

## THE VALUE OF PIG SELECTION EXPERIMENTS

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### INTRODUCTION

Short term selection experiments, which may be of less than ten generations, with production traits forming the selection objective, should estimate genetic parameters in the base population and genetic covariances with traits that are difficult to measure, after sufficient differences between selection lines have been achieved. Knowledge of genetic and phenotypic relationships between and within sets of production and non-production traits, for example physiological predictors of genetic merit, is required for the evaluation of alternative selection strategies. Information on relationships between traits may provide insight into the biological mechanisms involved in generating differences between selection lines. Selection experiments whose selection objective is a non-production trait are generally used for physiological studies, to establish genetically differing lines of animals, when the rate of genetic response in the selection objective is not of prime importance. To complement short term experiments, the long term selection experiments should be able to test for non-linearity of response, which includes selection limits, and to test theories on population size, such as predicted rates of inbreeding. Laboratory animals form appropriate populations for the examination of quantitative genetic theory using long term selection experiments, while short term selection experiments with meat, milk, egg or fibre producing animals should provide information that can be used directly in commercial breeding programmes. This paper briefly reviews pig selection experiments and some of the results obtained, to discuss aspects of selection experiments that should be considered for the continuation of existing experiments or before future pig selection experiments are established.

### EXPERIMENTAL POPULATIONS

The majority of European and North American pig selection studies have used Large White, Landrace or Duroc pigs, as they are the major breeds in pig production systems (Table 1). Studies with replicated selection experiments in different breeds (Hetzer and Miller, 1973; Kuhlers and Jungst, 1991 a,b), have not examined if experimental results are consistent between breeds. Division of experimental resources to have two replicates within a breed is not efficient, as direct estimation of the variance of responses will be based on only one degree of freedom. Given the small number of breeds, the large number of selection experiments and associated parameter estimates, there has not been a review of experimental results to determine if within-breed, between-study estimates are comparable. A comprehensive review is required to identify required areas of research and duplicated research subjects. At the start of a selection experiment, the experimental population should be screened for known single genes of large effect. For example, selection for aspects of lean growth has been associated with high frequency of the halothane gene (Vogeli et al, 1983;

Grashorn and Muller, 1985), such that differences between the selection lines are confounded with different frequencies of alleles of the gene. Several studies have substantially changed the selection criterion and assumed a new base population (Cleveland et al, 1982; Lamberson et al, 1991), when study of the correlated responses to selection on one trait has suggested alternative selection criteria. The effect of prior selection in the population may bias the rate of direct and indirect responses to secondary selection, compared to a population that had no previous selection on a correlated trait.

**Table 1.** Selection objectives, experimental designs and duration of several pig selection experiments

Selection objective	Design †	Generations	Breed ‡	Reference
Liveweight	U	6	D, LR	Kuhlers and Jungst (1991 a,b)
Backfat depth	D + C	16	D, LW	Hetzer and Miller (1973)
Growth rate (GR) and backfat (BF)	D + C	8	LR	Vangen (1979)
"	U	5	N	Cleveland et al (1982)
"	U	5	LR, LW	McPhee et al (1988)
"	D	7	LR	Vogeli et al (1983)
Growth rate, backfat, GR and BF	U	9	LR	Fredeen and Mikami (1986)
Food conversion ratio (FCR)	U	7	LR,LW	Webb and King (1983)
Growth rate, backfat and FCR	U	8	LW	Godfrey et al (1991)
"	U	10	LW	Henderson et al (1983)
Lean growth, efficiency, food intake	D	4	LR, LW	Cameron and Curran (1994)
Lean growth (restricted feeding)	D	4	LR, LW	Cameron et al (1994)
Lean weight, lean %	U	4	LW	Leymaster et al (1979)
Litter size	U	11	LW	Bolet et al (1989)
Ovulation rate	U	10	N	Cunningham et al (1979)
Ovulation rate and embryo survival	U	5	N	Neal et al (1989)
Sow productivity index	U	8	N	Lamberson et al (1991)
"	U	10	LR	Neal and Irvin (1992)
Leg weakness score	D + C	5	D	Rothschild and Christian (1988)
5 $\alpha$ -androstenone in backfat	D	5	LR	Willeke et al (1987)
Serum cholesterol	D	3	LR, LW	Pond et al (1992)
NADPH activity in backfat	D + C	8	LR	Mueller (1986)

† : Divergent selection with (D + C) or without (D) a control and uni-directional (U) selection with a control.

‡ : D : Duroc, LR : Landrace, LW : Large White or Yorkshire, N : Nebraska synthetic

## SELECTION OBJECTIVES AND CRITERIA

The majority of pig selection experiments can be grouped according to the selection objectives of either growth and carcass traits, reproductive performance or physiological traits. Several selection experiments are presented in Table 1, to illustrate the variety of selection objectives, experimental designs and duration the experiments. Selection lines have also been established to examine specific aspects of pig production, such as boar taint (Willeke et al, 1987) or leg weakness (Rothschild and Christian, 1988). The majority of studies have one selection objective, but a few studies have several selection objectives for direct comparison of selection strategies (Leymaster et al 1979; Fredeen and Mikami, 1986; Cameron and Curran, 1994; Cameron et al, 1994). Inclusion of two selection objectives enables measurement of the direct response in trait X, the correlated response in trait Y and *vice versa* in the complementary selection lines, and permits testing of predicted and realised responses to selection. For example, selection on ovulation rate (Cunningham et al, 1979) or on a linear index of ovulation rate and embryo survival (Neal et al, 1989), for improvement in litter size, without a selection line in litter size, has prevented direct comparison of the selection strategies. Selection on ovulation rate was suggested to be more efficient than selection on litter size (Haley and Lee, 1992), but indirect responses in litter size have not equalled expectation (Cunningham et al, 1979). An explanation for the difference between predicted and realised responses could be established, if complementary selection lines for litter size had existed, to enable measurement of correlated responses in ovulation rate, in the same environment.

Ovulation rate and embryo survival are components of litter size, such that measurement of correlated responses to selection on the components and their product, viz. litter size, may provide more information than selection on only one trait. In contrast, selection on highly correlated traits may be less informative than selection on component traits. For example, Kuhlers and Jungst (1990, 1991a) established separate selection lines for 70 day weight and 200 day weight, which are qualitatively similar traits, but the relative efficiency of the selection objectives has not been determined. Selection for several objectives may be more informative than selection for only one objective. For example, selection on carcass lean weight resulted in a greater correlated response in carcass lean % than the direct response (Leymaster et al, 1979), despite the higher heritability of carcass lean % (0.44 v 0.20). Comparable results have been reported for selection on lean growth or lean efficiency (Cameron and Curran, 1994). Therefore, selection experiments with more than one selection objective should be considered.

Several studies have selected on a correlated trait, rather than on the trait of interest. Ovulation rate (Cunningham et al, 1979), an index of ovulation rate and embryo survival (Neal et al, 1989) or testis size (Schinckel et al, 1984) have been selected on for improvement in litter size. Similarly, selection on the activity of NADPH-generating enzymes in backfat for improvement in carcass lean (Mueller, 1986). Regarding the latter study, other physiological traits may be more highly correlated with carcass lean than NADPH-generating enzymes and the choice of selection criterion may be directly related to the information from the study. Additionally, potential predictors of genetic merit may be more efficiently identified with selection on the trait of

interest rather than on a correlated trait, e.g. carcass lean content and NADPH-generating enzymes. Divergent selection lines have also been established to examine interaction of genotype and dietary fat, with selection for serum cholesterol (Pond et al, 1992).

#### **DIVERGENT OR UNI-DIRECTIONAL SELECTION WITH A CONTROL**

Divergent selection experiments with or without controls and uni-directional selection experiments with controls have been established, with uni-directional selection predominantly for reproductive performance and divergent selection for physiological studies (Table 1). For estimation of genetic response, divergent selection experiments are more efficient than uni-directional experiments with a control, as the ratio of the response to the variance of the response with divergent selection is double the ratio with uni-directional selection. However, the comparison is made assuming the selection lines are of the same structure as the control and responses are symmetric. For the divergent selection experiments in Table 1, asymmetric responses have been reported (Hetzer and Millar, 1973; Vangen, 1979; Cameron and Curran, 1994), with larger responses generally in the non-commercially viable lines (e.g. high backfat or slow growth), such that the precision of divergent selection may be lower than expected, compared to the experimental design. Despite the asymmetry, the efficiency of divergent selection, relative to uni-directional selection, can be determined from the contribution of information on genetic parameters by each selection line. Thompson and Atkins (1990) proposed a method to allocate information to within-lines and to between-line differences, which can be used to assess the merit of retaining the selection line showing least response in a divergent selection experiment. Uni-directional selection experiments with two selection objectives, but no controls, can be used to compare alternative selection strategies, provided the two selection groups are contemporaneous. These experiments have generally been used to examine genotype with environment interactions (Mitchell et al, 1990; Karlsson et al, 1993).

#### **ESTIMATION OF GENETIC PARAMETERS**

Selection experiments have routinely estimated realised heritabilities, but not genetic correlations. Evaluation of alternative selection strategies, from prediction of correlated responses, requires knowledge of heritabilities and genetic correlations. Similarly, the rate of genetic improvement per generation is frequently estimated, but the parameter is a function of the selection intensity, which will be specific to the experiment, and so provides little information. Recent developments in multi-variate mixed model methodologies (e.g. animal model residual maximum likelihood) have allowed estimation of heritabilities and genetic correlations for traits not in the selection criterion, to provide information for evaluation of alternative selection strategies. More information can therefore be obtained from selection experiments conditional on the experimental data being analysed with appropriate methodology. Selection on components of efficient lean growth has been associated with reduced reproductive performance (Vangen, 1980; Cleveland et al, 1988; Kerr and Cameron, 1994). It may be advantageous to include reproductive traits in the multi-variate analyses, to ensure that predicted responses are not over-estimated by not accounting for negative correlations between traits.

Similarly, additive genetic effects have been estimated in the analyses of several experiments, without testing for the significance of common environmental effects, maternal effects and the covariance between additive genetic and maternal effects in the model, so that the heritabilities may be over-estimated. The use of simplistic models may contribute to the discrepancies between realised and predicted responses of selection experiments. In several studies, heritabilities have been estimated from the regression of cumulative response on cumulative selection differential, but standard errors of heritabilities have been presented, which have not accounted for genetic drift. Cumulative responses are correlated and have heterogeneous variances, such that omission of genetic drift assumes homogeneous, uncorrelated variances (Hill, 1980). Therefore, the perceived information from such selection experiments will be over-estimated.

### CORRELATED TRAITS

The selection experiment provides an effective resource to estimate genetic covariances with traits in the selection criterion, particularly for traits which are either difficult or expensive to measure. For example, genetic relationships between carcass composition with meat and eating quality traits are required for the effective inclusion of meat and eating quality traits in breeding programmes and ultimately for the evaluation of alternative selection strategies. Correlated responses in reproductive performance, with selection on aspects of lean growth, have important implications on pig breeding programmes, such that knowledge of the genetic relationships between growth and reproduction is required. Measurement of correlated responses in physiological traits, for estimation of genetic correlations with traits in the selection objective, may identify physiological predictors of genetic merit for carcass composition (Scott et al, 1981; Lundstrom et al, 1983) or reproductive performance. Measurement of component traits of the selection objective, such as ovulation rate or embryo survival with selection for litter size (Kelly et al, 1988; Gama et al, 1990), may provide information on the biological mechanisms underlying the responses to selection. Mersmann et al (1984) and Stone (1984) used divergently selected lines for backfat deposition to examine the relationship between fat deposition and piglet mortality.

Several studies have reported no differences in physiological traits between selection lines, but the experimental power has been low as the probable inverse relationship between the number of animals measured and the difficulty or expense of a particular measurement, may result in limited numbers of animals being measured. The experimental power to detect a difference between selection lines is dependent on both the number of animals per line and the difference between the lines. One of the main reasons for seemingly conflicting results from physiological studies, based on selection experiments, is the low number of animals measured, leading to large between-study variation for the physiological trait.

Differing selection lines can be used to examine the biological mechanisms underlying lean tissue growth. For example, somatotrophin and  $\beta$ -agonists have been used to increase lean tissue growth in pigs, but the modes of action of somatotrophin and  $\beta$ -agonists are presently unclear. The selection lines provide a reference facility, with which treated animals can be compared to selected animals to determine if metabolic

changes resulting from treatment with somatotrophin (McPhee et al, 1991) and  $\beta$ -agonists (Mitchell et al, 1990) are of a similar nature to the metabolic differences between appropriate selection lines.

Data from commercial breeding organisations or central performance test stations has been analysed to estimate genetic parameters, rather than using data from selection experiments. Generally, traits have been measured on a subjective rather than an objective basis, e.g. meat and eating quality traits, or parameters have been estimated on a few easily measured traits, for which there is already a considerable amount of information in the literature, e.g. growth rate and backfat depth. Therefore, data from commercial breeding organisations should not be considered as an alternative to experimental data, for the estimation of genetic parameters, but as complementary. Further, estimation of the response to uni-directional selection with no control line, such as in a breeding organisation, will be dependent on the assumptions of the model, whereas measurement of the response to either divergent or uni-directional selection with a control, as in a designed selection experiment, requires no assumptions.

### GENOTYPE WITH ENVIRONMENT INTERACTION

Genotype with environment interactions (GxE) may be important in the choice of performance testing regime in nucleus herds, to take account of the regime in which commercial animals are reared. Several studies have evaluated the difference between two selection lines on high or low nutritional regimes and reported that the magnitude of the difference increased with nutritional status (Bereskin et al, 1990; MCPhee et al, 1991; Woltmann et al, 1991; Cameron, 1993). GxE were reported for growth traits, but not for backfat (Bereskin et al, 1990; Cameron, 1993) or food intake (Woltmann et al, 1992). Cameron (1993) estimated a genetic correlation of 0.9 for lean growth indices on *ad-libitum* and restricted feeding, which suggests that there may be no GxE for lean growth, but the combination of growth and backfat will be feeding regime dependent. Pond et al (1992) reported no GxE for level of dietary fat and selection for cholesterol, to reject a hypothesis regarding sensitivity to fat and cholesterol intake. Use of divergent selection lines in GxE studies has applications both for pig breeding programmes and for modelling non-porcine systems.

### GENETIC MARKERS

Divergent selection with control lines provide an experimental resource to identify genetic markers for quantitative traits. Selection lines could be screened to detect markers with different segregation patterns in the high and low selection lines. The presence or absence of a marker in a selection line may occur by chance and animals from the control line should be typed, to determine if the marker was segregating within the control line. Independent estimates of the effect of the marker on quantitative traits can be obtained from the between-selection line differences and from within the control line.

### SUMMARY

Potentially, pig selection experiments can provide a substantial amount of information. Knowledge of the genetic and phenotypic relationships between traits will enable evaluation of alternative selection

strategies, by comparison of predicted responses to selection. Information on genetic covariances with traits in the selection objective may identify useful predictors of genetic merit, such as physiological traits. Examination of correlated responses will provide information on the biological mechanisms underlying responses to selection. However, the potential value of pig selection experiments has not been fully utilised.

The majority of studies have selected on one criterion, but only a few studies have selected on several criteria to enable direct comparison of the selection strategies. Experimental results have often been limited to quantifying correlated responses, rather than estimation of heritabilities and genetic correlations between traits, which is possible with recent developments in multi-variate mixed model methodologies. Standard errors of heritabilities have been presented, which have not taken account of genetic drift, such that the perceived information from such selection experiments will be over-estimated. The range of measured correlated responses has often been limited, which restricts advances in biological information on the traits of interest. Several studies have reported no differences in physiological traits between selection lines, but the experimental power has been low, due to the limited number of animals measured.

The potential value of pig selection experiments can be attained for efficient estimation of genetic parameters, provided experimental data is analysed with appropriate methodology, and appropriate correlated traits are measured on sufficient animals, for detection of differences between selection lines.

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