 kg, after multiplying the regression coefficient for litter size at birth on inbreeding coefficient of Rodriguez *et al* (1994) by the average piglet birth weight of 1.3 kg. Therefore, inbreeding depression did not substantially contribute to the non-linear relationship between predicted breeding values for backfat depth and predicted breeding values for litter birth weight.

Prediction of responses in reproduction traits

In chapter 2 it was reported that the correlated responses in reproduction traits, with selection for components of efficient lean growth rate, were selection strategy dependent. Comprehensive evaluation of alternative selection strategies should include prediction of correlated responses in reproduction traits, which will require unbiased estimates of the genetic parameters. However, estimates of the genetic correlations were biased when data from only animals with both performance test and reproduction traits was analysed, as the effect of selection on performance test traits was not incorporated in the analyses (Meyer and Thompson, 1984; Sorensen and Johansson, 1992). Therefore, when the genetic correlations between performance test and reproduction traits are estimated, for the purpose of evaluating alternative selection strategies for a population, it is important that data from all animals in the population are analysed, to take account of previous selection in the population.

The reliability of a predicted response to selection is directly related to the precision of the estimated genetic parameters used to predicted the response to selection. In an analogous manner to the confidence interval of a parameter estimate, small standard errors of the genetic parameters will be indicative of reliable predictions of correlated responses. The precision of genetic parameters estimated from data on several divergent selection groups is expected to be higher than if parameters were estimated from data on either an unselected population or a population selected in one direction, due to the combination of both the between-selection line and the within-selection line information on the relationships between traits. In the present study, with divergent selection in the three *ad-libitum* fed selection groups, there was substantial between-selection line variation in growth, food intake, backfat and reproduction traits. The contribution of information from the between-selection line variation was similar to that resulting from variation within selection lines, as in the lean growth rate with *ad-libitum* feeding divergent selection group, the between-selection line information was proportionately equal to 0.42 of the total information (Cameron, 1994). Therefore, incorporation of several divergent selection groups in the experimental design has increased the precision of the genetic parameter estimates, such that predicted responses to alternative selection strategies can be evaluated with confidence.

Information on the genetic relationships between performance test and reproduction traits can be used to identify predictors of genetic merit for reproduction traits, in addition to predicting the correlated responses in reproduction traits to selection on performance test traits. A measure of the value of a performance test trait as a predictor of genetic merit for reproduction traits is the magnitude of the coheritability between traits. However, the long time interval between the end of performance test and farrowing and that the biological mechanisms of growth and reproduction are substantially different, suggest that traits measured at the end of performance test may not be the most informative for predicting correlated responses in reproduction traits. Therefore, the precision of predicted genetic merit for reproduction traits may be increased through measurement of additional growth traits, such as liveweight and ultrasonic backfat depth immediately prior to mating, to be used in conjunction with performance test traits. An experiment has now been established to provide information on the genetic and phenotypic relationships between performance test traits, the additional traits mentioned above and reproduction traits, such that the benefit from incorporating the additional traits to predict genetic merit for reproduction traits can be quantified.

In conclusion, the genetic correlation estimates, from the present study, indicate a positive genetic association between growth rate and daily food intake with reproduction traits. The correlated responses, reported in the previous chapter, indicated that selection for low daily food intake, either directly or indirectly through selection for high lean food conversion, would impair reproductive performance. Both of these results have the same implications, that selection strategies which result in low daily food intake may have a negative effect on reproductive performance.

Chapter 4

Responses in liveweight and backfat depth measured at the start of the mating period of boars and gilts

Introduction

In Chapter 2 it was confirmed that the magnitude of correlated responses in reproduction traits would be selection strategy dependent. For example, selection strategies which decreased daily food intake, either directly or indirectly by selecting for increased efficiency, would impair reproductive performance through combinations of reduced litter sizes and weights.

Comprehensive evaluation of selection strategies for growth and carcass traits should include prediction of responses in reproduction traits, which requires information on the genetic and phenotypic relationships between growth and carcass traits and reproduction traits. To optimise genetic improvement in growth, carcass and reproduction traits, identification of growth traits as predictors of genetic merit for reproduction traits is required. However, the long time interval between the end of performance test and farrowing and that the biological mechanisms of growth and reproduction are substantially different, suggest that traits measured at the end of performance test may not be the most informative for predicting genetic merit in reproduction traits. In chapter 3 it was suggested that measurement of additional growth traits prior to mating, used in conjunction with performance test traits, may increase the precision of predicted genetic merit for reproduction traits.

High conception rates are a primary requirement in pig production systems, particularly as failure to conceive is a major reason for culling in gilts (Meat and Livestock Commission, 1995). Therefore, the responses in conception rate with alternative selection strategies should be evaluated. Relationships between conception rate and liveweight and backfat depth at the start of the mating period need to be determined, to provide information on the biological basis of the selection strategy specific responses in reproductive performance with selection for components of efficient lean growth rate.

The following chapter reports the effects of alternative selection strategies on liveweight and backfat depth at the start of the mating period and on conception rate, after seven generations of divergent selection in a population of Large White pigs. The contribution of liveweight and backfat depth, measured at the start of the mating period, to the accuracy of predicted genetic merit for litter traits at birth was estimated.

Materials and methods

Animals

Data on mating traits were collected after seven generations of divergent selection for daily food intake (DFI), lean food conversion (LFC), lean growth rate (LGA) on *ad-libitum* feeding and lean growth rate on restricted or scale feeding (LGS), in a population of Large White pigs. Liveweight and backfat depth were measured at the start of a six-week mating period on the boars and gilts, at an average age of 282 and 278 days respectively, which had been selected to be parents of the next generation. All animals measured at the start of the mating period had information on performance test traits. Details on establishment of the selection lines are given in chapter 2.

Control lines were established to enable detection of asymmetric responses to selection and to provide genetic links between the four selection groups, as due to a batch farrowing management system, the selection groups farrowed at different times. The policy of mating control line boars from one selection group to control line gilts of the following selection group meant that control line boars were at least three months older than boars from the high or low lines at the start of a mating period. Information from control line boars was therefore not included in the analyses.

Pigs in the *ad-libitum* selection groups were performance tested over a fixed weight range with average start and finish weights of 30 and 85 kg. Pigs fed on restricted feeding were performance tested for a fixed time period of 84 days with an average start weight of 30 kg and food intake equal to 0.75 g/g of daily *ad-libitum* food intake. Animals were fed a high energy and high protein pelleted diet containing 224 g crude protein per kg dry matter (DM) and 15.9 MJ digestible energy (DE) per kg DM and all animals were individually penned during the performance test. At the end of test, ultrasonic measurements of backfat depth were taken at the mid-back (analogous to P2 carcass measurement) on both sides of the pig.

Matings were unsupervised and took place in outside paddocks. Individual boars were run with three gilts for six weeks and were inspected on a regular basis, so that inactive boars could be replaced. Pregnant gilts were given 2.5 kg food daily and farrowed sows up to 3.5 kg food twice daily of a diet containing 184 g crude protein per kg DM crude protein and 15.2 MJ DE per kg DM. All animals were farrowed in selection group batches. No cross fostering was practised.

Statistical analysis

Differences between the selection lines were estimated using residual maximum likelihood (REML) analysis (Patterson and Thompson, 1971), using the REML algorithm of GENSTAT (Genstat 5 Committee, 1993). The selection line with selection group interaction was fitted as a fixed effect, with sire included in the model as a random effect.

Phenotypic (co)variances between performance test, liveweight and backfat depth of gilts at the start of the mating period and the corresponding genetic covariances with litter size and litter weight at birth were estimated using an individual animal model in a multivariate REML analysis, using the REML algorithm of Meyer (1986). The selection line with selection group interaction was included in the model as a fixed effect, to reduce the bias in parameter estimates as a result of measuring animals from divergent selection lines (Meyer and Thompson, 1984).

The relationships between age, liveweight and backfat depth at the start of the mating period with conception rate were examined using a multiple regression procedure. A model was fitted with binomial errors and a probit link as conception rate was not normally distributed. Linear and quadratic terms were fitted for liveweight, backfat depth and age at the start of the mating period.

Results

Means and phenotypic standard deviations across selection lines, for each trait are presented in Table 4.1. In general, boars grew faster on test than gilts, but at the start of the mating period, mean ages and liveweights were similar. Increases in liveweight between the end of test and the start of the mating period for boars and gilts were comparable, but the backfat depth of boars decreased from the end of performance test to the start of the mating period. Mating traits were measured on 331 gilts and 74 boars, with farrowing information available for 259 of the gilts presented to a boar (Table 4.2). The total number of boars with measurements at mating was similar in each selection group, but the number of gilts measured within each selection group was more variable.

Performance of gilts

At the start of the mating period, gilts selected for high DFI, LGA or LGS had similar liveweights, but different backfat depths, while the low DFI, LGA and LGS lines had different liveweights, but similar backfat depths (Table 4.3). Gilts selected for high LFC had the lowest mean liveweight and backfat depth compared to gilts in the alternative selection strategies.

Table 4.1 *Means and phenotypic standard deviations of performance test traits, measured mating traits and litter traits at birth for gilts and boars*

	Gilts		Boars	
	Mean	s.d	Mean	s.d
Performance test				
Average daily gain (g/day) †	778	70	852	92
Mid backfat (mm) †	14.7	2.2	14.2	2.4
Final weight (kg) ‡	82	4	86	4
Mid backfat (mm) ‡	13.0	2.0	13.1	1.1
Start of the mating period				
Weight (kg)	129	12	132	15
Mid backfat (mm)	15.8	3.9	11.6	3.8
Age (days)	278	11	282	8
Litter traits at birth				
Conception rate §	77			
Farrow age	415	14.7		
Litter size	10.4	3.0		
Litter weight	13.7	3.5		

† Traits measured on *ad-libitum* fed selection groups only

‡ Traits measured on restricted fed selection group only

§ Conception rate of gilts x 100 on the observed scale

Between the end of performance test and the start of the mating period, backfat depth of gilts selected for low DFI increased to a greater extent than in gilts selected for high DFI, with no corresponding increase in liveweight (Table 4.3).

Table 4.2 *Number of animals with measurements at mating and number of gilts farrowing by selection line and group*

	Selection group											
	Daily food intake			Lean food conversion			Lean growth (*ad-libitum*)			Lean growth (restricted)		
	Cont	High	Low	Cont	High	Low	Cont	High	Low	Cont	high	Low
Start of mating period												
Boars	-	10	8	-	10	9	-	10	10	-	7	10
Gilts	30	30	18	30	30	30	29	30	28	30	16	30
Farrowing	25	21	11	25	25	26	22	23	20	26	10	25

In contrast, with selection for either high or low LFC, backfat depth did not change from the end of performance test to the start of the mating period, while liveweight increased. Gilts selected for low LGA were significantly lighter at the start of the mating period than gilts in the high LGA line, at the same age, due to continuation of the slower growth rate during performance test. Differences in liveweight and backfat depth between the high and low LGS selection lines were maintained from the end of test until measurement at the start of the mating period. Gilts selected for high LGS were significantly heavier with less backfat, at a younger age, than gilts in the low LGS line.

Conception rates of gilts selected for low DFI or high LGS were similar and lower than for the alternative selection strategies, but the low DFI gilts were significantly older at farrowing than gilts selected for high LGS (Table 4.4). Within the DFI and LGS selection groups, there were significant differences in the age at farrowing, but not in the LFC or LGA selection groups. There were no significant differences in number of piglets born or litter weight at birth within the selection groups, but litter birth weight was significantly higher in the high LGS line than in the high LFC line.

Table 4.3 *Estimates of the selection line effects for performance test traits and measured mating traits of gilts in each selection group, relative to the average control*

		Performance test			Start of the mating period		
Selection group	Selection line	Average daily gain (g/day)	Backfat (mm)	Final weight (kg)	Weight (kg)	Backfat (mm)	Age (days)
	Control	790	14.0		131	16.1	279
Daily food intake	High	93	4.2		4	4.2	-2
	Low	-15	-1.5		-2	1.4	-10
Lean food conversion	High	-38	-1.9		-17	-5.4	-9
	Low	-13	3.0		-8	-0.2	-3
Lean growth (*ad-libitum*)	High	33	-1.8		6	-2.1	5
	Low	-176	3.3		-14	1.7	6
Lean growth (scale)	Control †		13.3	81.4			
	High		-3.5	5.9	6	-4.8	-10
	Low		2.7	-3.5	-7	1.7	7
	s.e.d ‡	23	0.8	1.4	4.5	1.3	4.5

† Control line for lean growth on scale feeding selection group
‡ Standard error of the difference between the high and low selection lines

The number and weight of piglets born per 100 gilts put to the boar provided information on the selection line differences when conception rate, litter size and litter weight at birth were combined (Table 4.4). Litter size and litter weight at birth per 100 gilts put to the boar were highest for the low LFC and low LGS lines, but lowest for the high and low DFI selection lines, which was primarily due to differences in conception rate. There was a linear relationship between the selection line means, excluding the high LGS line, for litter size and litter weight at birth per 100 gilts put to the boar (Figure 4.1), with a regression coefficient of 1.7 (s.e. 0.35) kg/pig and the regression proportionately accounted for 0.77 of the variation in litter weight at birth per 100 gilts put to the boar. The high LGS line deviated substantially

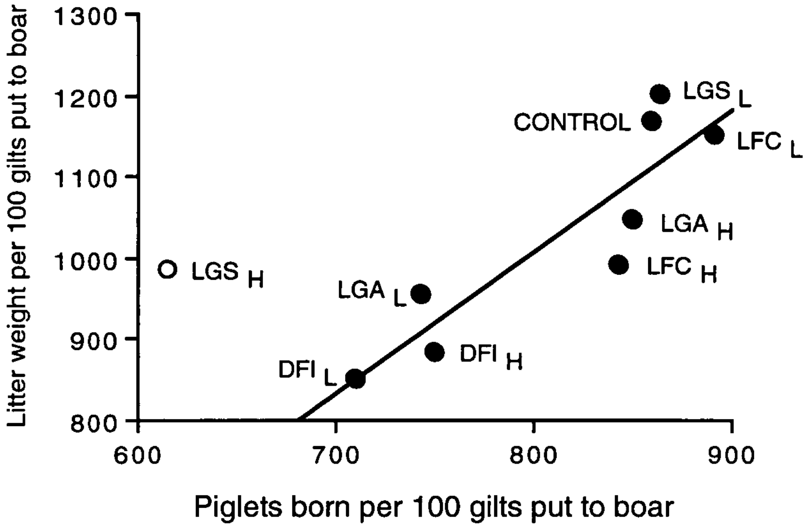

Figure 4.1. Piglets born and litter weight per 100 gilts put to the boar for the high (H), low (L) and control selection lines of the daily food intake (DFI), lean food conversion (LFC), lean growth (LGA) on *ad-libitum* feeding and lean growth on restricted feeding (LGS)

from the regression line, due to a higher litter birth weight than would be expected given the observed combination of conception rate and litter size at birth.

Table 4.4 *Estimates of the selection line effects of farrowing gilts for litter traits at birth in each selection group, relative to the average control*

		Litter traits at birth				Output/100 gilts put to the boar	
Selection group	Selection line	Conception rate †	Farrowing age (days)	Number born	Litter weight (kg)	Pigs born	Weight (kg)
	Control	83	416	10.3	14.0	859	1169
Daily food intake	High	-14	-10	0.5	-1.3	749	884
	Low	-21	8	1.0	-0.4	709	853
Lean food conversion	High	3	-8	-0.6	-2.6	843	994
	Low	1	-4	0.3	-0.3	890	1154
Lean growth (*ad-libitum*)	High	-8	4	0.9	-0.2	850	1047
	Low	-12	2	0.1	-0.6	743	957
Lean growth (scale)	High	-19	-8	-0.7	1.3	615	987
	Low	0	6	0.0	0.4	863	1202
	s.e.d ‡	12	5.5	1.1	1.2		

† Conception rate of gilts x100 on the observed scale

‡ Standard error of the difference between the high and low selection lines

Liveweight and backfat depth with conception rate

The test statistic for the regression model for conception rate with liveweight and backfat depth at the start of the mating period as explanatory variables was 1.3 with 4 and 325 d.f., which indicated that the model provided a poor fit to the data. Age at the start of mating provided little more information to account for variation in conception rate, as the test statistic increased to only 2.1 with 6 and 323 d.f.

Performance of boars

Boars in the high LGA and LGS selection lines were heavier at the start of the mating period than boars in the low LGA and LGS selection lines (Table 4.5). Boars selected for high DFI or low LFC, LGA and LGS had significantly higher backfat depths at the start of the mating period than in the low DFI, or high LFC, LGA and LGS selection lines. At the start of the mating period, high LGS boars were significantly younger and heavier than low LGS boars, while high LGA boars were heavier at the same age than low LGA boars. Backfat depth was reduced in all selection lines from the end of performance test to the start of the mating period, while liveweight increased. Reduction in backfat depth from the end of test to the start of the mating period was greatest in the fatter lines at the end of performance test, which were, respectively, the low LGA, low LFC and high DFI selection lines.

Table 4.5 *Estimates of the selection line effects for performance test traits and measured mating traits of boars in each selection group*

		Performance test			Start of the mating period		
Selection group	Selection line	Average daily gain (g/day)	Backfat (mm)	Final weight (kg)	Weight (kg)	Backfat (mm)	Age (days)
Daily food intake	High	996	16.8		136	13.8	276
	Low	789	11.2		122	8.8	272
Lean food conversion	High	876	10.8		127	9.0	276
	Low	790	16.9		128	12.9	284
Lean growth (*ad-libitum*)	High	944	11.4		153	10.5	290
	Low	700	17.8		123	13.8	290
Lean growth (scale)	High		10.1	93.3	141	9.6	273
	Low		15.2	81.7	125	13.4	290
	s.e.d †	41	1.6	1.9	6.6	1.7	3.8

‡ Standard error of the difference between the high and low selection lines

Relationships between traits

Estimates of the phenotypic correlations between performance test traits and traits measured at the start of the mating period are given in Table 4.6. Phenotypic correlations between average daily gain on test with liveweight at the start of the mating period and between backfat depth at the end of test with backfat depth at the start of the mating period were of a similar order of magnitude and significantly different from zero. The phenotypic correlation between average daily gain and backfat at the end of test was significantly lower than the correlation between liveweight and backfat depth measured at the start of the mating period. Coheritabilities were of similar magnitude to the corresponding phenotypic correlations, except for the coheritability between average daily gain and backfat at the end of performance test. Coheritabilities for litter size and litter weight at birth with average daily gain and backfat depth at the end of test were not significantly different from zero. However, for liveweight and backfat depth measured at the start of the mating period, the coheritabilities with litter size and weight at birth were similar and significantly different from zero.

Heritabilities for litter size and weight at birth were 0.12 (s.e. 0.06) and 0.16 (s.e. 0.11), which indicated that the accuracies of predicted genetic merit for the litter traits were 0.35 and 0.40, respectively, when genetic merit was determined using information from each litter trait. Incorporation of information on average daily gain and backfat depth at the end of test into the selection criteria, increased the accuracies of predicted genetic merit to 0.56 and 0.60, respectively. The accuracies of predicted genetic merit were further increased to 0.90 and 0.89, when measurements of liveweight and backfat depth at the start of the mating period were included in the selection criteria. The considerable increases in accuracy were due to the high heritability estimate for liveweight and high genetic correlation estimates between litter traits and liveweight at the start of the mating period, rather than to the high estimated genetic correlation between backfat depth and litter traits. The genetic parameter estimates were based on a relatively small data set with selected females only, such that the parameter estimates were imprecise, with s.e. of 0.1. However, when the genetic parameters for liveweight were proportionately reduced by 0.20, the accuracies decreased to 0.72, which was still substantially higher than when only performance test traits were included in the selection criteria. In a commercial breeding scheme however, the incorporation of traits measured after performance test into selection indices is probably not a realistic objective since the selection of animals would be delayed and the benefits would most likely be outweighed by the costs.

Table 4.6 *Phenotypic correlations (x100) and coheritabilities (x100) between performance test traits and traits measured at the start of the mating period and the corresponding coheritabilities with litter size and weight at birth*

	Average daily gain	Backfat depth	Weight at mating †	Backfat at mating †
Average daily gain		17 ‡	33	5
Backfat depth	-16 ‡		4	30
Weight at mating	44	4		62
Backfat at mating	16	44	42	
Litter size at birth §	16	6	27	23
Litter weight at birth §	14	15	29	30

† Measurement at the start of the mating period

‡ Phenotypic correlations between performance test and mating traits above the diagonal, with coheritabilities below the diagonal. Standard errors of phenotypic correlations = 0.08, coheritabilities = 0.15

§ Coheritabilities between weight and backfat traits with litter traits. Standard errors of coheritabilites = 0.09 for litter size and 0.12 for litter weight

Discussion

Liveweight and backfat depth measured at the start of the mating period differed significantly between and within-selection groups after seven generations of divergent selection for components of efficient lean growth rate. The correlated responses in traits measured at the start of the mating period indicated that the genetic covariances with traits in the selection criteria would be different from zero. Indices for predicting genetic merit for litter size or litter weight at birth, derived using information on the genetic and phenotypic relationships between traits measured at the start of the mating period, in conjunction with performance test traits, had higher accuracies than indices based on information from performance test traits only. However, the genetic parameter estimates were based on a relatively small data set with selected females only, such that the parameter estimates were imprecise. Although, the value of using information on traits measured at the start of the mating period to estimate breeding values for reproduction traits or for the prediction of responses in reproduction traits to selection for components of efficient lean growth was demonstrated the use of traits measured at the start of the mating period in selection indices in commercial practice may not be realistic.

Performance of gilts

An understanding of the influence of correlated responses in liveweight, backfat depth and age on reproduction traits is required, such that responses in reproduction traits can be rationalised. However, a comprehensive relationship between measurements of liveweight, backfat depth and age at the start of the mating period with reproduction traits could not be determined, when data from the four selection groups was combined, as there was evidence that the relationships were selection strategy dependent.

Selection for low DFI resulted in a greater increase in backfat depth between the end of test and the start of the mating period than in the high DFI selection line, but there was no difference in liveweight gain. The implied difference in rates of fat deposition in the high and low DFI selection lines suggested that at a similar liveweight, low DFI gilts may be at later stage of their respective growth curve (Taylor, 1985). Therefore, low DFI gilts may have lower mature weight, reached at an earlier age, than high DFI gilts (Taylor, 1980). If there is a relationship between the age at puberty and the age at mature weight, then on a physiological time scale, gilts selected for low DFI would be expected to farrow at an earlier age than gilts selected for high DFI, if conception was at the same oestrus cycle. However, gilts selected for low DFI were older at farrowing than gilts in the high DFI line, which indicated either a delay in the onset of puberty or conception at a later oestrus cycle. The inconsistency between the observed and expected difference in farrowing ages of the high and low DFI selection lines indicated that the two hypotheses : (1) low DFI gilts may be at a later stage of their respective growth curve compared to the high DFI gilts and (2) age at puberty and the age at mature weight are related, did not fully account for the observations.

The increased age at farrowing of the low DFI gilts, implying later conception relative to the high DFI gilts, may be a result of correlated responses in traits, other than liveweight, backfat depth and age at the start of the mating period. For example, the daily food intake of pigs selected for low DFI was 0.80 g/g relative to high DFI gilts (1861 *v.* 2330 g/day. s.e.d. 48 g/day) during performance test, which may have contributed to the increase in farrowing age. Ogle and Dalin (1989) reported that low food intake from 15 kg liveweight increased age at first detected oestrus, relative to pigs on a higher plane of nutrition, with low food intake equal to 0.55 g/g of high daily food intake. The Ogle and Dalin (1989) study implied an increase in age at farrowing of pigs with low food intake, as all pigs were mated at the same oestrus cycle. Therefore, both the DFI selection group and the Ogle and Dalin (1989) study suggest that low daily food intake over a long time period would increase farrowing age, while the effects of liveweight and backfat depth at the start of the mating period on farrowing age would be inconsequential.

Gilts selected for high LGS were younger at farrowing than gilts selected for low LGS, implying onset of puberty at an earlier age or conception at an earlier oestrus cycle. Selection on LGS imposed a restriction on daily food intake of 0.75 g/g of *ad-libitum* daily food intake, during performance test. The level of food restriction was relatively greater in the high LGS line, as when performance tested on *ad-libitum* feeding, the daily food intake of the high LGS line was greater than the low LGS line (Cameron and Curran, 1995). Therefore, the lower age at farrowing and higher level of food restriction of the high LGS line, relative to the low LGS line, was not consistent with the suggestion of Ogle and Dalin (1989) that food restriction would delay puberty onset.

The negative effect of a higher level of restriction in daily food intake in the high LGS line may have been compensated by the significantly higher liveweight at a fixed age, as a consequence of selection for increased lean growth rate. Kirkwood and Aherne (1985) suggested that minimum threshold values for liveweight, backfat and age characteristics must be achieved before sexual maturity can occur. Therefore, assuming that the threshold level for age was reached, faster growing high LGS gilts may realise the threshold level for liveweight sooner, with puberty attained at an earlier age than low LGS gilts. Given the differences between the high and low LGS lines and combining the hypothesis of Kirkwood and Aherne (1985) with that of Ogle and Dalin (1989), it is implied that the age at puberty of restricted fed pigs would be influenced to a greater extent by growth traits, than by the level of feed restriction. Kirkwood and Aherne (1985) did not define the minimum threshold values for liveweight, backfat depth and age characteristics, or the relative importance of each characteristic in determining the onset of puberty in gilts. Therefore, the relationships between liveweight, backfat depth and age traits with age at puberty should be determined, such that the proposed hypothesis can be tested.

Results from the current study have shown that the relationships between liveweight, backfat depth, age and food intake with particular reproduction traits are clearly selection strategy dependant. Therefore, the relationships observed between traits within selection groups will not necessarily be applicable between selection groups. For example, in the LFC selection group, significant between-selection line differences in backfat depth and liveweight at the start of the mating period were not associated with differences in conception rate or age at farrowing. However, backfat depths at the start of the mating period with selection for high LFC or high LGS were similar, but conception rates were substantially different, such that low backfat depth may be associated with poor conception with selection for high LGS but not high LFC. Similarly, there were comparably low rates of conception with selection for low DFI or for high LGS, but pigs selected for low DFI were significantly fatter at the start of the mating period. The lower daily food intake during performance test with selection for low DFI was associated with an increase in farrowing age which implied a delay in puberty onset or conception at a later oestrus cycle, relative to the high DFI selection line. Food intake was also restricted in both LGS selection lines, but farrowing age was decreased with selection for high LGS, which indicated different nutritional effects on reproductive development in the low DFI or high LGS selection lines.

Given that the responses in reproduction traits were dependent on the selection strategy, and that a comprehensive relationship between measurements of liveweight, backfat depth and age at the start of the mating period with reproduction traits could not be determined, identification of relationships between growth and reproduction traits will require measurement of additional growth traits at an earlier age than in the current study. Further, gilts in the current study were older at the start of the mating period than in commercial practice (Whittemore, 1993), such that even if a consistent relationship between traits had been detected, the information would be of limited practical value. Therefore, sequential measurements of growth characteristics from the end of performance test until conception are required to establish the relationships between growth and reproduction traits (e.g. age at puberty and age at conception), such that predictor traits for genetic merit in reproductive performance may be identified.

Performance of boars

In each selection group, backfat depth of boars was lower at the start of the mating period than at the end of performance test, while liveweight was greater. The reduction in backfat depth may have been attributable to higher levels of activity and aggressive behaviour observed when boars were grouped together, at the end of performance test, than when the animals were individually penned during performance test. When boars were group penned, the food allocation of 2.5 kg/day per pig was marginally lower than the daily food intake during the last week of test, 2.7 kg on average (Cameron, 1995). The combination of increased liveweight and that daily food intake was less than *ad-libitum* between the end of performance test and the start of the mating period, implied that mobilisation of fat reserves would be necessary to sustain lean growth rate. Therefore, measurements of *ad-libitum* food intake, liveweight and backfat depth at intervals between the end of performance test and the start of the mating period are required to provide information on the basis for the reduction in backfat depth in boars.

In conclusion, the accuracy of predicted genetic merit in reproduction traits was increased when measurements of liveweight and backfat depth at the start of the mating period were used in conjunction with performance test traits. Relationships between liveweight and backfat depth at the start of the mating period with conception rate were not consistent between selection groups, which suggested that reproductive development and conception rate may be determined by selection strategy dependant combinations of liveweight, backfat, age, and food intake.

Chapter 5

Responses in gilt post-farrowing traits and pre-weaning piglet growth

Introduction

Selection strategies which decrease daily food intake may be detrimental to pre-weaning piglet growth rate (chapter 2), through a combination of lower maternal rearing ability and reduced genetic merit for piglet growth rate. Information on the relative contribution of the factors influencing pre-weaning piglet growth are required, to determine the relationships between post-farrowing sow traits and piglet pre-weaning growth, for comprehensive evaluation of alternative selection strategies.

Responses in litter traits with selection on growth rate and backfat depth have been reported in several studies (for example, Vangen, 1980a; DeNise, Irvin, Swiger and Plimpton, 1983; Cleveland, Johnson, and Cunningham, 1988), but responses in sow liveweight and backfat depth at farrowing and at weaning have not been examined. Consequently, there is little information on the relationships between post-farrowing sow traits and piglet pre-weaning growth determined from selection experiments. Although the effects of changes in liveweight and subcutaneous fat depth during lactation on pre-weaning piglet growth rate have been determined in experiments which have imposed treatments on sows, such as different feeding levels, (for example, Yang, Eastham, Phillips and Whittemore, 1989; Noblet, Dourmad and Etienne, 1990), the effect of genotype has not been considered.

The following chapter reports the responses to divergent selection for components of efficient lean growth rate on gilt traits at farrowing and during lactation and on pre-weaning piglet growth rate in a population of Large White pigs. The relative importance of food intake, changes in liveweight and backfat depth of gilts during lactation on pre-weaning piglet growth rate were evaluated.

Materials and methods

Animals

Data on gilt and piglet traits at parturition and at weaning were collected after seven generations of divergent selection for daily food intake (DFI), lean food conversion (LFC), lean growth rate (LGA) on *ad-libitum* feeding and lean growth rate on restricted feeding (LGS), in a population of Large White pigs. Details on establishment of the selection lines are given in chapter 2.

Matings, at approximately 298 days of age, were unsupervised and took place in outside paddocks, as there were not adequate indoor facilities to enable supervised matings and recording of mating dates. Individual boars were run with three gilts for six weeks and were inspected on a regular basis, so that inactive boars could be replaced. Pregnant gilts were transferred from the mating paddocks into a group penning system, with four gilts per pen, before entering the farrowing crates on average 10 (s.d. 5) days before they were due to farrow. The number of days spent in the farrowing crates before farrowing was variable since the exact mating dates were unknown. Liveweight and backfat depth of gilts were measured on entering the farrowing crates and at weaning, after a 35 (s.d. 2) day lactation. Backfat depth was measured at the mid-back (analogous to the P2 site) on both sides of the pig. Pregnant gilts were given 2.5 kg food daily of a diet containing 184 g crude protein per kg DM and 15.2 MJ DE per kg DM. There was no change in the composition of the diet after farrowing and the food intake of gilts during lactation was measured daily. Piglets were weighed at birth, at 21 days of age and at weaning. Piglets were offered supplementary creep feed containing 264 g crude protein per kg DM and 18.0 MJ DE per kg DM from 22 days of age. No cross fostering was practised.

Statistical analysis

Differences between the selection lines were estimated using residual maximum likelihood (REML) analysis (Patterson and Thompson, 1971), using the REML algorithm of GENSTAT (Genstat 5 Committee, 1993). The selection line with selection group interaction was fitted as a fixed effect, with sire included in the model as a random effect. Sex was also included as a fixed effect in the analysis of individual piglet traits.

The total daily energy input, to milk production, calculated from the food intake and the mobilisation of body lipid of the gilt during the first 21 days of lactation was compared with the energy output in litter gain, from birth to 21 days of age. Dietary energy was equal to 12.7 MJ metabolisable energy (ME) per kg of food. Energy requirements for maintenance of gilts during lactation were calculated as a function of metabolic body weight (Whittemore, Kerr and Cameron, 1995). The food energy available for milk production was equal to the difference between dietary energy and the energy required for maintenance, with the efficiency of conversion of dietary energy to milk energy assumed to be 0.7 (Whittemore and Morgan, 1990). The total body lipid mobilised by gilts during lactation was estimated using the formula of Whittemore and Yang (1989), which was based on measurements of liveweight and ultrasonic backfat depth at farrowing and at weaning, with liveweight at farrowing adjusted for the products of conception. The energy available for milk production from mobilisation of body lipid was determined assuming that the energy content of lipid was 39.3 MJ ME per kg (Webster, 1977) and the efficiency of conversion of lipid to milk energy was 0.85 (Whittemore, 1993). The energy required for litter gain was assumed to be 22 MJ ME per kg (Whittemore and Morgan, 1990).

Differences between the selection lines in food conversion ratio (Cameron and Curran; 1994 and Cameron, Curran and Kerr; 1994) suggested that the efficiencies of conversion of dietary energy to milk energy by the gilt or the conversion of milk energy to litter gain may also differ between selection lines. Therefore, in an analysis of litter gain, separate regression coefficients for food intake and changes in liveweight and backfat depth during lactation were fitted for each selection group.

Results

Means and standard deviations of gilt and individual piglet traits measured prior to farrowing, at 21 days post-farrowing and at weaning are presented in Table 5.1. Liveweight and backfat depth of gilts decreased from farrowing to weaning by 44 kg and 7.5 mm, on average. There were 49, 71, 63 and 59 farrowing gilts in the DFI, LFC, LGA and LGS selection groups respectively (Table 5.2), with 20 gilts on average in the high, low and control lines, except in the low DFI selection line, in which there were only 8 gilts with farrowing records.

Responses in gilt traits

At farrowing, liveweights and backfat depths of gilts selected for low DFI, LFC, LGA and LGS were similar (Table 5.3). The backfat depth of gilts in the high DFI line was greater than gilts in the low selection lines. Backfat depth of gilts in the high LFC, LGA and LGS lines was less than in the low selection lines. Liveweight of gilts selected for high LFC was significantly lower than with selection for high DFI, LGA or LGS. There was a substantial response in liveweight with divergent selection on LGA, while the response in backfat depth was significantly different from zero in all four selection groups.

There was no difference in liveweight loss during lactation between gilts in the high selection lines or the low selection lines (Table 5.3).

Table 5.1 *Means and phenotypic standard deviations for gilt and piglet traits measured at farrowing, 21 days post-farrowing and at weaning*

Trait	Farrowing		21 days post-farrowing		Weaning	
	Mean	s.d.	Mean	s.d.	Mean	s.d.
Liveweight (kg)	209	21			165	20
Backfat (mm)	24.6	5.3			17.1	5.0
Total food intake (kg)					133	17
Age (days)	415	15			449	15
Litter size	10.9	3.0	8.9	2.5	8.8	2.5
Litter weight (kg)	13.8	3.4	47.1	12.0	75.5	19.1
Litter growth rate (kg/day)			1.6	0.5	2.1	0.7
Piglet weight (kg)	1.3	0.3	5.3	1.3	8.6	2.0
Piglet growth rate (g/day)			190	53	236	86
Mortality (x 100) from birth			18		19	
Creep feed intake (kg)					4.1	5.1

Table 5.2 *Number of animals with measurements by selection line and group*

Selection group	Daily food intake	Lean food conversion	Lean growth (*ad-libitum*)	Lean growth (restricted)
Control	18	20	23	11
High	23	28	21	27
Low	8	23	19	21

The reduction in backfat depth during lactation was significantly lower in the high LFC and LGA selection lines than in the high DFI and low LFC lines. There was substantial variation between selection lines in food intake during lactation. Gilts in the low LGA and LGS lines had the lowest food intakes, and gilts in the high DFI and low LFC lines the highest food intakes during lactation. Reductions in liveweight and backfat depth during lactation were similar for the high and low DFI selection lines, but gilts selected for low DFI consumed significantly less food during lactation. Reductions in liveweight and backfat depth were lower with selection for high LFC than with selection for low LFC and food intake during lactation was also lower. The reductions in liveweight and backfat depth during lactation for the high and low lines of the LGA and LGS selection groups were similar. Gilts selected for high LGA had substantially higher food intake during lactation than gilts selected for low LGA, while food intakes of the high and low LGS selection lines were similar.

Table 5.3 *Mean values of the selection lines for gilt traits measured at farrowing and during lactation, relative to the average of the control lines*

	Farrowing			Lactation		
Selection group	Selection line	Weight (kg)	Backfat (mm)	Weight loss (kg)	Backfat loss (mm)	Total food (kg)
	Control	216	25.0	46	7.7	133
Daily food intake	High	2	5.8	-5	0.9	17
	Low	-10	0.9	-6	0.1	-8
Lean food conversion	High	-26	-5.4	-9	-1.8	-3
	Low	-14	0.8	2	1.1	16
Lean growth (*ad-libitum*)	High	4	-4.2	-5	-2.2	4
	Low	-19	0.1	0.3	-1.0	-12
Lean growth (restricted)	High	-6	-5.1	-7	0.3	-8
	Low	-7	2.1	-6	-0.1	-15
	s.e.d †	7	1.5	5	1.3	4

†Standard error of the difference between the high and low selection lines

Responses in litter and individual piglet traits

There were no significant differences in litter size at birth or at 21 days post-farrowing between or within selection groups (Table 5.4).

Table 5.4 *Mean values of the selection lines for litter traits, relative to the average of the control lines*

Selection group	Selection line	Litter size		Mortality (x 100) †	Litter weight (kg)		
		Birth	21 days		Birth	21 days	Weaning
	Control	10.7	9.0	16	14.2	48.7	78.6
Daily food intake	High	0.0	-0.6	5	-1.8	-4.2	-4.2
	Low	0.5	-1.0	13	-0.7	-11.2	-18.3
Lean food conversion	High	-0.9	-0.9	0	-2.7	-8.6	-15.4
	Low	0.0	-0.5	4	-0.4	-2.1	-0.9
Lean growth (*ad-libitum*)	High	0.6	0.5	0	-0.3	1.7	0.9
	Low	0.0	0.6	-6	-0.4	-0.6	0.5
Lean growth (restricted)	High	1.6	0.0	9	1.1	-1.2	-9.6
	Low	0.9	0.2	4	0.9	-0.7	-5.3
	s.e.d ‡	1.0	0.8	5	1.1	4.0	6.4

† Mortality (x 100) from birth to 21 days

‡ Standard error of the difference between the high and low selection lines

Mortality from birth to 21 days post-farrowing was similar for all selection lines but the low LGA and DFI selection lines had respectively, the lowest and highest mortality. Litter birth weights were heaviest with selection for high or low LGS, but were lightest with selection for high DFI or high LFC. Litter weights at birth were similar within the DFI, LGA and LGS selection groups, but were greater in the high LFC line than in low LFC line. At 21 days post-farrowing and also at weaning, litter weights were highest with selection for high or low LGA. Selection for low DFI or high LFC resulted in substantially lower litter weights at weaning than selection for high DFI or low LFC. There were no responses in litter weights at 21 days post-farrowing or at weaning in the LGA and LGS selection groups.

Table 5.5 *Mean values of the selection lines for piglet traits, relative to the average of the control lines*

		Piglet weight (kg)			Piglet growth rate (g/day)	
Selection group	Selection line	Birth	21 days	Weaning	Birth-21 days	21 days-weaning
	Control	1.31	5.50	8.9	196.0	249.4
Daily food intake	High	-0.16	-0.17	0.2	-1.6	17.0
	Low	-0.05	-0.64	-0.9	-28.9	-6.4
Lean food conversion	High	-0.14	-0.49	-1.0	-17.0	-42.1
	Low	-0.02	0.00	-0.1	0.2	-10.4
Lean growth (*ad-libitum*)	High	-0.07	-0.12	-0.4	-1.8	-1.9
	Low	0.01	-0.17	-0.5	-7.2	-12.4
Lean growth (restricted)	High	-0.02	-0.02	-0.4	-2.0	-40.0
	Low	0.07	-0.24	-0.6	-12.2	-14.3
	s.e.d †	0.06	0.25	0.4	10.8	18.9

† Standard error of the difference between the high and low selection lines

Individual piglet weights at birth were not significantly different between the high and low lines in the DFI, LGA or LGS selection groups, but were lower with selection for high LFC than with selection for low LFC (Table 5.5). At 21 days post-farrowing, piglets in the low DFI and high LFC selection lines were lighter than piglets in the high DFI and low LFC selection lines. At weaning selection for low DFI or high LFC resulted in lighter piglets, but the weaning weights of piglets in the high and low LGS selection lines were similar. In the LGA selection group responses in piglet weights at 21 days post-farrowing and at weaning were similar in the high and low selection lines. Growth rate from birth to 21 days post-farrowing was significantly higher in the high DFI selection line compared to the low line. Creep feed intake from 21 days post-farrowing until weaning was less than 6 kg, per litter, in all selection lines with no substantial differences between selection lines.

Energy for litter gain during the first 21 days post-farrowing

The predicted energy inputs available from food and mobilisation of body lipid for litter gain in each selection line are presented in Table 5.6. In the high DFI and low LFC lines, there was significantly more energy available from food for litter gain than in the low DFI and high LFC lines, but food energy was similar in the high and low LGA and LGS selection lines. There were no significant differences between the high and low lines in the four selection groups in energy from the mobilisation of body lipid. The energy in the daily litter gain was higher with selection for high DFI than in the low DFI line, but there was no difference between the high and low lines in the LFC, LGA or LGS selection strategies.

The energy used for litter gain was similar to the energy provided by the gilt, from food and lipid mobilisation, for the high and low lines in the DFI and LFC selection groups. In the LGA and LGS selection groups, the energy for litter gain was greater than the predicted energy available from food and lipid mobilisation. Therefore, the energy provided by gilts in the LGA and LGS selection groups was apparently insufficient to meet the energy required for litter gain, assuming no variation between genotypes in the efficiency of conversion of dietary energy to milk energy by the gilt and in the conversion of milk energy to litter gain.

Table 5.6 *Daily energy inputs from food and mobilisation of body lipid for milk production compared to the daily energy output in litter gain, from birth to 21 days of age, by selection line and group*

Selection group	Selection line	Energy inputs (MJ ME/day) † Food	Lipid	Energy output (MJ ME/day) Litter gain	Energy deficit (MJ ME/day) ‡
	Control	18.7	13.5	36.4	-3.6
Daily food intake	High	20.5	14.3	33.6	1.7
	Low	17.1	12.6	25.1	5.1
Lean food conversion	High	18.9	11.2	30.0	0.6
	Low	22.9	15.1	34.4	3.0
Lean growth (*ad-libitum*)	High	19.8	10.6	38.3	-7.8
	Low	17.3	13.3	37.0	-6.3
Lean growth (restricted)	High	16.4	12.4	33.6	-4.5
	Low	15.2	11.9	34.5	-7.4
	s.e.d §	0.9	2.0	3.6	2.9

† Energy inputs from food intake and body lipid mobilised, where food energy is adjusted for the maintenance requirements of the gilt

‡ The difference between total energy inputs and energy output

§ Standard error of the difference between the high and low selection lines

In the analysis of energy for litter gain, the regression coefficients for changes in liveweight and backfat depth during lactation were similar between selection groups (15.1 (s.e. 1.8) and 20.3 (s.e. 6.6)), but the regression coefficients for energy available from food intake were selection strategy dependent. In the DFI and LGS selection groups, the regression coefficients of 1.45 (s.e. 0.27) and 1.72 (s.e. 0.45) were higher than the coefficients for the LFC and LGA selection groups of 0.97 and 0.60 (s.e. 0.27). The relatively larger standard error for the regression coefficient for change in backfat depth than for change in liveweight indicated that contribution of the change in backfat to the prediction of energy available from lipid mobilisation to litter gain was less than from the change in liveweight. In a log-log regression analysis of backfat depth at farrowing with backfat depth at weaning, the regression coefficient and intercept were 1.02 (s.e. 0.06) and -0.47 (s.e. 0.20), which indicated that the change in backfat depth was a constant proportion of backfat depth at farrowing.

Discussion

The responses in gilt traits during lactation and in piglet pre-weaning growth were selection strategy dependent. Gilts in the high DFI and low LFC selection lines were heavier at farrowing and had a higher food intake during lactation with heavier litters at weaning than gilts in the low DFI and high LFC selection lines. Given the similarity between the selection lines in the energy available from lipid mobilisation, the importance of food intake during lactation to provide energy for pre-weaning piglet growth was emphasised. Therefore, selection strategies which reduce voluntary food intake during lactation or which result in a reduction in liveweight and backfat depth at farrowing will be detrimental to pre-weaning piglet growth rate.

Selection strategy dependent responses

Whittemore and Morgan (1990) indicated that litter size, food intake of the gilt and the mobilisation of body reserves during lactation were the primary determinants of pre-weaning piglet growth. In the current study, differences between the selection lines in litter size were small, such that variation in litter growth rate was only a result of selection strategy dependent combinations of gilt food intake during lactation and mobilisation of body reserves, which were indicated by changes in liveweight and backfat depth during lactation.

Selection for low DFI resulted in lighter gilts with less backfat at farrowing, a substantially lower food intake during lactation, but similar reductions in liveweight and backfat depth than with selection for high DFI. Therefore, the lower piglet growth rate with selection for low DFI compared to selection for high DFI was due only to lower food intake of the gilts, which constrained milk production and as such piglet pre-weaning gain. In contrast, with selection for high LFC, the combination of relatively smaller changes in liveweight and backfat depth and a lower food intake during lactation than gilts in the low LFC selection line, resulted in lower litter and piglet pre-weaning growth. The higher food intake of high LGA gilts compensated for the relatively lower reductions in liveweight and backfat depth during lactation compared to the low LGA line, such that piglet pre-weaning growth rates were similar in the two selection lines. Litter growth rates of the high and low LGS selection lines were not different as a result of similar food intakes and changes in liveweight and backfat depth during lactation.

Differences between the selection lines in pre-weaning piglet growth may have been partially due to differences in maternal rearing ability, as influenced by the food available and the genetic merit of the lactating gilt for food intake and mobilisation of body reserves. Piglet pre-weaning growth may also be determined by genetic merit of the piglets for growth rate. However, the ability of piglets to express their genetic merit for growth will be, to a large extent, dependant on the availability of food during lactation, the appetite of the gilt and her ability to mobilise body tissues. If there is a marginal under-supply of dietary nutrients to the gilt, then maternal catabolism of both lipid and protein will be required to meet the energy demands for milk production (Eastham, Smith, Whittemore and Phillips, 1988). Whittemore, Smith and Phillips (1988) suggested that there may be an upper limit to the extent of lipid mobilisation, as indicated by reduction in backfat depth. Therefore, if the under supply of nutrients is greater than can be compensated for by mobilisation of body reserves, then milk production may be constrained and piglet expression of genetic merit for growth will be suppressed. Given the information from the current study, however, it was not possible to comprehensively differentiate between the relative contributions of the genetic component of the piglet, the genetic component of the gilt and the environmental influences on pre-weaning piglet growth rate.

Gilts which had lower backfat depths at farrowing (for example with selection for low DFI , high LFC, LGA and LGS) also had lower backfat depths at weaning. A reduced backfat depth at weaning has been associated with a prolonged weaning to oestrus interval and a reduction in number of gilts conceiving for the second parity (Yang, Eastham, Phillips and Whittemore, 1989). Low backfat depth at weaning of the low DFI, high LFC, LGA and LGS selection lines may be indicative of a reduction in long term reproductive efficiency over several parities, assuming the association reported by Yang *et al* (1989) is valid for different genotypes. Reproductive performance of the low DFI and high LFC selection lines was lower than in the high DFI and low LFC lines, which coupled with the lower backfat depth at weaning, suggests that litter performance may be further reduced in later parities. However, in the high LGA and LGS selection lines, there was no difference in reproductive performance of gilts, such that first parity litter performance may not be a good indicator of performance in subsequent parities, because of the lower backfat depth at weaning. Therefore, the reproductive performance of the alternative selection strategies should be evaluated over several parities to determine the long term effects of selection for components of efficient lean growth rate on reproduction traits.

Nutritional studies have reported relatively small changes in litter weight gain to increases in gilt food intake during lactation. Noblet and Etienne (1986) indicated that litter gains were unaffected by the energy intake of lactating gilts and Eastham, Smith, Whittemore and Phillips (1988) estimated a regression coefficient of litter weight gain on food consumption during lactation of 0.09 (s.e. 0.03). In the current study, the regression coefficient of litter weight gain on daily food intake during lactation was 0.39 (s.e. 0.08), which was substantially greater than in the studies of Noblet and Etienne (1986) and Eastham *et al* (1988). The responses in food intake during lactation of the DFI, LFC and LGA selection groups were a consequence of selection strategy rather than as a result of an imposed treatment, as in the studies of Noblet and Etienne (1986) and Eastham *et al* (1988). The difference between the results of the current study and the Noblet and Etienne (1986) and Eastham *et al* (1988) studies suggests that the biological mechanisms controlling food intake and pre-weaning piglet growth rate are different when food intake is determined by genetic merit or by nutritional treatment. Therefore, comparison of the two types of study may be inappropriate.

Responses in gilt food intake during lactation and pre-weaning piglet growth rate have not been previously examined given selection on performance test traits, such as growth rate and backfat depth. Correlated responses in reproduction traits measured at birth and weaning have been limited to litter size and weight (for example Vangen, 1980; DeNise *et al*, 1983; Cleveland *et al*, 1988). Consequently, there is no information from selection experiments on the relationships between gilt food intake during lactation and piglet pre-weaning growth.

Energy for litter gain during the first 21 days post-farrowing

The energy available for litter gain from food and mobilisation of body lipid was similar to the energy in litter gain for the DFI and LFC selection groups, but was apparently less than the energy in litter gain of the LGA and LGS selection groups. The primary sources of energy for litter gain were from food and body lipid, with average values of 18.6 and 13.0 MJ ME, respectively. The contribution of energy from the reduction in body protein to litter gain was negligible, as the average predicted rates of reduction in body lipid and protein of 388 g/day and 88 g/day, respectively, corresponded to energy of 15.2 and 0.4 MJ ME/day (Webster, 1977). Therefore, the difference between the energy provided from food and from mobilisation of body lipid relative to the energy utilised in litter gain may be due to between-genotype differences in the efficiency of conversion of dietary energy to milk energy and in the conversion of milk energy to litter gain. The higher regression coefficients of energy utilised in litter weight gain on energy available from food for the DFI and LGS selection groups compared to the LFC and LGA selection groups, indicated between-genotype variation in the efficiency of conversion of energy from food into litter gain.

An alternative explanation for the difference between the energy provided from food and from mobilisation of body lipid relative to the energy utilised in litter gain is that the prediction equations for body lipid content were genotype specific, such that the reduction in body lipid content was under-estimated in the LGA and LGS selection groups. Use of the Whittemore and Yang (1989) prediction equation assumed that the relationship between liveweight and backfat depth with body lipid content was independent of genotype. Cameron and Curran (1995) reported differences between selection strategies in the distribution of fat in 85 kg carcasses. Therefore, information on the body lipid content of gilts from each selection strategy at farrowing and weaning is required in order to determine the appropriate equations to predicted reduction in body lipid, during lactation, in the alternative selection strategies.

An objective of the study was to determine the relative importance of gilt food intake and predicted body lipid mobilisation during lactation to pre-weaning piglet growth rate. The within-selection group regression coefficients for energy provided from food and from mobilisation of body lipid for litter gain of 1.11 (s.e. 0.16) and 0.96 (s.e. 0.09), together with the phenotypic correlation coefficients (0.30 and 0.47, s.e. 0.06) indicated similar relationships between food intake and body lipid mobilisation in terms of the energy utilised for litter gain. However, constraints on the current study prevented comprehensive conclusions being drawn regarding between-genotype differences in the relative contributions of food intake, changes in liveweight and backfat depth of gilts during lactation to pre-weaning piglet growth rate. For example, body lipid content of gilts at farrowing was predicted from gilt body weight and backfat depth measured ten days prior to farrowing. Defining gilt body weight immediately post-farrowing as liveweight prior to farrowing minus litter birth weight did not account for either the weight of amniotic fluid or litter weight gain between the time of gilt measurement and birth. Further, there were no measurements on gilts taken at 21 days post-farrowing, when creep food was first offered to piglets, such that the mobilisation body lipid by gilts was calculated for a 35 day lactation, rather than on the basis of a 21 day lactation, before supplementary creep feed was available to piglets. Ideally, gilt liveweight and backfat depth would have been measured immediately post-farrowing and after 21 days, for prediction of body lipid content and to coincide with measurements of pre-weaning piglet growth.

The results from the present study have provided evidence that selection at the end of performance test, based on performance in growth traits, influences the rearing ability of gilts through responses in gilt liveweight, backfat depth and lactation feed intake. However, in the present study, all animals were fed the same diet, which may not have been equally appropriate for all genotypes, given the differences between genotypes in food intake during lactation. It is reasonable to assume that the various selection strategies will have different nutritional requirements during gestation and lactation, as the genotypes differed in terms of both growth (Cameron and Curran, 1994; Cameron *et al*, 1994) and reproductive characteristics (chapter 2). Therefore, the sensitivity of genotypes to diets differing in the ratio of energy to essential amino acids should be determined during both gestation and lactation in first and subsequent parities. Information on the genotype with nutrition interaction for reproduction traits may enable the detrimental effects of low food intake of particular genotypes on reproduction traits to be alleviated by the identification of appropriate feeding strategies.

In conclusion, the responses to selection for components of efficient lean growth indicated that selection strategies which reduce liveweight at farrowing and reduce voluntary food intake during lactation have a negative effect on pre-weaning piglet growth rate. However, knowledge of the correlated responses alone is insufficient for the comprehensive evaluation of alternative selection strategies, since the correlated responses do not provide all the information that is available from selection experiments. Prediction of correlated responses given alternative selection strategies for lean growth requires information on the genetic and phenotypic relationships between performance test traits and gilt reproduction traits during gestation and lactation.

Chapter 6

General discussion

The reproductive performance of Large White gilts

The choice of selection strategy may influence the magnitude of responses in reproduction traits and therefore the correlated responses in reproduction traits given various selection strategies for efficient lean growth rate should be determined. The correlated responses to selection provide quantitative information on the effects of alternative selection strategies on reproduction traits, but not the information that is required to evaluate selection strategies. Estimates of the genetic and phenotypic relationships between the traits in the selection criteria and reproduction traits are required for the comprehensive evaluation of alternative selection strategies. Therefore, the main objectives of the study were to determine the responses in reproduction traits to selection for components of efficient lean growth rate and, secondly, to estimate the genetic and phenotypic relationships between growth and reproduction traits.

Litter size and weight at both birth and weaning were reduced with selection for low DFI and high LFC compared to selection for high DFI or low LFC. In the LGA and LGS selection groups, the responses in litter size and weight at birth and at weaning were not significantly different from zero. Estimates of the genetic correlations for litter traits at birth and weaning with daily food intake and growth rate during performance test were positive and significantly different from zero, but correlations with backfat depth, for *ad-libitum* fed pigs, were not significantly different from zero. The DFI and LFC selection strategies, which resulted in a low voluntary food intake during lactation or low liveweight and backfat depth at farrowing, had a negative effect on pre-weaning piglet growth rate. Selection strategies for LGA or LGS did not significantly affect pre-weaning piglet growth rate. In conclusion, selection for low daily food intake either directly of indirectly through selection for high LFC impaired reproductive performance.

Litter size

Litter size at both birth and weaning are traits of high economic value in commercial pig breeding schemes and an extra piglet in a litter will have a favourable impact on improving the efficiency of pig production (see review of Haley *et al*, 1988). Selection strategies for growth and carcass traits which result in reduced litter size will therefore be detrimental to the rate of genetic improvement in performance test traits, due to a reduced selection differential. The substantial responses in litter size with selection for DFI or LFC, suggested that selection strategies which result in low daily food intake either directly or indirectly may have a lower rate of genetic improvement than selection strategies for lean growth rate, assuming similar accuracies for the selection strategies.

Estimates of the genetic correlation between performance test traits and litter size at birth and weaning between studies have been variable (for example Johansson and Kennedy, 1983; Crump, 1992; Short *et al*, 1994; Rydhmer *et al*, 1995) and smaller in magnitude than estimates for growth rate and food intake with litter size in the current study. However, the underlying conclusions from the studies are broadly similar, that selection strategies for increased lean growth rate will not have a negative effect on the litter size of selected gilts at birth or at weaning, while selection strategies which reduce food intake or growth rate will be detrimental to litter size. The reductions in litter size should be of concern to the industry, as even small changes will have severe negative consequences to the breeding efficiency of selected pig populations. The economic success and the rates of genetic improvement in growth and carcass traits are dependent on achieving a high level of performance in both growth and litter traits. In dam lines, litter size would be a component of both the selection criterion and selection objective, while in terminal sire genotypes, litter size could be incorporated as part of the selection objective, such that the correlated responses in litter size could be accounted for in the breeding programme.

Litter weights, piglet weights and pre-weaning growth rate

Although litter size has probably been the most widely considered reproduction trait in selection experiments (Haley *et al*, 1988), selection strategies which result in low litter and piglet weights and low pre-weaning piglet growth rates will have negative consequences on the rate of genetic improvement in growth traits. Chapter 2 demonstrated that higher pre-weaning mortality was associated with low piglet birth weight, which confirmed the results of Vangen (1972) that piglet birth weight was positively related to survival. Therefore, given the negative relationship between litter size at birth and individual piglet weight (chapter 2), increasing litter size at birth may not necessarily increase the number of piglets that can be weaned in a litter.

Selection strategies for low DFI or high LFC had a negative effect on litter and individual piglet weight at birth and particularly at weaning (chapters 2 and 5). The higher genetic correlations between growth rate and daily food intake with litter weight than with litter size, but the relatively similar heritabilities for litter weight and size reported in chapter 3, suggested that selection strategies which change growth and daily food intake may result in relatively greater changes in litter weight than in litter size. Rydhmer, Johansson, Stern and Eliasson-Selling (1992) and Vangen (1980a) also indicated, perhaps not surprisingly, that the genetic correlations between the growth rate of the gilt and piglet birth weights were positive. Further, Rydhmer *et al* (1989) reported that piglet weight was positively related to growth rate, from 25 to 90 kg, indicating that genetic merit for growth rate may be expressed at a very early age. Therefore, selection strategies for increased lean growth rate will result in heavier individual piglets at birth. Heavier piglets will be more likely to survive (chapter 2), and will have increased growth rates compared to piglets with lower birth weights. Therefore, a high rate of piglet survival from birth to weaning coupled with faster growth rates will result in larger litters of heavier piglets at weaning .

Pre-weaning piglet growth rate is also influenced by the ability of the lactating gilt to supply nutrients, in the form of milk energy, to the piglets (Whittemore and Morgan, 1990). The ability of the gilt to supply the piglets with a level of nutrition to meet requirements for growth is determined by the adequate provision of nutrients to the gilt, and the genetic merit of the gilt for food intake and mobilisation of body reserves. There are therefore three factors influencing the rate of pre-weaning piglet growth rate: the genetic merit of the piglet, for growth, the genetic merit of the gilt to provide nutrients to the piglet and the environmental influences which control, for example, the amount of food available to the lactating gilt. The experiments reported in chapters 4 and 5 were not designed to provide the information to distinguish between the three factors. However, the genetic merit for piglet growth could be determined for example, by artificially rearing piglets, producing reciprocal crosses between the divergent high and low selection lines or using embryo transfer. The genetic merit of the gilt may be estimated by controlling litter size and gilt food intake during lactation. Information regarding the environmental influences on pre-weaning piglet growth is also required to fully remove constraints on pre-weaning piglet growth.

Differences in piglet pre-weaning growth rate between the selection groups may have been due in part, to a lack of knowledge of the appropriate feeding for different genotypes of gilts during gestation and lactation, to allow gilts to express genetic merit for growth, food intake and reproduction traits. Given the substantial differences between the alternative selection strategies in growth characteristics during performance test (Cameron and Curran, 1994; Cameron *et al*, 1994), it is unrealistic to assume that the nutrient requirements of divergently selected pigs will be the same. Therefore, since all pigs were fed the same diet during gestation and lactation, the differences in litter weights and piglet growth were inevitable and may have been substantially reduced if information on the appropriate feeding strategies of the different genotypes had been available. Given the optimal nutritional regime, the low voluntary food intake of particular genotypes may not necessarily have been a disadvantage. For example, in the breeding herd, an advantage of small mature size, with a low voluntary food intake, will be a low cost of maintenance. However, the advantages will be realised only if the gilts, which have a small mature size and low food intake, also have a fast rate of daily gain, which suggests that the shape of the growth curve must change. Gilts of small mature size and low growth rate will produce smaller piglets at birth, with low growth rates, which will not be cost effective to producers.

Gilt liveweight, backfat depth and food intake at mating, farrowing and weaning

The effects of differences in liveweight, backfat depth and food intake of gilts, on age at sexual maturity, on gilt performance during lactation and on pre-weaning piglet growth rate have been variable (see review of Whittemore and Morgan, 1990). Previous experiments have generally used dietary treatments to achieve differences in liveweight, backfat depth and food intake of gilts rather than consider the effects of genetic differences. The four divergent selection groups considered in the present study have also resulted in differences in liveweight, backfat depth and food intake during performance test (Cameron and Curran, 1994; Cameron *et al*, 1994), at mating (chapter 4), at farrowing and at weaning (chapter 5). However, the between selection line regression coefficient of litter weight gain on daily food intake during lactation was substantially higher in the present study (chapter 4) than in the nutritional experiments (Noblet and Etienne, 1986; Eastham *et al*, 1988). The difference between the current study and the nutritional studies suggests that the biological mechanisms controlling growth and reproduction traits are not the same, when food intake is determined by nutritional treatment or by genetic merit. Therefore, direct comparison of the two types of study is probably not appropriate.

Responses in gilt liveweight, backfat depth and food intake at mating, farrowing and weaning have not been previously examined when selection has been on performance test traits, as correlated responses in reproduction traits have generally been limited to litter size and weight (for example Vangen, 1980; DeNise *et al*, 1883; Cleveland *et al*, 1988). The rather narrow consideration of reproduction traits in previous selection experiments does not provide sufficient information to fully understand the relationships between traits given alternative selection strategies. Selection on growth and food intake during performance test will not only affect litter and piglet traits directly, as indicated by the positive genetic correlations estimated between growth rate and food intake with litter traits, but also indirectly, through the correlated responses in gilt liveweight, body lipid content at mating and farrowing, and food intake during lactation on maternal rearing ability. Therefore, comprehensive evaluation of selection strategies requires information on the relationships between performance test traits and post-farrowing traits of the gilt.

Relationships between performance test and reproduction traits

Knowledge of the correlated responses in reproduction traits, resulting from various selection strategies for efficient lean growth rate alone, is insufficient for the comprehensive evaluation of alternative selection strategies. The correlated responses do not provide all the information that is available from selection experiments and information on the genetic and phenotypic relationships between performance test and reproduction traits is required. The responses in litter and piglet traits (chapter 2), in gilt traits measured at mating (chapter 4), at farrowing and during lactation (chapter 5) demonstrated that there is genetic covariation between growth and reproduction traits. Therefore, information on the genetic and phenotypic relationships between performance test and reproduction traits are required to predict responses in reproduction traits, for the evaluation of alternative selection strategies.

Obtaining unbiased estimates of genetic parameters for reproduction traits may be problematic, since reproduction traits are normally only measured on sexually mature selected females, following selection based on performance in growth traits (chapter 3). Estimates of genetic correlations between performance test and reproduction traits may be biased if only information on the selected females which have measurements on both performance test and reproduction traits are included in the analyses, as the effects of selection on performance test traits will not be fully accounted for (Meyer and Thompson, 1984; Sorenson and Johansson, 1992). Therefore, when estimating genetic correlations between performance test and reproduction traits, it is imperative that data from all individuals in the population, for example in a nucleus breeding herd, are included in the multivariate analysis of all traits included in the selection criterion.

In previous studies, there have been few estimates of the genetic relationships between performance test and reproduction traits and estimates have been variable in both sign and magnitude (for example, Short *et al*, 1994; Rydhmer *et al*, 1995; Crump, 1992; Johansson and Kennedy, 1983; Vangen, 1980a). To a large extent, estimates from previous studies have been inconsistent with those from the current study, particularly for growth and food intake. The lack of consistency between studies suggests that the estimated genetic relationships between growth and reproduction traits are population specific, due to the confounding of genotype/animals/population and environment. Therefore, estimates of genetic parameters from one population may not be appropriate to a different population (Falconer, 1989). It may also be naive to assume that estimated genetic relationships between growth traits, measured during performance test, and reproduction traits, measured up to eight months later, will be repeatable across studies. Traits measured at the end of performance test may not be the most informative for predicting the correlated responses in reproduction traits, since the biological mechanisms which control growth and reproduction traits are substantially different. The results reported in chapter 4 indicated that additional measurements of growth traits at the start of the mating period, when used in conjunction with performance test traits, would increase the accuracy of predicted genetic merit in reproduction traits. In a commercial breeding scheme, the cost-benefit implications of incorporating traits measured after performance test into selection criterion would need to be evaluated, since the timing of selection of animals would be delayed.

Estimation of the genetic correlations between traits measures the linear relationship between traits. The between-selection line variation in backfat depth was sufficient to detect the presence of a non-linear relationship between the predicted breeding values for average backfat depth and the predicted breeding values for litter weight at birth, indicating that extreme fat and lean genotypes for backfat depth would have lower litter birth weights than average (chapter 3). Some support for the novel conclusion was provided by Vangen (1980a), but the presence of a non-linear relationship between traits raises questions regarding the assumptions of the models that are currently used for the estimation of the genetic relationships between traits. If the relationship between backfat depth and litter traits is non-linear, then estimates of the genetic correlations may be close to zero, when a linear relationship between traits is measured. Information on the genetic relationships between performance test and reproduction traits is required to predict genetic merit for reproduction traits and the correlated responses in reproduction traits, given selection on performance test traits. If the relationship between backfat depth and reproduction traits is non-linear, then the predicted responses in reproduction traits to selection on an index including backfat depth may be uninformative, if a linear relationship between the traits is assumed.

Experimental design

The lean growth selection experiment was designed to examine the relationships between growth and carcass traits given various selection strategies for efficient lean growth. However, as selection experiments are efficient systems for measuring direct responses, they are also efficient for measuring correlated responses (Hill, 1971). Therefore, the correlated responses in reproduction traits for the different selection strategies were also evaluated. Aspects of the management of the animals during the reproductive phase were not ideal, which may have influenced the results from the experiment. For example, after performance test animals were moved to outside paddocks for mating, as there were not adequate facilities to house all animals indoors. Outdoors, animals were group penned rather than individually penned, as during performance test. The change of environment coupled with the mixing of individuals for the first time may have had negative effects on the performance of some animals. Food provisions were similar for each individual when the animals were outside, but as food allocation was on a pen basis, there may have been variation in food intake between animals due to competition. Further, variation in external temperature may have affected the growth of some individuals more than others. Since all individuals were under the same management system and a control line linked the four selection groups, then the environmental effects may have been removed, in the analysis of the data. If on the other hand there was a genotype by environment interaction for growth characteristics, then the ranking of the selection lines during performance test and post-performance test for growth characteristics, when pigs were housed in groups outside, may have been different.

The timing of data collection for the experiments reported in chapters 4 and 5 was not ideal to provide the maximum information on the relationships between traits measured at mating and farrowing and subsequent reproductive performance. Matings were unsupervised and there was no information on age at puberty in each of the selection groups or on exact mating dates. Gilts were older at mating than gilts in commercial practice (Whittemore, 1993), which may limit the value of the information from the experiment. The practical value of the estimated relationships between growth and reproduction characteristics would have been substantially enhanced if measurements of age at puberty and conception had been available. Constraints on data collection also prevented comprehensive conclusions being drawn regarding the contribution of food intake, changes in liveweight and backfat during lactation to pre-weaning piglet growth rate. Measurement of gilt liveweight was on average 10 days prior to farrowing and therefore changes in the weight of the unborn litter or of the gilt herself between the time of measurement and birth were not accounted for in the calculation of liveweight change during lactation. Further, there were no measurements of liveweight and backfat depth of gilts at 21 days post farrowing, such that the contribution of mobilisation of body reserves by the gilt to piglet growth, before creep feed was offered to the piglets, could not be accurately determined. Ideally, measurement of gilt liveweight and backfat depth would have been taken immediately after farrowing and at 21 days post-farrowing to determine contribution of body lipid mobilisation by the gilt to pre-weaning piglet growth rate.

The major reasons for the apparently inadequate design of the experiments reported in chapters 4 and 5 were the management of the pigs and the lack of facilities on the farm to accommodate the requirements of the experiments. For example, mating of gilts was delayed to allow animals longer to acclimatise to the outdoor environment before being mated. There were no facilities for recording individual feed intake in the outside pens. Frequent measurement of liveweights and backfat depths of pigs in outside accommodation was practically infeasible. Similarly, measurements of liveweight and backfat depth in the farrowing house, immediately after farrowing and at 21 days post-farrowing were difficult in practice and considered to be excessively stressful to the animals.

Breeding for performance and reproduction traits

The decrease in voluntary food intake with selection for increased lean content, with selection pressure on feed efficiency has been reported in previous studies (for example Ellis *et al*, 1983; McPhee, 1981). In the present study, selection for high LFC also produced a significant reduction in food intake, which was associated with reduced reproductive performance. Similarly, selection for low food intake during performance test reduced reproductive performance. In contrast, there was no associated reduction in reproductive performance with selection for lean growth rate on either *ad-libitum* or restricted feeding. However, selection for high LGA resulted in faster growing pigs than with selection for low LGA (Cameron and Curran, 1994), resulting in heavier pigs at a fixed age, which may ultimately be selection for a larger animal. Larger mature size may not be desirable in a breeding herd given the associated increased cost of maintenance and inevitable consequences on for example nutrient requirements and management of breeding sows (Whittemore, 1994). With selection for high LGS, performance in litter traits was not significantly reduced, but the number of gilts conceiving within the allotted mating period was considerably lower than for the alternative selection strategies. Selection for high LGS may have either reduced conception rate or delayed age at puberty, which may not be economic. The selection strategy dependant responses in both growth and reproduction traits indicate that in a breeding programme there may be advantages but also disadvantages of each selection strategies evaluated. The results from the study illustrate that both growth and reproduction traits should be considered in the design of breeding programmes based on selection for growth and carcass traits particularly in dam lines.

Further research

The study has provided a substantial amount of information on the effects of alternative selection strategies for components of efficient lean growth rate on reproductive performance in primiparous sows. However, the underling biological basis for responses in reproduction traits given differing genotypes of pigs was not determined. There are therefore several areas of research required, to provide a comprehensive evaluation of the selection strategies.

The results have indicated that food intake prior to farrowing and during lactation influences reproductive performance. Differences between selection strategies in reproductive performance may be due to a lack of knowledge in terms of the managerial and nutritional requirements of superior genotypes to maximise performance in both growth and reproduction traits. Presently, there is no information on the relationships between feeding strategies, growth and reproduction in pigs. Information on the interaction between genotype, nutrition and reproduction is required by the British pig breeding industry to identify optimal combinations of feeds and genotypes to minimise the constraints on reproduction performance.

A high proportion on animals in breeding herds are second parity or older. Therefore, information on the effects of alternative feeding regimes on the reproductive performance of multiparious sows is required. Information on the effects of nutrition on reproductive performance over at least two parities is required as the nutritional requirements of first parity sows will include a growth component, while information from second parity sows will be a more robust indicator of the reproductive performance of mature animals given different feeding regimes.

Information on the factors contributing to responses in reproduction traits will allow determination of the appropriate nutritional and managerial requirements of superior pig genotypes. Ultrasonic scanning techniques may be used to enable the contribution of ovulation rate and embryo survival to differences between the selection strategies to be determined.

General conclusions

The conclusions that can be drawn from the project can be summarised as follows:

1. Selection strategies for lean growth rate on either an *ad-libitum* or restricted feeding regime did not affect performance in litter traits, while selection for low daily food intake or high lean food conversion was associated with reduced litter performance.

2. Genetic correlation estimates indicated positive associations between growth rate and daily food intake during performance test with litter traits. A non-linear relationship between the predicted breeding values for backfat depth with the predicted breeding values for litter birth weight was detected, which has substantial implications for the design of selection criteria.

3. The relationships between liveweight and backfat depth measured at the start of the mating period with conception rate were not consistent between different genotypes of pigs such that conception rate may be determined by selection strategy dependent combinations of liveweight, age, food intake and body lipid content.

4. The accuracy of predicted genetic merit in reproduction traits may be increased when measurements of liveweight and backfat depth, measured at the start of the mating period, are used in selection indices in conjunction with performance test traits

5. Selection strategies which result in a low liveweight at farrowing or low voluntary food intake of gilts during lactation may have a negative influence on pre-weaning piglet growth rate.

The overall conclusion from the study is that selection strategies for components of efficient lean growth rate will not be detrimental to reproductive performance, in first parity sows, provided that there is no associated reduction in voluntary food intake.

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Reproductive performance of pigs selected for components of efficient lean growth

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Abstract

Correlated responses in reproductive performance to five generations of divergent selection for daily food intake (DFI), lean food conversion (LFC), lean growth rate on ad-libitum *feeding (LGA), and lean growth rate on scale feeding (LGS) were studied. Litter traits were measured on 1220 Large White gilts. Mean litter weights at birth and weaning were 12·9 kg and 63·5 kg, with average litter sizes of 10·3 and 7·9. Responses to selection in the high and low lines for litter size in the DFI and LFC selection groups were 1·9 and –1·5 (s.e.d. 1·1) at birth and 0·9 and –1·8 (s.e.d. 1·2) at weaning. Responses in litter birth weights were respectively positive and negative for DFI and LFC (3·0 and –2·8 (s.e.d. 1·4) kg) and the response in LGS (3 kg) was greater than in LGA (–0·1 kg). Selection line differences in litter weaning weight followed a similar pattern to birth weight for DFI and LFC (17·5 and –17·3 (s.e.d. 10·1) kg). Responses in litter weights were a result of selection line differences in both litter sizes and piglet weights. The relationships between litter size, litter weights and piglet weights at birth and weaning were essentially linear. An extra piglet at birth and weaning corresponded to an increase of 1·0 (s.e. 0·02) kg and 6·9 (s.e. 0·1) kg in litter weights. Piglet birth and weaning weights were decreased by 0·03 (s.e. 0·003) kg and 0·19 (s.e. 0·02) kg. A uterine constraint on piglet growth was implied, but there was no evidence for a limit to uterine capacity. Heritabilities for litter size, weight and piglet weight at birth of 0·06, 0·11 (s.e. 0·04) and 0·16 (s.e. 0·02) respectively were similar to those at weaning. Common environmental effects on piglet weights at birth and weaning were substantially higher than the heritabilities (0·38 and 0·45, s.e. 0·01). The study indicated that selection for lean growth on either an* ad-libitum *or restricted feeding regime did not significantly affect reproductive performance, but the high lean food conversion ratio and low daily food intake selection lines had impaired reproductive performance.*

Keywords: *genetics, lean growth, pigs, reproduction, selection.*

Introduction

Selection for growth and efficiency in commercial pig breeding schemes has been based on performance test traits, such as growth rate, food intake and on predicted carcass traits. In several selection experiments, pigs have been selected on the basis of one trait (e.g. growth or backfat; Kuhlers and Jungst, 1991a and b; Fredeen and Mikami, 1986a and b) or on an index of growth rate and backfat depth (Jungst, Christian and Kuhlers, 1981; Cleveland, Cunningham and Peo, 1982; McPhee, Rathmell, Daniels and Cameron, 1988). Although, selection on reproductive traits has been subject to less attention in commercial breeding programmes (see review of Haley, Avalos and Smith, 1988), the correlated responses in reproductive performance should be considered in the design of breeding programmes, based on selection for growth and carcass traits. Several studies have measured the responses in reproductive traits with selection on lean growth (Fredeen and Mikami, 1986c; Cleveland, Johnson and Cunningham, 1988; Kuhlers and Jungst, 1992), but in general, the responses have not been significantly different from zero. However, Cameron (1994) noted that the cumulative selection differential of animals selected for low daily food intake was substantially lower than with selection for high daily food intake, due to reduced reproductive performance. These results suggest that the choice of selection strategy will determine the magnitude of the correlated responses in reproductive traits and this has serious implications to the pig breeding industry.

The purpose of the current study was to determine the correlated responses in reproductive performance after five generations of divergent selection for components of efficient lean growth rate in a Large White population and to estimate the genetic and phenotypic parameters for reproductive traits.

Material and methods

Animals

Data were collected from five generations of Large White pigs divergently selected for daily food intake (DFI), lean food conversion (LFC), lean growth rate on *ad-libitum* feeding (LGA) and lean growth rate on restricted or scale feeding (LGS). Details on the establishment of the selection lines were given by Cameron (1994) and Cameron and Curran (1994). In each of the four selection groups, there were high, low and control lines and each line was designed to consist of 10 sires and 20 dams, with a generation interval of 1 year. Control lines were established to enable detection of asymmetric responses to selection and to provide genetic links between the four selection groups, as due to a batch farrowing management system, the selection groups farrowed at different times.

Pigs in the *ad-libitum* selection groups were performance tested over a fixed weight range with average start and finish weights of 30 and 85 kg. Pigs on restricted feeding were performance tested for a fixed time period of 84 days with an average starting weight of 30 kg and food intake equal to 0·75 g/g of daily *ad-libitum* food intake. All animals were individually penned during the performance test. At the end of test, ultrasonic measurements of backfat depth were taken at the shoulder, mid back (analogous to P2 carcass measurement) and the loin on both sides of the pig.

The selection objectives were to obtain equal correlated responses, measured in phenotypic standard deviation units, in carcass lean content and growth rate (or food conversion ratio) in the LGA and LGS (or LFC) selection groups. In the DFI selection group, the objective was daily food intake. In the LGA, LGS and LFC selection groups animals were selected on indices combining measurements of performance test traits (Cameron, 1994; Cameron, Curran and Kerr, 1994). Selection in the high, low and control lines of each selection group was based on both the selection criterion value and the parentage of the animal, the latter to avoid increases in the rate of inbreeding, such that selection was partially on a within-sire basis rather than solely on mass selection. At generation four, the average inbreeding coefficient for the selection lines was 5·8%.

All animals were mated between 9 and 10 months of age, about 8 weeks after the end of performance test. Matings were unsupervised and took place in outside paddocks. Individual boars were run with three gilts for 6 weeks and were inspected on a regular basis, so that inactive boars could be replaced. Pregnant gilts were given 2·5 kg food daily and farrowed sows up to 3·5 kg food twice daily of a diet containing 184 g/kg dry matter (DM) crude protein and 15·2 MJ digestible energy (DE) per kg DM. All animals were farrowed in selection group batches at an average age of 414 (s.d. 19) days. The coefficient of variation for farrowing age was 0·05 due to the short mating period. No cross fostering was practised. Piglets were offered creep food containing 264 g/kg DM crude protein and 18·0 MJ DE per kg DM from 14 days of age and were weaned at an average of 35 (s.d. 3) days.

Litter traits were measured on a total of 1220 Large White gilts, with 13 030 records of piglet birth weights including stillborn piglets and 9951 records of piglet weaning weights. For each gilt, litter size and weight at birth and weaning were measured, with piglet weights at birth and weaning also recorded.

Statistical analysis

Additive genetic (co)variances for the gilt traits were estimated using an individual animal model. Full pedigree information was included in a multivariate residual maximum likelihood (REML) analysis (Patterson and Thompson, 1971), using the REML algorithm of Meyer (1985). Additive genetic and common environmental (co)variances for individual piglet traits were estimated using an individual animal model in a multivariate derivative-free residual maximum likelihood (DFREML) analysis (Graser, Smith and Tier, 1987), adapted from the univariate DFREML algorithm of Meyer (1989), as proposed by Thompson and Hill (1990). For the estimation of variance components, fixed effects were not included in the analysis of gilt traits, as selection group-generation subclasses were confounded with months and years. Sex was included, as a fixed effect, in the analysis of piglet traits. Standard errors of heritabilities and common environmental effects were obtained using a similar procedure to Smith and Graser (1986). Standard errors of genetic correlations were estimated using the formulae of Robertson (1959).

The mortality of piglets, from birth to weaning, was not normally distributed and was analysed as a trait of the dam, using a generalized linear mixed model with binomial errors and a logistic link. The model was the marginal model of Breslow and Clayton (1993), fitted by the generalized linear mixed model procedure (Welham, 1993) for the GENSTAT statistical package (GENSTAT 5.3 Committee, 1993). Sires were included as random terms in the model with the selection group, line and generation subclass of each animal as fixed effects. The sire variance component was obtained from the generalized linear mixed model and the dam variance component was approximated from the estimate of the over-dispersion parameter, which was derived from the over-dispersed binomial variance using model III of Williams (1982). The residual variance on the logistic scale was equal to $\pi^2/3$ (Waddington, Welham, Gilmour and Thompson, 1994). The heritability of mortality, on the logistic scale, was calculated from estimates of the sire and dam variance components and the residual variance.

Maternal effects on litter size at birth were examined by daughter-dam regression, using a univariate DFREML (Meyer, 1989) analysis, including the litter size into which the dam was born as a linear covariate. Additive genetic effects, maternal genetic effects and the genetic covariance between the additive and maternal effects were estimated for the gilt traits using a univariate DFREML analysis as described by Meyer (1989).

A model including genetic group as a fixed effect was used to estimate the correlated responses at generation five, where genetic group corresponded to the selection group, line and generation subclass of each individual. Relationships between litter and piglet weights at birth and weaning with litter size at birth and weaning were examined to determine the relationship between litter size and weight and the existence of uterine constraints on pre-natal piglet growth and litter size.

Results

Correlated responses to selection

Means and phenotypic standard deviations for each trait are presented in Table 1. The observed mortality rate from birth to weaning included stillborn piglets and was comparable with the Meat and Livestock Commission (MLC) 1994 average (23·1 *v.* 20·4) (MLC, 1994). The total number of gilts farrowing and the number of piglets born and weaned by selection group are given in Table 2. The number of gilts farrowing in the LFC selection group was substantially less than in the other selection groups and consequently there were fewer piglets born and weaned. There were on average 20 fewer gilts farrowing in the LFC selection group in generations 2, 4 and 5, than in the DFI, LGS and LGA selection groups. In particular, in generations 4 and 5 the lower number of farrowing gilts was restricted to the LFC high line, the reasons for this are not yet apparent.

Table 1 *Means and phenotypic standard deviations of measured reproductive traits*

Trait	Mean	s.d.
Litter size at birth	10·3	2·9
Litter size at weaning	7·9	3·1
Mortality† Observed	23·1	
Logistic‡	−1·2	0·5
Litter birth weight (kg)	12·9	3·6
Litter weaning weight (kg)	63·5	24·8
Piglet birth weight (kg)	1·3	0·3
Piglet weaning weight (kg)	8·1	2·0

† Mortality rate of piglets from birth to weaning × 100 on the observed and logistic scale.

‡ Mortality rate on the logistic scale equalled $\log_e(p/(1-p))$.

Table 2 *Total number of gilts farrowing, number of piglets born and weaned by selection group*

Selection group	Gilts farrowing	Piglets born	Piglets weaned
Daily food intake	330	3471	2580
Lean food conversion	246	2678	1980
Lean growth (*ad libitum*)	308	3146	2449
Lean growth (scale)	336	3735	2942

Litter size and weight at birth and weaning showed slight negative skewness (average −0·46 and −0·63, s.e. 0·14). When litters of less than four piglets at birth and less than two piglets at weaning were removed from the data set, the skewness coefficients were reduced (average −0·05 and −0·16). It was not considered appropriate to transform the data to correct for skewness or to delete the small number of records contributing to the effect, as they comprised proportionately only 0·06 of the data. Individual piglet weights were normally distributed.

Correlated responses in reproductive performance after five generations of divergent selection for components of efficient lean growth are presented in Table 3. Differences between the high and low lines in litter size at birth and weaning were not statistically significant in the four selection groups

Table 3 *Estimates of selection line effects, within each selection group, for reproductive traits after five generations of selection for each selection group*

Selection group	Selection line	Litter size Birth	Litter size Weaning	Mortality† Observed	Mortality† Logit	Litter weight (kg) Birth	Litter weight (kg) Weaning	Piglet weight (kg) Birth	Piglet weight (kg) Weaning
Daily food intake	High	11·5	7·5	33	−0·7	13·2	63·5	1·10	8·5
	Control	11·1	8·9	19	−1·5	13·7	76·4	1·23	8·6
	Low	9·6	6·6	30	−0·9	10·2	46·0	1·05	7·2
Lean food conversion	High	9·1	7·1	21	−1·3	10·7	57·0	1·18	8·4
	Control	10·7	9·0	14	−1·8	13·7	68·5	1·31	7·9
	Low	10·4	8·9	14	−1·8	13·5	74·3	1·26	8·4
Lean growth (*ad libitum*)	High	10·9	8·6	20	−1·4	12·6	67·6	1·13	8·2
	Control	10·8	9·2	13	−1·9	13·9	72·7	1·28	8·2
	Low	9·9	8·4	15	−1·8	12·7	68·1	1·33	8·5
Lean growth (scale)	High	10·2	7·3	29	−0·9	14·0	56·6	1·38	7·9
	Control	11·0	8·4	23	−1·2	13·8	67·8	1·25	8·0
	Low	9·6	8·1	15	−1·8	11·0	61·0	1·16	8·1
	s.e.d.‡	1·1	1·2	§	0·4	1·4	10·1	0·13	0·5

† Mortality rate from birth to weaning × 100 on the observed and logistic (logit) scale.
‡ Average standard error of the difference between the high and low selection lines at generation 5.
§ Standard error not estimated as observations on a 0,1 scale.

(Table 3), although the low DFI and high LFC lines had lower litter sizes than the alternative lines. Although, average s.e.d. are presented in the Tables, the significance of responses to selection were tested using the appropriate s.e.d. for each comparison. Mortality rate between birth and weaning was statistically significantly higher in the high LGS line than in the corresponding low line. The highest incidence of postnatal death occurred when litter size at birth was low. There was a proportional reduction of 0·12 in mortality for every piglet increase in litter size at birth until litter size equalled five (Figure 1), after which there was a proportionate increase in mortality of 0·01 per unit increase in litter size. Piglet pre-weaning mortality decreased rapidly with increasing piglet birth weight, with mortality less than 0·10 for piglets with a birth weight greater than 1·5 kg (Figure 2).

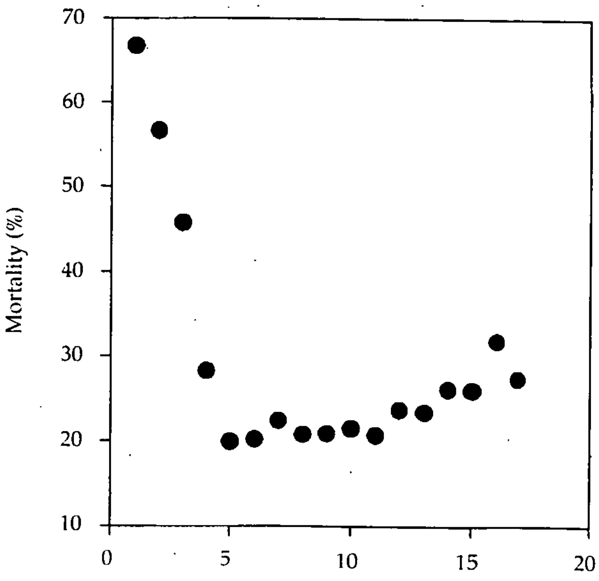

Figure 1 Pre-weaning mortality at a given litter size.

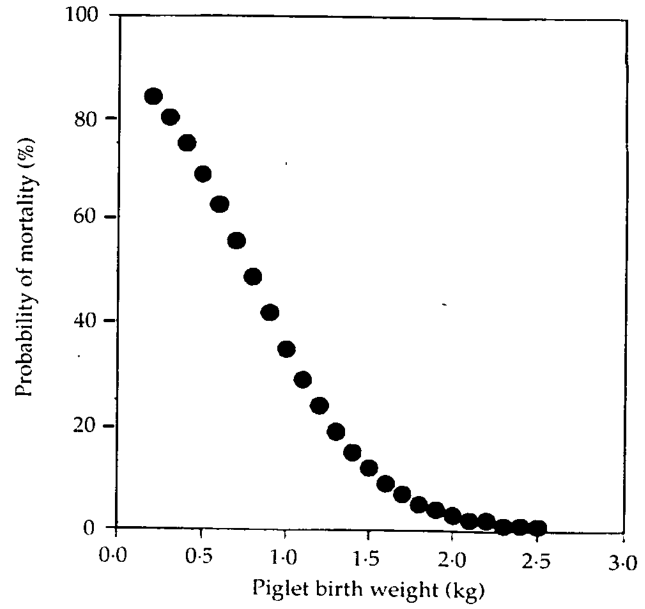

Figure 2 Pre-weaning mortality at a given birth weight.

The low DFI, high LFC and low LGS lines had significantly lower litter weights at birth than the complementary selection lines and the control lines, but there were no responses in piglet birth weights. The high and low line differences in litter and piglet weaning weight were not statistically significant, except for the low DFI line, which had lighter piglets at weaning than in the high DFI and control lines (Table 3), with no difference in weaning age (1·5 (s.e.d. 2·5) days).

Relationships between litter and individual piglet weights with litter size at birth and weaning

The essentially linear relationships between litter and piglet weights at birth and weaning with corresponding litter sizes are illustrated in Figures 3 and 4, respectively. At extreme litter sizes, variation in mean piglet weights, about the regression line, was a result of comparatively few observations at these points. The linear regression coefficients indicated a 1·0 (s.e. 0·02) kg increase in litter birth weight and a 6·9 (s.e. 0·1) kg increase in litter weaning weight for every piglet increase in litter size at birth and weaning, respectively. Conversely, with increased litter size, piglet birth and weaning weights decreased by 0·03 (s.e. 0·003) kg and 0·19 (s.e. 0·02) kg respectively. Within-selection group regression coefficients were not statistically different from each other or from the overall coefficients.

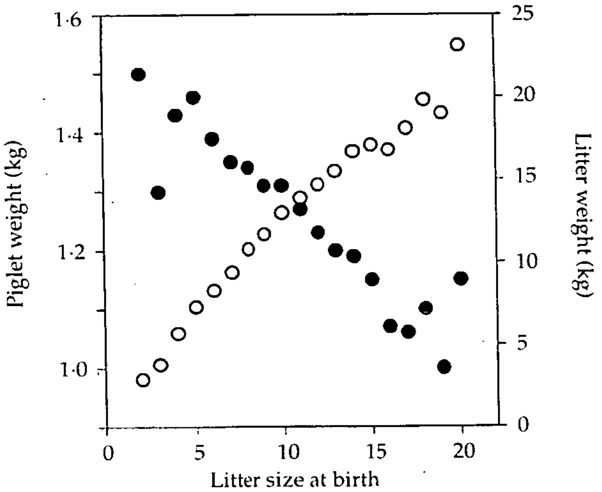

Figure 3 Average litter weight (○) and piglet weight at birth (●) with litter size at birth.

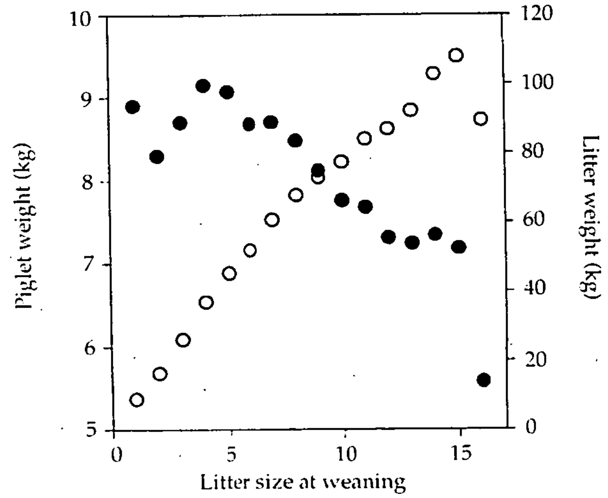

Figure 4 Average litter weight (○) and piglet weight at weaning (●) with litter size at weaning.

Incorporation of litter size as a covariate substantially increased the proportion of variation in litter weights at birth and weaning, which was accounted for by the model (Table 4). Linear adjustment of litter weight for litter size at birth and weaning markedly reduced residual variances of both traits and the genetic variance of litter weight at weaning, but there was little change in the genetic variance of litter weight at birth (Table 4). Estimates of variance components of piglet weights at birth and weaning were not changed by inclusion of a linear or quadratic term for litter size.

Table 4 *Comparison of linear and quadratic models including litter size at birth or weaning for litter weights*

Dependant trait	Covariate in model	Variance components: Genetic	Residual	R^2†
Litter birth weight (kg)		1·47	11·8	11
	Linear	1·65	2·4	82
	Quadratic	1·66	2·2	84
Litter weaning weight (kg)		87·5	525·0	14
	Linear	22·4	113·1	82
	Quadratic	23·7	102·0	83

† R^2 = (Model sums of squares/total sums of squares) × 100.

Adjustment of litter birth and weaning weights to constant litter sizes diminished the differences between the high and low selection lines in litter weight traits, except in the LGA selection group, while responses in the LGS and DFI groups for litter birth and weaning weights, respectively, remained (Table 5). Adjustment of piglet birth weight to constant litter size did not significantly change the magnitude of responses in any of the selection groups. Selection line differences in piglet weaning weights were unchanged when adjusted to constant litter size.

Table 5 *Comparison of high – low line differences in litter and piglet weights at birth and weaning when litter size at birth or weaning was included or not included as a covariate in the model*

Selection group	Litter weight (kg)				Piglet weight (kg)			
	Birth		Weaning		Birth		Weaning	
Litter size†	Included	–	Included	–	Included	–	Included	–
Daily food intake	0·8	3·0	11·3	17·5	0·14	–0·05	1·4	1·3
Lean food conversion	–1·3	–2·8	–3·9	–17·3	–0·13	–0·08	–0·3	0·0
Lean growth (*ad-libitum*)	–1·1	–0·1	–1·8	–0·5	–0·08	–0·20	–0·2	–0·3
Lean growth (scale)	2·1	3·0	0·8	–4·4	0·27	0·22	–0·2	–0·2
s.e.d.‡	0·9	1·4	4·6	10·1	0·06	0·13	0·3	0·5

† Litter size included or not included as a covariate in the model.
‡ Average standard error of the difference between the high and low selection lines at generation 5.

Genetic parameters

Heritabilities, genetic and phenotypic correlations for litter size and weights at birth and weaning are given in Table 6. Heritability estimates for litter size and weight were of similar magnitude at birth and at weaning. Phenotypic correlations between traits were high and positive. Genetic correlations were marginally lower than the phenotypic correlations, except for the genetic correlations between litter size at birth and litter weights. Piglet birth and weaning weights had high positive phenotypic and genetic correlations (Table 7). Residual and common environmental correlations were of the same order of magnitude, with common environmental effects being substantially greater than the heritability estimates, especially for piglet weaning weights. Estimates of heritability and the common environmental effect from a univariate analysis of piglet birth weight were similar to estimates from a multivariate analysis (0·14 (s.e. 0·02) and 0·37 (s.e. 0·01)). The heritability of mortality was estimated as 0·04 on the logistic scale.

Table 6 *Genetic and phenotypic parameter estimates for litter sizes and weights at birth and weaning*

Trait	NBORN	NWEAN	LBWt	LWWt
Litter size at birth (NBORN)	**0·06†**	0·69	0·84	0·55
Litter size at weaning (NWEAN)	0·53	**0·08**	0·72	0·88
Litter weight at birth (LBWt)	0·25	0·46	**0·11**	0·69
Litter weight at weaning (LWWt)	0·21	0·87	0·61	**0·14**

† Heritability estimates (in bold) on diagonal with phenotypic correlations (r_P) in upper triangle and genetic correlations (r_A) in lower triangle. s.e. (h^2) = 0·04, s.e. (r_P) = 0·02, average s.e. (r_A) = 0·24, except s.e. (r_A = 0·87) = 0·06.

Table 7 *Genetic, phenotypic and common environmental parameters estimates for individual piglet weights at birth and weaning*

Trait	Piglet weight (kg)	
	Birth	Weaning
Genetic and phenotypic		
Piglet birth weight (kg)	**0·16†**	0·46
Piglet weaning weight (kg)	0·67	**0·08**
Common environmental		
Piglet birth weight (kg)	**0·38‡**	0·45
Piglet weaning weight (kg)	0·42	**0·45**

† Heritability estimates (in bold) on diagonal with phenotypic correlation (r_P) in upper triangle and genetic correlations (r_A) in lower triangle. s.e. (h^2) = 0·02, s.e. (r_P) = 0·01, average s.e. (r_A) = 0·09.

‡ Common environmental effects (in bold) on diagonal with residual correlation (r_E) in upper triangle and common environmental correlation (r_C) in lower triangle. s.e. (c^2) = 0·01, s.e. (r_E and r_C) = 0·01.

Maternal effects, as estimated from daughter-dam regression coefficients (Table 8) on litter size at birth, were not significantly different from zero in any of

Table 8 *Daughter-dam regression coefficients and maternal effects for litter size at birth, within each selection group*

Selection group	Regression coefficient	s.e.	Maternal effect
Daily food intake	–0·11	0·06	–0·14
Lean food conversion	–0·10	0·07	–0·13
Lean growth (*ad libitum*)	–0·10	0·07	–0·13
Lean growth (scale)	–0·01	0·07	–0·04

the selection groups, although all estimates were non-positive. Similarly, estimates of maternal genetic effects of the dam for litter size and weights at birth and weaning were not significantly different from zero, as the difference between log likelihoods from models which included or did not include a maternal genetic effect were less than 1·0 for each trait.

Discussion

Correlated responses to selection

Correlated responses in reproductive performance to divergent selection for components of efficient lean growth rate in Large White pigs have demonstrated that selection for particular aspects of efficient lean growth adversely affects reproductive performance. Litter size at birth and weaning were reduced with selection for low DFI or high LFC, but not in the complementary selection lines. Selection for low DFI also resulted in decreased piglet weaning weight. The asymmetric responses to selection, primarily in lines which have reduced daily food intake, suggest that low daily food intake during performance test is maintained during pregnancy, such that prenatal piglet development is impaired. There were no significant responses in reproductive traits with divergent selection for LGA or LGS, except for decreased litter birth weight with selection for low LGS. Vangen (1980b) also found no difference in litter size and piglet weight at birth when pigs were divergently selected on an index based on growth and backfat, which was similar to the LGA selection criterion.

In several studies, it has been proposed that body composition is closely related to reproductive development and performance in pigs. For example, a negative genetic correlation between backfat and age at puberty was reported (Eliasson, Rydhmer, Einarsson and Andersson, 1991), while the estimated correlation between backfat and litter size was positive (Johansson and Kennedy, 1983). Similarly, Rydhmer, Johansson, Stern and Eliasson-Selling (1992) reported a positive and negative genetic correlation for pubertal age with leanness and growth rate, respectively. Results from the above studies support the suggestion of Kirkwood and Aherne (1985) that selection for carcass lean content may be indicative of selection for increased mature size, which, at a given age, produces a physiologically younger animal with a later onset of puberty, implying reduced reproductive performance compared to fatter animals at the same age. Therefore, an experiment has now been established to specifically examine the relationships between sow body composition at mating with subsequent litter size and piglet performance, in each of the four selection groups. The results from this experiment will be reported in a subsequent paper.

Vangen (1972) and Mersmann, Pond, Stone, Yen and Lindvall (1984) reported that the pre-weaning mortality rate was greater in piglets born to leaner rather than fatter dams. Mersmann *et al.* (1984) suggested that fatter sows may provide more energy or critical nutrients to new born pigs, through a greater concentration of lipid in milk, which may influence their survivability. Increased pre-weaning mortality may also be attributed to higher restlessness observed in leaner sows (Vangen, 1980a; McKay, 1993). Results from the current study were similar to those of Vangen (1972), that a higher rate of pre-weaning mortality was associated with low piglet birth weight and high litter size. In contrast, the high mortality in litters of less than five piglets was not closely related to birth weight.

Adjustment of litter and piglet weights for litter size at birth and weaning

Inclusion of litter size as a covariate in the model for litter and piglet weight at birth and weaning indicated that the relationships between these traits were essentially linear. Similar results have been reported by Crump (1992). Between-litter variation in piglet weights was larger when litters were small, but there were comparatively fewer records at extreme litter sizes. A substantial amount of variation in litter weights at birth and weaning was attributed to litter size. For example, responses in litter weights at birth in the DFI and LFC selection groups were mainly due to changes in litter size. However, in the LGS selection group, heavier litter weights at birth were primarily due to heavier piglets at birth, while the response in litter weight at weaning in the DFI selection group was attributable to both differences in litter size and piglet weight.

The negative relationship between piglet weight and litter size at birth implies a uterine constraint on pre-natal piglet growth, due to increased competition among embryos/foetuses for uterine resources (Christenson, Leymaster and Young, 1987). The positive linear relationship between litter weight and litter size at birth, with litter size ranging from one to 20 piglets, does not support the suggestion of an upper limit to uterine capacity, defined as the maximum number of foetuses that an individual can carry to term (Bennett and Leymaster, 1989). However, the existence of uterine constraints on pre-natal piglet growth may be implied by the magnitude of the regression coefficient, which was significantly less than the average piglet weight at birth.

Genetic parameters

The parameter estimates may be biased as reproductive traits were measured on selected females only and that selection was based on their performance in non-reproductive traits. The effect of selection on genetic parameter estimates for correlated traits has been well documented (Meyer and Thompson, 1984; Sorensen and Kennedy, 1984). In a univariate situation, inclusion of a complete relationship matrix in a REML analysis can take account of the effect of selection (Sorensen and Kennedy, 1986; Kennedy, 1990). Although all pedigree information was included in the model, selection on several traits may induce bias in genetic parameter estimates (Sorensen and Johansson, 1992). Therefore, genetic and phenotypic relationships between performance test and reproductive traits will be estimated in a multivariate analysis, in a subsequent study.

The reported selection line differences in reproductive traits were estimated from measurements on selected gilts within each selection line, rather than from all gilts within a line, such that the selection line differences will be overestimated. The extent of overestimation is the product of the selection differential in the last generation and the phenotypic regression of the reproductive trait on the selection criterion. In the experimental design, 20 out of 50 gilts were selected from the high and low lines each generation, within each selection group, such that the maximum selection differential per generation was 1·9 σ_p. Therefore, the maximum value for the over-estimate of the response, as a result of measuring only the selected females, will be 1·9 $r_p\sigma_p$, where r_p and σ_p are the phenotypic correlation and standard deviation, respectively. For example, in the DFI selection group, given a preliminary estimate of the phenotypic correlation between daily food intake and litter weight at weaning of 0·07, the lower limit for the response would be 14·2 kg compared with the measured response in litter weight at weaning of 17·5 kg.

Heritability estimates for litter size were similar to those of previous studies (see review of Haley *et al.* 1988). Similarly, heritability estimates for litter and piglet weights at birth and weaning were consistent with estimates of Vangen (1980b) and Crump (1992). Common environmental effects for piglet weights were substantially larger than heritability estimates, which indicated a high intraclass correlation between litter mates. The similarity between litter mates is expected as birth weights are influenced by uterine constraints and litter size, while weaning weights will be limited by nutrient supply from the dam. The low heritability estimate, on the logistic scale, for pre-weaning mortality suggests that there is little potential for genetic improvement in pre-weaning mortality with either direct or indirect selection. It may be more effective to select for reduced variation in litter size, rather than selecting for increased litter size, given that mortality increases with litter size and that the genetic effect on mortality is negligible.

Regression coefficients of the litter size an animal produced on the litter size into which it was born, from the current study were similar within each *ad-libitum* fed selection group and to those of Rutledge (1980). The regression coefficient is equal to $[h^2/(2 - m)] + m$, where h^2 is the heritability of litter size and m is the maternal effect (Falconer, 1965). The average maternal effect for the three *ad-libitum* fed selection groups was equal to −0·13, such that an increase of one pig in the litter of the dam would result in a reduction of 0·13 pigs in her daughters' litters. The estimate of the maternal effect from the current study was of the same order of magnitude as that of Van der Steen (1985). Standardization of litters at birth, through cross fostering, was suggested by Van der Steen (1985) to reduce the negative maternal influence on an animal's subsequent litter size. Given the negative relationship of litter size with piglet birth and weaning weights it may be necessary to take account of the post-natal maternal effect when selecting for piglet growth traits. However, selection line differences in piglet weights and estimates of genetic and residual variances at both birth and weaning were unchanged, when adjusted to constant litter size, which is analogous to standardization of litter size at birth as suggested by Van der Steen (1985). The adjusted selection line differences provide little evidence to suggest that selection for piglet growth will be adversely affected by maternal effects.

There was no evidence of maternal genetic effects for litter size and weights at birth and weaning in the present study, which was consistent with results of Haley and Lee (1992). However, Southwood and Kennedy (1990) reported significant maternal genetic effects for litter size at birth and weaning, although the magnitude of the effects was dependent on the dam's genotype. There are few estimates of maternal genetic effects, but the above studies suggest that the relative importance of maternal genetic effects may be population specific and dependent on both the data structure and the method of analysis.

The study has indicated that selection for lean growth on either an *ad-libitum* or restricted feeding regime did not significantly affect reproductive performance, while animals in the high lean food conversion ratio or low daily food intake lines had reduced reproductive performance. However, to understand the biological basis for responses in litter size, measurements of additional traits are necessary. Weight and ultrasonic backfat depth at mating need to be measured to establish the relationship between body composition of the sow with conception rate, litter size and piglet growth. Laparoscopic measurement of ovulation rate is required to assess potential litter size and embryo survival. The responses in reproductive performance have implications for the design of breeding programmes. Genetic and phenotypic relationships between performance test and reproductive traits will be estimated in a subsequent study, as prediction of responses in reproductive traits is required for the design of breeding programmes based on selection for growth and carcass traits.

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Selection for components of efficient lean growth rate in pigs
3. Responses to selection with a restricted feeding regime

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Abstract

Responses to four generations of divergent selection in pigs for lean growth rate (LGS) with restricted feeding were studied. The selection criterion was designed to obtain equal correlated responses in growth rate and carcass lean content, measured in phenotypic s.d. Animals were to be performance tested in individual pens with a mean starting weight of 30 kg for a period of 84 days. Daily food intake was equal to 0·75 g/g of the daily food intake for pigs offered food ad-libitum. *In the high, low and control lines, there were 1250 Large White-Edinburgh (LW) pigs and 875 British Landrace-Wye (LR) pigs. Each selection line consisted of 10 sires and 20 dams, with a generation interval of 1 year.*

After four generations of selection, cumulative selection differentials were 5·9 and 4·8 phenotypic s.d. for LW and LR populations, with similar responses, 1·8 (s.e. 0·17) phenotypic s.d. Mean weight at the end of test, growth rate and backfat depths at the shoulder, mid back and loin were 89 kg, 712 g/day, 26, 13 and 13 mm for LW and for LR pigs were 87 kg, 683 g/day, 28, 10 and 10 mm. High line pigs were heavier at the end of test (4·3 (s.e.d. 1·4) kg and 4·0 (s.e.d. 1·6) kg) for LW and LR populations, with corresponding responses in growth rate (54 (s.e.d. 16) g/day and 47 (s.e.d. 18) g/day). Responses in the three backfat depths were −4·1 (s.e.d. 1·2) mm, −2·6 (s.e.d. 0·7) mm and −2·9 (s.e.d. 0·7) mm for LW and −2·2 (s.e.d. 0·05) mm, −2·2 (s.e.d. 0·4) mm and −2·4 (s.e.d. 0·5) mm for LR populations. Responses in weight off test and backfat depths were symmetric about the control lines.

Heritabilities for LGS were 0·34 and 0·28 (s.e.d. 0·5) for the LW and LR populations, when estimated by residual maximum likelihood. Common environmental effects for LGS were 0·11 (s.e. 0·03) for LW and 0·17 (s.e. 0·04) for LR. Heritabilities for growth rate and average backfat depth were similar for LW and LR populations (0·17 and 0·29, s.e. 0·05), as were common environmental effects (0·10 s.e. 0·04). Average phenotypic and genetic correlations between growth rate and backfat, for LW and LR populations, were small (0·15 (s.e. 0·03) and −0·06 (s.e. 0·16), respectively).

Responses to selection and genetic parameter estimates demonstrate that there is substantial genetic variation in growth and fat deposition when pigs are performance tested on restricted feeding.

Keywords: *genetic parameters, lean growth, pigs, restricted feeding, selection.*

Introduction

Fowler, Bichard and Pease (1976) discussed the qualitative responses to selection on lean food conversion with *ad-libitum* feeding and to selection on lean growth rate with *ad-libitum* or restricted feeding. Responses to selection on an *ad-libitum* feeding regime may be partially due to correlated responses in daily food intake. Selection for lean growth rate on restricted feeding may be a result of increased efficiency, since variation in food intake is constrained. However, there may be limited selection pressure on food intake with selection on a restricted feeding regime, as the restriction may be relatively greater for some animals due to genetic variation in daily food intake.

Establishment of an experiment with divergent selection lines for daily food intake, lean growth rate and lean food conversion ratio was outlined by Webb and Curran (1986) and described by Cameron (1994) and Cameron and Curran (1994). Divergent selection lines for lean growth rate with restricted feeding were also included in the experimental design, to complement the lean growth rate selection lines on *ad-libitum* feeding and to enable subsequent examination of genotype with environment interactions. The Fowler and Ensminger (1960) study provided evidence for a genotype with feeding regime interaction, as pigs selected on restricted feeding had higher growth rates than animals selected on *ad-libitum* feeding, when tested on both restricted and on *ad-libitum* feeding regimes. McPhee, Rathmell, Daniels and Cameron (1988) reported results with uni-directional lines of pigs, which were consistent with those of Fowler and Ensminger (1960). Responses to selection for lean growth with restricted feeding and with *ad-libitum* feeding need to be examined to determine the optimal feeding regime for performance test, when the selection objective is increased lean growth with an *ad-libitum* feeding regime.

This paper examines the selection pressure applied and the responses to divergent selection for lean growth rate with a restricted feeding regime in Large White-Edinburgh (LW) and British Landrace-Wye (LR) populations. Genetic and phenotypic parameters for the selection criterion and the component performance test traits are estimated. Subsequent papers will examine the genotype with feeding regime interaction and describe the responses in carcass composition.

Material and methods

Animals

LW and LR boars and gilts were purchased from eight British nucleus herds and boars from national artificial insemination centres in 1982. All pigs were mated to halothane positive pigs, with their progeny halothane tested to identify homozygous or heterozygous halothane positive pigs (Southwood, Simpson, Curran and Webb, 1988). Pigs identified as halothane negative formed the base population and their progeny formed generation 0. LW and LR selection lines were established at Edinburgh and Wye, respectively, such that population and location were confounded.

Selection lines

In generation 0, full-sibs were allocated at random to either *ad-libitum* or restricted feeding for a genotype with environment interaction study (Cameron, Curran and Thompson, 1988). Pigs performance tested on restricted feeding were allocated to the lean growth selection group with restricted or scale (LGS) feeding. Restricted fed, generation 0 LW pigs were the progeny of 31 sires and 57 dams, with 19 sires and 67 dams for the LR population. Within each population, high and low selection lines were intended to consist of 10 sires and 20 dams. Control lines were also established. Ideally, three boars and three gilts from each of 20 litters per selection line were to be performance tested. Avoidance of half- and full-sib matings and by not mating half- and full-sib gilts to the same boar was used to restrict the rate of inbreeding. After four generations of selection, two-thirds of the animals within each selection line were performance tested on the restricted feeding regime, and the remaining animals were tested on *ad-libitum* feeding for the study of a genotype with environment interaction.

LW pigs from the high and low selection lines were mated at 9·5 months of age, on average, to maintain a generation interval of 13·5 months. All matings took place in outside paddocks, as there were no facilities to mate pigs inside. Selected animals were identified after all animals had completed test, as due to batch farrowing, animals within a selection group completed test over a 9- to 10-week period, on average. LR pigs were mated at 8 months of age with continuous farrowing throughout the year. All matings were supervised with boars introduced to gilts, in indoor mating pens. Due to continuous farrowing, selection groups were not tested in batches and pigs were identified for mating on a continuous basis until the required number of selected pigs, in each selection line, had been achieved. For the LR population, the period at start of test effect was fitted, with a period consisting of 3 months, as due to the practice of continuous farrowing the number of pigs starting test in each month was not large.

Performance test

Pigs were weaned at 5 weeks of age. For 4 days before the start of test, the test diet was mixed with the post-weaning diet to acclimatize pigs to the test diet. The performance test was over a fixed time period of 84 days with a start weight intended to be 30 kg and all pigs were individually penned. There were two similar testing houses for LW pigs and three testing houses for LR pigs. A high energy (15·9 MJ digestible energy per kg dry matter (DM)) and high protein (224 g/kg DM crude protein) pelleted diet was chosen to reduce nutritional constraints on pigs' genetic ability for protein and lipid deposition. At the end of test, ultrasonic back fat measurements were made at 6·5 cm off the mid line at the shoulder, mid back (analogous to P2 carcass measurement) and loin on both sides of the pig.

Food intake on test was determined by time on test and was intended to be 0·75 g/g per day of *ad-libitum* fed pigs. The weights of food provided daily in each

Table 1 *Restricted feeding scale (kg/day) by time on test in generations zero to two and three to four and the daily* ad-libitum *food intake of a sample of 50 Large White-Edinburgh pigs from the daily food intake control line in generation three*

	Week of test											
	1	2	3	4	5	6	7	8	9	10	11	12
Generation												
0, 1 and 2	0·95	1·1	1·2	1·4	1·65	1·8	2·0	2·2	2·3	2·3	2·3	2·3
3 and 4†	1·25	1·25	1·3	1·4	1·45	1·6	1·7	1·8	1·85	1·85	1·85	1·85
Ad-libitum intake	1·69	1·68	1·77	1·85	1·96	2·15	2·27	2·41	2·48	2·50	2·47	2·49
Pigs leaving food in generation 2†	2	3	3	5	12	16	36	41	48	36	29	25

† Large White-Edinburgh pigs only.

week of test are given in Table 1. In generations 0, 1 and 2, several LW pigs had not consumed the majority of the daily allowance, particularly after 7 weeks of test. For example, the numbers of times in generation 2 when a substantial amount of food was left, on at least 1 day during a test week, are given in Table 1. An appropriate feeding scale for the LW population was determined by measuring, over a period of 12 weeks, the weekly food intakes of 50 *ad-libitum* fed LW boars and gilts from the daily food intake control line of generation three. The results of the trial suggested that restricted-fed LW pigs were under-fed during the first 3 weeks of test and over-fed in the last 6 weeks of test (Table 1). The LW feeding scale used from generation 3 (Table 1), was calculated as 0·75 g/g of the measured *ad-libitum* food intake of the 50 LW pigs. The relationship between the two feeding scales was essentially linear, as the regression equation of the new scale on the old scale (OS) was 0·73 + 0·48 (s.e. 0·02) OS, which proportionately accounted for 0·98 of the variation in food intake on the new scale. In generation two, the maximum amount of food refused was less than 6 kg for 40 LW pigs, out of 87 LW pigs not consuming all food given. After changing the feeding scale in generation three, of the 79 LW pigs refusing some food, a total of 64 LW pigs refused less than 6 kg of food. In generation four, 15 LW pigs out of only 22 LW pigs refusing some food, refused less than 6 kg. The total amount of food given during test for LW pigs was 150·5 kg in generations zero, one and two, but 134·0 kg in generations three and four.

Over the four generations of the experiment, only 84 out of 875 LR pigs did not consume all the daily allowance, although the reduction in food intake was small. The average total food intake of the 84 LR pigs was equal to 142·0 kg, with the lowest food intake equal to 132·5 kg, compared with the allocated food of 150·5 kg.

Selection objective and criterion

The selection objective was to achieve equal correlated responses, measured in phenotypic standard deviations units, in carcass lean content and average daily gain, respectively. The selection criterion used throughout the experiment in both populations was

$$17{\cdot}25\ ADG_S - 22{\cdot}88\ BFAT_S$$

where ADG_S and $BFAT_S$ are the standardized deviations from the mean for each animal for average daily gain and average backfat depth at the shoulder, mid back and loin, measured at the end of test. Derivation of the selection criterion coefficients, with genetic and phenotypic parameters taken from a review of the literature, are given in the **Appendix**. Standardized traits, which had zero mean and unit phenotypic variance, were used for selection purposes to maintain constant selection pressure on each trait in the selection criterion, due to potential between-generation variation in phenotypic variances. The selection criterion was scaled to have an arbitrary standard deviation of 30 units.

Statistical analysis

Retrospective selection criterion was calculated for each animal, using estimates of phenotypic variances from univariate derivative free residual maximum likelihood analyses (see below) of average daily gain and backfat depth, to standardize traits in the selection criterion, rather than using the within-generation variances. Mean values of the retrospective selection criterion accumulated over generations unlike the actual selection criteria used for selection purposes, which were expressed as deviations from a within-generation mean value.

Cumulative selection differentials (CSDs) were calculated using the method of Thompson and Juga (1989). The selection criterion was adjusted for fixed effects of sex, testing house and month or period at the start of test, estimated by least-squares analysis of variance, before calculation of cumulative selection differentials.

Inbreeding coefficients were calculated directly from the pedigree using the same method as Van Vleck (1988).

Additive genetic, common environmental and residual (co)variances were estimated with an individual animal model in a multivariate derivative free residual maximum likelihood (DFREML) analysis (Graser, Smith and Tier, 1987), using a modification of the DFREML algorithm of Meyer (1989), as proposed by Thompson and Hill (1990). To calculate the selection criterion for each animal, the phenotypic regression coefficient for average backfat with weight on test was determined from phenotypic (co)variances estimated in a bivariate DFREML analysis of average backfat and weight on test, to take account of genetic variation in weight on test. In the analysis of weight off test and the three backfat measurements, weight on test was fitted as a covariate. Average backfat depth was pre-adjusted for weight on test in the bivariate analysis with average daily gain, as the DFREML package required equal design matrices. Fixed effects for sex, testing house and month or period at start of performance test were included in the model. Iterations were assumed to have converged when the difference in variances of successive log likelihoods was less than 10^{-9}. Standard errors of parameter estimates were obtained using a similar procedure to Smith and Graser (1986). Standard errors of genetic correlation estimates were calculated as suggested by Robertson (1959).

Table 2 *Means and phenotypic stardard deviations of performance test traits by population*

	Population			
	Large White-Edinburgh		Landrace-Wye	
	Mean	s.d.	Mean	s.d.
Average daily gain (g/day)	712	64	683	73
Average backfat depth (mm)†	17·0	2·42	16·2	1·59
Shoulder (mm)	25·6	3·54	28·3	1·93
Mid back (mm)	12·7	2·01	9·5	1·38
Loin (mm)	12·7	2·38	10·8	1·75
Weight on test (kg)	28·8	1·2	30·3	1·3
Weight off test (kg)	89·0	5·4	87·2	6·0

† Average of the shoulder, mid back andd loin backfat depths.

Direct and correlated responses to selection were determined from the mean within-generation and selection line predicted breeding values, which were calculated using a best linear unbiased prediction (BLUP) procedure, using estimates of the additive genetic, common environmental and residual variances from DFREML analyses. Variances of direct and correlated responses, at generation four, were calculated using the method of Tier and Smith (1989). Phenotypic responses to selection were estimated as the phenotypic mean values of animals within a generation and selection line group, after adjusting the data for fixed effects.

Results

Means and phenotypic standard deviations for performance test traits, from all generations, are given in Table 2. Growth rates and backfat depths were similar between populations, but variation in backfat depths was greater in the LW than in LR population. Numbers of animals tested each generation are given in Table 3. In generations one,

Table 3 *Total number of animals performance tested* (N_i) *in each generation, the inbreeding coefficient (F) (and s.d.) at generation four, by selection line, and the total numbers of litters per generation per population*

	Population							
	Large White-Edinburgh				Landrace-Wye			
	High	Control	Low	No. of Litters	High	Control	Low	No. of Litters
N_0		186		57		172		67
N_1	51	100	89	38	71	43	74	49
N_2	75	121	107	48	70	39	76	54
N_3	76	119	114	56	60	21	85	45
N_4	69	69	74	57	58	49	57	58
Total†	271	409	384		259	152	292	
F (%)	4·91	1·26	4·59		3·65	1·63	7·23	
s.d.	3·18	1·62	2·26		0·79	2·04	1·69	

† Total number of animals performance tested in generations 1 to 4.

Table 4 *Cumulative selection differentials by selection line, in selection criterion units, in each generation, by population*

	Population			
	Large White-Edinburgh		Landrace-Wye	
	High	Low	High	Low
Generation				
0	33·4	−27·3	30·8	−38·0
1	39·0	−47·0	42·4	−56·7
2	53·6	−66·4	46·4	−67·0
3	69·7	−82·3	51·5	−77·5

two and three, there was an average of 33 and 52 pigs of each sex tested in the high and low LW lines and corresponding averages of 33 and 39 LR pigs of each sex. On average, there were 8·2 LW sires and 15·1 dams with 9·2 LR sires and 17·9 dams, per selection line. Inbreeding coefficients in the high and low lines were similar (Table 3) and higher than in the control lines, due to the experimental design.

CSDs in the low selection lines were marginally greater than in the high lines, in both populations (Table 4). After four generations of selection, the LW and LR CSDs were equal to 5·9 and 4·8 phenotypic standard deviations, respectively. Direct responses after four generations in the two populations were similar, 46·6 index units, on average (Table 5), equivalent to 1·8 phenotypic standard deviations. Phenotypic responses were comparable with direct responses, calculated from predicted breeding values (Table 5).

Heritabilities for the selection criterion, estimated by DFREML, of 0·34 and 0·28 (s.e. 0·05) for LW and LR populations (Table 6) were similar to the estimates of 0·34 and 0·22 from the Thompson and Juga (1989) method and to the realized heritability, estimated by weighted regression of cumulative response on CSD of 0·32 and 0·30 (s.e. 0·06). Common environmental effects (c^2) were significantly greater than zero (Table 6), particularly for the LR population. The phenotypic variance of the LGS selection criterion was intended to equal 900; but actual variances in the LW and LR populations were 669 and 715, respectively. Given the selection criterion coefficients, the reason for low variances was the difference between the actual phenotypic correlation for growth rate and backfat depth of 0·19 and 0·11 for the LW and LR populations, respectively (Table 8), and the value of −0·10 used in design of the selection criterion.

Table 5 *Direct and phenotypic responses in the selection criterion, by population*

	Population					
	Large White-Edinburgh			Landrace-Wye		
	High	Control	Low	High	Control	Low
Generation						
1	13·3	0·7	−15·0	10·0	−1·8	−5·1
2	12·3	0·0	−21·3	16·4	−4·5	−10·1
3	13·1	−1·0	−25·0	20·2	−6·1	−14·8
4†	17·3	−0·6	−29·6	25·6	−3·3	−20·7
s.e.d. (H-L)‡		4·4			4·6	
H-L§	17·4	−0·6	−29·4	26·9	−6·4	−23·4

† Response estimated as the difference between the mean predicted breeding value of animals in each generation relative to mean predicted breeding value of the base generation.
‡ Standard error of the difference between the high and low selection lines at generation four.
§ Response estimated as the difference between the mean phenotype of high line animals minus the mean phenotype of low line animals, in generation 4, after adjustment for fixed effects.

Correlated responses to selection are presented in Table 7, with estimates of the genetic and phenotypic parameters. High line pigs were heavier with less backfat than low line pigs and within-population selection line differences were of similar magnitude. The corresponding selection line differences in growth rate and average backfat depth were similar for LW and LR pigs (Table 8). Responses in average backfat depth, measured in phenotypic s.d. were larger (1·32 and 1·45 for LW and LR) than the responses in growth rate (0·84 and 0·64 for LW and LR).

Table 6 *Genetic and phenotypic parameter estimates for the selection criterion, by population*

	Population	
	Large White-Edinburgh	Landrace-Wye
Variance components		
Additive genetic σ_A^2	224	198
Common environmental σ_C^2	76	122
Residual σ_E^2	368	396
Phenotypic σ_P^2	669	715
heritability (h^2)	0·34	0·28
s.e.	0·05	0·05
common environment (c^2)	0·11	0·17
s.e.	0·03	0·04

Table 7 *Correlated responses at generation four for weight off test (Wtoff) and backfat depths at the end of test with estimates of the genetic and phenotypic relationships between traits, by population*

		Population							
		Large White-Edinburgh				Landrace-Wye			
		Wtoff (kg)	Shoulder (mm)	Backfat mid-back (mm)	Loin (mm)	Wtoff (kg)	Shoulder (mm)	Backfat mid-back (mm)	Loin (mm)
Correlated responses to selection	High line	1·80	−1·40	−0·86	−1·12	2·66	−1·13	−1·12	−1·13
	Control	0·51	0·15	0·27	0·27	−0·26	0·23	0·16	0·17
	Low line	−2·49	2·66	1·71	1·83	−1·32	1·08	1·08	1·25
	s.e. (H-L)	1·40	1·21	0·66	0·71	1·55	0·52	0·40	0·50
Genetic phenotypic	Wtoff†	**0·18**	0·14	0·18	0·21	**0·17**	0·11	0·14	0·13
	Shoulder	−0·32	**0·20**	0·74	0·70	−0·09	**0·21**	0·80	0·80
	Mid-back	−0·04	0·70	**0·37**	0·84	−0·07	0·99	**0·30**	0·90
	Loin	0·13	0·76	0·88	**0·35**	0·02	0·99	0·99	**0·26**
	s.e. (h^2)§	0·04	0·04	0·06	0·06	0·05	0·05	0·05	0·06
	s.e. (r_A)§	0·14	0·06	0·03		0·17	0·02	0·02	
Environmental parameters	Wtoff‡	**0·12**	0·27	0·30	0·28	**0·11**	0·18	0·25	0·19
	Shoulder	0·13	**0·08**	0·75	0·64	0·00	**0·15**	0·66	0·68
	Mid-back	0·06	0·99	**0·07**	0·80	0·01	0·99	**0·16**	0·83
	Loin	0·08	0·99	0·96	**0·08**	0·04	0·98	0·97	**0·19**
	s.e. (c^2)	0·03	0·03	0·02	0·02	0·04	0·04	0·04	0·05

† Heritabilities (in bold) on the diagonal, with genetic and phenotypic correlations below and above the diagonal.

‡ Common environmental effects (in bold) on the diagonal, with common environmental and residual correlations below and above the diagonal.

§ Standard errors of heritability estimates and average standard errors of genetic correlation estimates, by column.

Heritability estimates for weight off test, growth rate and backfat depths in the two populations were essentially equal (Tables 7 and 8). Similarly, phenotypic and residual correlations between growth rate and backfat depths, for both populations, were positive, with residual correlations

Table 8 *Correlated responses at generation four for average daily gain (ADG) and backfat depth with estimates of the genetic and phenotypic relationships between traits, by population*

		Population			
		Large White-Edinburgh		Landrace-Wye	
		ADG (g/day)	Backfat (mm)	ADG (g/day)	Backfat (mm)
Correlated responses to selection	High line	23	−1·14	32	−1·15
	Control	7	0·25	−2	0·19
	Low line	−31	2·10	−15	1·17
	s.e. (H-L)	16	0·70	18	0·46
Genetic and phenotypic parameters	ADG†	**0·17** (0·05)	0·19 (0·03)	**0·16** (0·05)	0·11 (0·03)
	Backfat	−0·10 (0·16)	**0·29** (0·05)	−0·02 (0·17)	**0·28** (0·05)
Environmental parameters	ADG‡	**0·10** (0·03)	0·31	**0·10** (0·04)	0·19
	Backfat	0·09	**0·11** (0·03)	−0·01	**0·19** (0·04)

† Heritabilities (in bold) on the diagonal, with genetic and phenotypic correlations below and above the diagonal with standard errors in parentheses.

‡ Common environmental effects (in bold) on the diagonal, with common environmental and residual correlations below and above the diagonal.

being marginally greater, but correlations between common environmental effects were zero. Genetic correlations between growth rate and backfat depths were not significantly different from zero, while correlations between the three backfat measurements were equal to unity in the LR population, but significantly less than one in LW population. As with the selection criterion, common environmental effects for weight off test, growth rate and backfat depths were significantly greater than zero, particularly for LR population.

Discussion

Fowler, Bichard and Pease (1976) used a biological model to qualitatively predict responses in components of efficient lean growth rate to selection for lean tissue food conversion (LTFC) or lean tissue growth rate (LTGR) on an *ad-libitum* or restricted feeding regime. Selection for increased LTFC on *ad-libitum* feeding would be primarily achieved by reduced food intake, while increased LTGR, in the long term, would be a result of increased food intake. In contrast, selection for increased LTGR on restricted feeding would increase efficiency as variation in food intake would be constrained. However, the majority of experiments with selection on lean growth rate have tested pigs on *ad-libitum* feeding (Sather and Fredeen, 1978; Vangen, 1979; McPhee, 1981; Cleveland, Cunningham and Peo, 1982; Ellis, Chadwick, Smith and Laird, 1988), rather than on restricted feeding regimes (Fowler and Ensminger, 1960; McPhee *et al.*, 1988). No experiment has selected for LTGR on both feeding regimes, although, Fowler and Ensminger (1960) did select for growth rate on high and low planes of nutrition. To test the hypotheses of Fowler *et al.* (1976), Smith and Fowler (1978) argued for the establishment of a comprehensive selection experiment with lines selected for different criteria on *ad-libitum* or restricted feeding regimes and measurement of correlated responses on the alternative feeding regimes. Performance testing of pigs on a restricted feeding regime has been used by several breeding companies (Gu, Haley and Thompson, 1989; Crump, 1992). In the current experiment, the food restriction was intended to be 0·75 g/g of the mean *ad-libitum* food intake to limit variation in food intake, although the restriction will be relatively greater for some animals due to genetic variation in appetite.

Selection for lean growth on restricted feeding may identify animals which preferentially partition energy towards protein deposition rather than towards fat deposition, due to the higher energy cost of fat deposition (Webster, 1977). In the LW population, proportionally more energy was credited to protein deposition in the high selection line than in the low line (0·25 *v.* 0·21) and conversely less to lipid deposition (0·37 *v.* 0·41), with the control line intermediate (0·23 and 0·39), using formulae of Whittemore, Kerr and Cameron (1994) for energy requirements, assuming energy for maintenance is solely a function of live weight. Vangen (1980) compared lines divergently selected for lean growth and suggested that the lower maintenance requirement of the high lean growth line was due to less energy being required to retain protein than to retain fat depots. However, Kanis (1990) suggested that energy partition towards protein deposition was negatively associated with food intake capacity, such that on restricted feeding with no intended variation in food intake, genetically lean animals with low food intake capacity would have similar growth rates, but higher maintenance requirements than fat animals. An interpretation of Kanis's (1990) hypothesis, which is consistent with the results of Vangen (1980) and the formulae of Whittemore *et al.* (1994), is that genetically lean animals have higher rates of protein turn-over, such that energy requirements per g of protein retained (synthesized – degraded) were greater than in genetically fat animals, assuming that energy requirements per g of protein and fat deposited and for maintenance were similar between selection lines.

Less variation in growth rate and backfat depth with restricted feeding compared with *ad-libitum* feeding has been reported (Cameron *et al.*, 1988; Gu *et al.*, 1989). In the present study, phenotypic variances for growth rate and average backfat depth with restricted feeding were proportionately equal to 0·34 and 0·67 of the variances with *ad-libitum* feeding for both populations, although the mean values were proportionately reduced by only 0·83 and 0·93, respectively. On restricted feeding, fat deposition was sustained, with marginally less variation than with *ad-libitum* feeding, but variation in growth rate was substantially reduced to a greater extent than expected from reduction in the mean value. The maintenance of fat deposition with restricted feeding, seemingly at the expense of growth rate, suggests that around 80 to 100 kg there may be a preference for fat deposition rather than muscle growth. Therefore, selection line differences in fat deposition may be expected to be relatively greater than differences in weight off test. In the LW and LR populations, the selection line differences in mid-back fat depths and weight off test, relative to the mean, were 0·21 and 0·05, respectively.

Heritability estimates for growth rate and average backfat depth were equal to half of those used in the design of the selection criterion. Estimates of phenotypic and genetic correlations between growth rate and average backfat depth were of similar magnitude, but of opposite sign to the selection criterion parameters. However, the impact of the differences between the two sets of parameters may have little effect on the correlated responses in growth rate and carcass lean content as the ratio of the selection criterion coefficients was −1·33, which was similar to the value of −1·24, when the estimated parameters were used to determine the selection criterion. Examination of the correlated responses in carcass composition, in a subsequent paper, will determine the validity of the above hypothesis.

There are few estimates of genetic correlations for growth and backfat, with pigs on restricted feeding regimes (McPhee *et al.*, 1988; Gu *et al.*, 1989; Crump, 1992). The estimates of Gu *et al.* (1989) and Crump (1992) were dependent on the extent of the food restriction. Gilts were restricted to a greater extent than boars and the average genetic and phenotypic correlations between growth and backfat, for the two studies, were −0·40 and −0·13 for gilts and 0·04 and 0·20 for boars. The restricted feeding regime of McPhee *et al.* (1988) was equal to 0·80 of *ad-libitum* food intake and the genetic and phenotypic correlations of −0·22 and −0·05, were more similar to the gilt estimates of Gu *et al.* (1989) and Crump (1992). Parameter estimates from the present study, −0·06 and 0·15, were closer to the boar estimates of Gu *et al.* (1989) and Crump (1992). In each study, genetic correlations were less than phenotypic correlations and the magnitude of the genetic correlation was determined by the level of food restriction.

Comparison of the direct response on one feeding regime with the correlated response given selection on the alternative feeding regime will determine the relative merit of each selection strategy and provide information on the genotype with environment interaction. Fowler and Ensminger (1960) selected for growth rate on high and low nutritional planes and measured the direct and correlated responses for each plane of nutrition. McPhee *et al.* (1988) selected for lean growth on restricted feeding and measured responses on *ad-libitum* and restricted feeding regimes. Both Fowler and Ensminger (1960) and McPhee *et al.* (1988) concluded that selection on restricted feeding may be preferable to selection on *ad-libitum* feeding, when progeny were grown on an *ad-libitum* feeding regime. Fowler and Ensminger (1960) estimated genetic correlations of 0·74 and 0·67 from the pairs of direct and correlated responses, which suggested a genotype with environment interaction for growth. They suggested that increased growth on restricted feeding was a result of increased efficiency, but on *ad-libitum* feeding the response was due to increased food intake. A subsequent genotype with environment interaction study, of a similar form to that of Fowler and Ensminger (1960), but for all four selection groups from the current experiment, will provide further information on the genotype with environment interaction.

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Appendix

The selection objective was to achieve equal correlated responses, measured in phenotypic standard deviations units, in carcass lean and average daily gain.

The selection criterion was determined by calculating selection index coefficients for average daily gain (ADG) and average backfat (BFAT), which were then scaled such that the selection criterion had a standard deviation of 30.

Formula for calculating the selection criterion coefficients for the index: b_1 ADG + b_2 BFAT are:

$$b_1 = 1 \text{ and } b_2 = (r_{AL} h_{ADG} h_{LEAN} + h^2_{ADG}) / (r_{BL} h_{BFAT} h_{LEAN} + r_{AB} h_{ADG} h_{BFAT})$$

where r_{AL} and h^2_{ADG} are the genetic correlation between average daily gain with carcass lean and the heritability of average daily gain, respectively. The variance (V) of the index was $1 + 2b_2 r_P + b_2^2$ where r_P is the phenotypic correlation between ADG and BFAT. Scaled selection index coefficients, b_i^*, were equal to $(30/\sqrt{V})\, b_i$.

The LGS selection criterion was then equal to b_1^* ADG + b_2^* BFAT.

Table *Phenotypic and genetic parameters used in the design of the selection criteria*

	Average daily gain	Backfat depth	Carcass lean
Average daily gain	**0·30**†	−0·10	
Backfat depth	0·00	**0·50**	
Carcass lean	0·10	−0·50	**0·45**

† Heritabilities on the diagonal (in bold), genetic and phenotypic correlations are below and above the diagonal, respectively.

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An Approach to Prediction of Feed Intake in Growing Pigs Using Simple Body Measurements

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ABSTRACT

*Several data sets were used to test the proposition that feed intakes can be predicted from knowledge of simple measurements of pig live weight and fatness. Key equations are the prediction of lipid mass (*Lt*) and protein mass (*Pt*) from* P2 *fat depth and live weight (*Wt*);* $\mathrm{Lt} = 1{\cdot}12\,(0{\cdot}19\mathrm{Wt} + 0{\cdot}78\mathrm{P2} - 9{\cdot}2)$, $\mathrm{Pt} = 0{\cdot}439(0{\cdot}41\mathrm{Wt} - 0{\cdot}52\mathrm{P2} + 2{\cdot}4)$*, and the prediction of daily metabolisable energy intake (*EIp*) as the sum of the needs for protein retention (*Pr*), lipid retention (*Lr*) and maintenance,* $\mathrm{EIp} = 52\mathrm{Pr} + 53\mathrm{Lr} + 0{\cdot}44\mathrm{Wt}^{0{\cdot}75}$*. The approach is found to be sound for the prediction of the average daily intake of groups of pigs over a given weight range; but was less accurate in the prediction of the feed intake of individual pigs in some, but not all, of the populations examined. For the 10 groups of pigs tested, mean actual and predicted feed intakes (kg/day) were respectively: 2·31 and 2·35; 2·14 and 2·18; 3·15 and 3·03; 2·81 and 2·80; 1·87 and 2·08; 1·96 and 2·24; 2·01 and 2·04; 2·03 and 2·06; 2·20 and 2·12, 1·88 and 1·78.*

INTRODUCTION

Prediction of feed intake in pigs is difficult but necessary for effective simulation of growth, diet formulation, and determination of optimum feeding strategies on *ad libitum* feeding regimes (see review of Whittemore, 1994). But despite the apparent *prima facie* case for the feed intake potential of different pig types to be known, such information is not readily available for practical use. Empirical measurement of the feed intakes of populations of pigs has allowed construction of regression relationships which may result in the estimation of intake as a function of, for example, body weight. But general descriptors of feed intake based upon energy consumption and showing a curvilinear increase in digestible energy (*DE*) intake with weight (*Wt*), such as those of ARC (1981), DE (MJ/day) = $55(1-e^{-0{\cdot}0204Wt})$, and of NRC (1987), DE (MJ/day) = $55(1-e^{-0{\cdot}0176Wt})$ are not sufficient, first because there is variation in appetite potential found between different pig populations, and second because a simple exponent is unlikely to adequately describe change in the energy costs of maintenance and growth as the animal increases in weight. It may be deduced that any inaccuracy which occurs lies in body weight itself reflecting only maintenance, a relatively minor component of feed usage in the growing pig. The position may be improved if the algorithm were to account for the two major components of feed usage: the rate of growth and the composition of growth; the latter possibly being predicted from weight and ultrasonic backfat depth. The paper will examine this proposition using sample populations of UK white pigs which show some range in their feed intake. It will suggest that significant advancement of the methodology for intake prediction is possible, but will also demonstrate limitations to the concept.

The hypothesis for the framework follows from the propositions of Emmans & Fisher (1986) and Whittemore (1994) which may be adumbrated as follows. Feed intake and growth are related, as the second is resultant from the first. The digestibility of nutrients by pigs is not greatly influenced by the rate of ingestion, and the ability of the pig to lose digested energy absorbed in excess of need by increased heat loss to the environment is limited. Growth is dependent upon nutrients available after the costs of daily maintenance have been deducted. Maintenance costs may be determined as a simple function of body weight. The nutrient requirement for growth is related to the energetic costs of protein and lipid deposition, and the relative rates of growth of these tissues. It is possible that the mass of protein and lipid in the body of the pig may be predicted from knowledge of body weight and ultrasonically measured backfat depth. Determination of mass and fat depth at points separated in time allows determination of daily gains of protein and lipid. The daily feed intake of an individual pig is the sum of its daily costs of maintenance, and daily protein and lipid deposition.

The problem addressed here is the prediction of expected feed intakes of different groups of pigs which may differ, due to their genetic makeup, in their intrinsic appetite. Feed intake appears about 0·4 heritable

(Cameron, 1992) and is highly positively genetically correlated to growth rate (0·8) and also, although more weakly, positively correlated to fatness (0·4). While these values are higher than other earlier estimates, selection against fatness would, nevertheless, tend to reduce feed intake unless there was also counterbalancing selection pressure for growth rate, which has not always been the case in many selection programmes with low emphasis on growth rate. In practice, selection against backfat has been found consistently to result in reduced feed intake (Sather & Fredeen, 1978; McPhee, 1981; Ellis *et al.*, 1988), especially if efficiency is also included in the index (Cameron, 1992). Webb (1989) presents a collated table from the work of McPhee (1981, 1985), showing how selection for efficiency and leanness had, after five generations, reduced average daily feed intake from 2·24 to 2·07 kg. Cameron (1994) has shown how divergent selection for daily feed intake, after only four generations of selection, has created pig populations whose average feed intakes over the live weight range 30–85 kg differ by 0·315 kg daily (2·198 kg vs 1·883 kg). Earlier, a comparison of commercial products from UK breeding companies (MLC, 1982) had shown widely ranging *ad libitum* daily feed intakes for the different company genotypes. Average daily feed intakes for the 27–85 kg test period for 10 genotypes ranged between 2·16 and 2·61 kg/day; the genotype with the highest feed intake having an appetite some 20% greater than that with the lowest feed intake. Breed differences in daily feed intake have long been accepted, with halothane-positive strains showing lower appetites than halothane-negative (Webb, 1989). Kalm (1986) measured average daily feed intakes between 30 and 90 kg live weight of 2·2 kg for Large White pigs, but only 1·9 for the Pietrain. In practical production circumstances, the fast-growing Large White, Landrace and Duroc breeds, and their crosses, all tend to have similar feed intakes which are higher than the rather slower growing Pietrain and Belgian Landrace meat-line types; the appetites of the latter being up to 20% less than the former (Whittemore, unpublished). The review of Henry (1985) indicates Pietrain pigs eat 81% of the amount eaten by French Landrace, and the Belgian Landrace breed eat 92%.

Whilst the relationship between feed intake and growth rate appears to be positive in a comparison of pig breeds or strains, this may not necessarily be the case for an individual animal. Therefore, a given pig may grow faster on the same amount of feed due to preferential partition of nutrients to protein retention rather than lipid, or conceivably due to enhanced biochemical efficiency for some aspect of metabolism. The prediction of feed intake as a function of its needs is addressed by Emmans & Fisher (1986), Emmans (1989) and Whittemore (1993), the former having suggested that 'an animal seeks to eat because it seeks to grow'. Given an effective description of energy needs for maintenance and for the components of growth, and assuming no differences between and within populations in the efficiency of biochemical transformations, feed intake may therefore be calculated as the simple sum of requirements; and this is likely to create a need for dependable information on protein and lipid retention rates. The axiom is logical but awaits verification.

Determination of parameters that might allow prediction of potential feed intake necessarily demands conditions where there is no evident constraint upon desired feed intake. An acceptable health status must be assumed. Environmental limitations to the expression of potential feed intake have been reviewed by Emmans & Fisher (1986) and by Kyriazakis (1994) and include excessive environmental temperature, dietary nutrient imbalance, and diet bulk density. Animals in environmental temperatures below their comfort temperature will, of course, incur energy costs for cold thermogenesis, and this would encourage *pro rata* increased feed consumption. Such constraints, however, are better seen as modifiers to predicted feed intake; potential feed intake requiring to be estimated as independently as possible of environmental effects.

A PRELIMINARY TEST OF THE PROPOSITIONS

To examine the proposition that feed intake may be determined as the sum of the nutrient needs, a data set collected for an unrelated purpose by a UK breeding company (1992), and independent of the present considerations, has been used (Table 1). The pigs were derived from the Large White breed by *c.* 15 generations of selection for lean tissue growth rate and fed a diet of 14·3 MJ *DE*/kg under *ad libitum* conditions

TABLE 1

Feed Intakes and Daily Gains of Pigs (Males, $n = 78$; Females, $n = 41$)

	Notation	*55–75 kg live weight*		*95–110 kg live weight*	
		Males	*Females*	*Males*	*Females*
Average liveweight (kg)	Wt	65	65	102·5	102·5
Average daily live weight gain (kg/day)	Wg	1·082	0·954	1·165	1·034
Average feed intake (kg/day)	FI	2·31	2·14	3·15	2·81
Using first prediction method:					
Average predicted feed intake (kg/day)	FIp^1	2·38	2·19	2·81	2·61
Using second prediction method:					
Average predicted feed intake (kg/day)	FIp^2	2·35	2·18	3·03	2·80

allowing individual recording. Table 1 shows the recorded values for live weight (Wt), feed intake (FI) and daily live weight gain (Wg).

First prediction method

If the composition of the live weight gain during growth is presumed to be in the ratio of 1 : 1 : 3 for the daily retentions of lipid, protein and water, and if the energy costs (MJ ME/kg) of protein and fat retention are 52 and 53, respectively, then the energy cost of gain will be 21 MJ ME/kg ($[52Pr + 53Lr]/5$). A first estimate of the predicted energy intake (EIp^1) can be estimated from the sum of the requirements for maintenance (0·44 MJ ME per kg $Wt^{0\cdot75}$) and for growth, assuming a protein : lipid ratio of 1:1 and no cost of cold thermogenesis. For a detailed discussion of the choice of values for the energy costs of protein deposition, lipid deposition and maintenance, see ARC (1981), Whittemore (1983, 1993, 1994). Thus

$$EIp^1 \text{ (MJ } ME\text{/day)} = 21\,Wg + 0{\cdot}44\,Wt^{0\cdot75} \qquad (1)$$

Since DE is 1·04ME, and the diet contained 14·3 MJ DE/kg, then predicted feed intake (FIp^1) can be calculated (Table 1). Given the simplistic nature of eqn (1), the effectiveness of the prediction is encouraging for the lighter pigs but disappointing for the heavier animals. The main deficiency of eqn (1) is the assumption that energy for growth is used with constant efficiency above maintenance. Energy partitioning between protein and lipid retention is variable, especially with levels of feed consumption and pig size, and the water component of the gain is almost wholly associated with the protein moiety. Thus, where the lipid gains are greater than the 1 : 1 ratio proposed above, feed intake would be underestimated by eqn (1).

Second prediction method

Lipid retention (Lr) and protein retention (Pr) may be estimated by regression from measurement of live weight and ultrasonic measurement of fat depth at different points in the course of growth. In the study described in Table 1, fat depths at the $P2$ site were taken at 75, 95 and 110 kg live weight (Table 2). Total lipid mass (Lt) and total protein mass (Pt) may be estimated from the following equations from the review of Whittemore (1983):

$$Lt = 1{\cdot}12\,(0{\cdot}19\,Wt + 0{\cdot}78\,P2 - 9{\cdot}2) \qquad (2)$$
$$Pt = 0{\cdot}439\,(0{\cdot}41\,Wt - 0{\cdot}52\,P2 + 2{\cdot}4) \qquad (3)$$

which related to UK white cross-bred pigs.

TABLE 2

Fat Depths [*P2*(mm)] of Pigs, together with Estimated Protein and Lipid Masses and Gains

	75 kg live weight		*95 kg live weight*		*110 kg live weight*	
	Males	*Females*	*Males*	*Females*	*Males*	*Females*
Fat depth (mm)	7·6	8·2	9·1	9·8	10·4	11·1
Lipid mass (kg)(*Lt*)	12·3	12·8	17·9	18·5	22·2	22·8
Protein mass (kg)(*Pt*)	12·8	12·7	16·1	15·9	18·5	18·3
Lipid gains 75–95 kg (*Lr*)	—	—	0·301	0·269	—	—
Lipid gains 95–110 kg (*Lr*)	—	—	—	—	0·337	0·298
Protein gains 75–95 kg (*Pr*)	—	—	0·176	0·155	—	—
Protein gains 95–110 kg (*Pr*)	—	—	—	—	0·186	0·165
Lipid : protein gain 75–95 kg (*Lr/Pr*)	—	—	1·71	1·74	—	—
Lipid : protein gain 95–110 kg (*Lr/Pr*)	—	—	—	—	1·81	1·81

Estimates of total lipid and protein mass, using eqns (2) and (3), and daily rates of retention are presented in Table 2. Even though the equations relate to a different population of pigs from that under study, and relationships between fat depth and protein mass may be to some extent population specific, it is evident that presumptive composition of the weight gain used for eqn (1) was indeed in error, and it would therefore be beneficial to consider energy requirements for growth in terms of the protein and lipid components themselves rather than attempt to estimate crudely the composition of live weight gain. Using energy costs for protein and lipid deposition of 52 and 53 MJ *ME*/kg, respectively, the following equation may be described;

$$Elp(\text{MJ } ME/\text{day}) = 52Pr + 53Lr + 0{\cdot}44Wt^{0{\cdot}75} \qquad (4)$$

Using the values in Table 2, eqn (4) now gives much improved feed intake predictions (FIp^2) for the 95–110 kg growth phase (Table 1). *Lr* and *Pr* are not directly calculable for the 55–75 kg growth phase as *P2* measurements were not taken at 55 kg. However, linear extrapolation of the 75–95 kg and 95–110 kg phases would indicate supposed rates of lipid and protein retention of 0·26 and 0·16 kg for males, and 0·24 and 0·14 for females at 65 kg live weight (for the 55–75 kg phase). Respective *Pt* and *Lt* values are calculated to be 11·3 and 9·48 for males, and 11·1 and 9·96 for females. Estimates for FIp^2 for the 55–75 kg growth phase are also given in Table 1. The close agreement between actual and predicted feed intakes supports the contention that, provided the composition of the gain is determinable, feed intake can be predicted from the sum of the nutrient needs for protein growth, lipid growth and maintenance. Further, the data required for such a prediction need to be no more than the live weight of the pig, and the *P2* backfat ultrasonic measurement at a single pair of points sufficiently widely spaced in time to allow measurement of gain. The exercise confirms the validity of the energy cost coefficients used in eqn (4), and the predictions for *Lt* and *Pt* used in eqns (2) and (3). Knowledge of easily measured live weight, growth and *P2* fat change allows prediction of rates for *Pr* and *Lr*, which in turn allows estimation of the intake necessary to achieve those rates.

A SUBSTANTIVE TEST OF THE PROPOSITIONS

The data set of Cameron & Curran (1994) comes from the fourth generation of three groups of animals selected for (High) and against (Low) lean growth, lean efficiency, and daily feed intake (for details of selection traits and population characteristics see Cameron, 1994). Entire male and female Large White pigs were grown from 30–85 kg, fed *ad libitum* a diet of 13·9 MJ *DE*/kg and penned individually. Measurement of time taken (days) to grow from 30–85 kg and of *P2* backfat depth at 85 kg allowed estimation of average metabolic weight, $Wt^{0\cdot75}$, according to

$$(Wt_1^{1\cdot75} - Wt_0^{1\cdot75})/1\cdot75(Wt_1 - Wt_0) \qquad (5)$$

where Wt_0 is the start weight and Wt_1 is the final weight, and also enabled estimation of final protein and lipid mass from eqns (2) and (3). Protein and lipid gains were estimated assuming that the proportions of protein and lipid at the start of test were $0\cdot17Wt_0$ and $0\cdot15Wt_0$; a presumption which may be open to some error as pigs with differing propensities to fatten during growth may also have differing fatnesses at the start of the test. The average actual daily feed intakes (*FI*) for the six groups of pig genotypes, and the predicted feed intake (FIp^2), estimated from eqn (4) and the knowledge that the *ME* value of the diet is 13·4 MJ/kg (13·9/1·04), is given in Table 3.

As evidenced in Table 3, the data set provided six groups of pigs sufficiently different in actual daily feed intake and appropriate to allow a substantive test of the propositions and equations for the prediction of feed intake. Actual and predicted average daily feed intake for the two groups of pigs selected for High and Low lean growth were similar, while the match for the other four groups may be considered acceptable, there being over-prediction by some 200 g/day (10%) in the lean efficiency group and under-prediction by some 100 g/day (5%) in the daily feed intake line. The prediction method provided a good first approximation for

TABLE 3
Actual and Predicted Average Food intake for the Six Pig Groups Described in the Data Set of Cameron (1994)

	Average actual daily feed intake (FI)(kg ± SE[a]*)*	*Average predicted daily feed intake (FIp^2)(kg ± SE*[a]*)*
Efficiency line (n = 135)		
High	1·87 (± 0·20)	2·08 (± 0·21)
Low	1·96 (± 0·23)	2·24 (± 0·28)
Growth line (n = 138)		
High	2·01 (± 0·23)	2·04 (± 0·21)
Low	2·03 (± 0·27)	2·06 (± 0·27)
Feed line (n = 139)		
High	2·20 (± 0·24)	2·12 (± 0·22)
Low	1·88 (± 0·22)	1·78 (± 0·15)

[a] Standard error of treatment mean, √ variance. Differences between actual and predicted values were not significantly different.

feed intake but the match between actual and predicted average feed intake was selection-group dependent. Prediction for the first data set (Table 1) was more accurate than the second (Table 3), which may have been related to the weight range under consideration being smaller.

PREDICTION OF INDIVIDUAL PIG FEED INTAKE

The data set of Cameron (1994) also allowed comparison of the predicted feed intakes with actual feed intakes of individual animals. Regression equations of individual pig actual feed intake upon individual pig predicted feed intake for the six groups were:

Growth line
High Actual feed intake (kg) = −0·107(± 0·196) + 0·992(± 0·092) Predicted feed intake $r^2 = 0{\cdot}67$
Low Actual feed intake (kg) = 0·365(± 0·158) + 0·813(± 0·077) Predicted feed intake $r^2 = 0{\cdot}60$

Efficiency line
High Actual feed intake (kg) = 0·721(± 0·276) + 0·551(± 0·125) Predicted feed intake $r^2 = 0{\cdot}29$
Low Actual feed intake (kg) = 0·150(± 0·118) + 0·840(± 0·051) Predicted feed intake $r^2 = 0{\cdot}80$

Feed line

High Actual feed intake (kg) = 0·597(± 0·221) + 0·618(± 0·101) Predicted feed intake $r^2 = 0{\cdot}39$

Low Actual feed intake (kg) = −0·034(± 0·285) + 0·921(± 0·152) Predicted feed intake $r^2 = 0{\cdot}35$

Satisfactory prediction would be evidenced by a coefficient which is close to unity (with a low SE) and a high r^2 value. Evidently the ability of the methodology, as proposed, to predict the feed intake of individual pigs within groups is not as good as for the groups as a whole. Individual pigs may behave differently from the expectations from eqns (2), (3) and (4). In the case of three of the six groups, more than 60% of the variance in actual feed intake was satisfactorily explained by the prediction equations, and in the case of four of the six groups the regression coefficients were encouragingly close to unity; but in the remaining groups less than 40% of the variance was explained.

The causes of the anomalies in prediction of feed intake merit further consideration: (a) in relation to the number of individual pigs which may be needed to make up a satisfactory cohort for prediction of the feed intake of pig groups; and especially (b) as variation in biochemical efficiencies of utilisation of nutrients for protein deposition, lipid deposition and maintenance may be implicated.

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